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Filling holes in regional carbon budgets: Predicting peat depth in a north temperate lake district

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[1] Peat deposits contain on the order of 1/6 of the Earth's terrestrial fixed carbon (C), but uncertainty in peat depth precludes precise estimates of peat C storage. To assess peat C in the Northern Highlands Lake District (NHLD), a ~7000 km^2 region in northern Wisconsin, United States, with 20% peatland by area, we sampled 21 peatlands. In each peatland, peat depth (including basal organic lake sediment, where present) was measured on a grid and interpolated to calculate mean depth. Our study addressed three questions: (1) How spatially variable is peat depth? (2) To what degree can mean peat depth be predicted from other field measurements (water chemistry, water table depth, vegetation cover, slope) and/or remotely sensed spatial data? (3) How much C is stored in NHLD peatlands? Site mean peat depth ranged from 0.1 to 5.1 m. Most of the peatlands had been formed by the in-filling of small lake basins (terrestrialization), and depths up to 15 m were observed. Mean peat depth for small peat basins could be best predicted from basin edge slope at the peatland/upland interface, either measured in the field or calculated from digital elevation (DEM) data (Adj. R^2 = 0.70). Upscaling using the DEM-based regression gave a regional mean peat depth of 2.1 ± 0.2 m (including ~0.1–0.4 m of organic lake sediment) and 144 ± 21 Tg-C in total. As DEM data are widely available, this technique has the potential to improve C storage estimates in regions with peatlands formed primarily by terrestrialization.

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1. Introduction

[2] Peatlands have long been recognized as providing a wide range of ecosystem services valuable to humans [*Huels*, 1915; *Soper*, 1917]. In recent decades their role in the global climate and particularly their importance in long-term carbon (C) sequestration has come into focus [*Belyea and Malmer*, 2004; *Gorham*, 1991; *Sjörs*, 1950, 1981]. Peatlands are a quantitatively important C pool globally and in many regions, yet the size of this pool is highly uncertain. Although they cover only 3% of the land area, northern peatlands contain about 1/3 of the total pool of soil C in the world [*Post et al.*, 1982], or 1/6 of the globe's terrestrial fixed C, equivalent to about 40% of the C in the atmosphere [*Sjörs*, 1981]. The estimate of the amount of C stored in northern peatlands still ranges by twofold [*Gorham*, 1991; *Turunen et al.*, 2002], from about 220–460 Pg C (1 Pg = 10^{15} g), reflecting uncertainty in area, depth and bulk density of peat [*Gorham*, 1991].

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[3] There is a pressing need for the development of knowledge and models of peat C storage at regional scales (~100 to ~10,000 km^2), as many management decisions at these scales affect land use and ultimately C stores and fluxes. However, for areas ranging from dozens to millions of square kilometers, recent detailed surveys of peat C pools in the UK, Canada and Siberia have differed from previous estimates by ~40% to >200% [*Beilman et al.*, 2008; *Garnett et al.*, 2001; *Sheng et al.*, 2004], suggesting that current regional estimates for peat C storage should be treated with caution. An emerging theme from the studies of C storage in northern/boreal regions is that peat is highly important, and commonly the largest regional C pool [*Beilman et al.*, 2008; *Garnett et al.*, 2001; *Weishampel et al.*, 2009].

[4] Uncertainty in peat depth is the largest remaining obstacle to estimating the size of regional and global peatland C pools. The global estimated mean peat depth of 2.3 m is admittedly uncertain [*Gorham*, 1991], and within many regions information on peat depth is lacking, contributing to uncertainty in C storage [*Beilman et al.*, 2008]. One such region is the Northern Highlands Lake District, a ~7000 km^2 lake-rich region in northern Wisconsin, United States, with 20% peatland coverage by area. This north temperate region lies on the southern fringe of the peat-rich areas of North America [*Conway*, 1949; *Vitt et al.*, 2000].

Available information about peat depth in the NHLD is sparse but suggests that the peat depth varies substantially among wetlands [*Curtis*, 1959; *Huels*, 1915]. This lack of knowledge on peat depth is a major gap in the ongoing efforts to construct a C budget for the region including long-term storage.

[5] Models relating peat depth to surface characteristics would be useful in upscaling C pool size estimates, particularly if the surface characteristics can be obtained from remote sensing. Extensive progress has been made in upscaling forest C stocks and fluxes using remotely sensed images [e.g., *Chen et al.*, 2003; *Desai et al.*, 2007], but there is less information available on peatland C stores and their relationship to surface characteristics. For some peatlands, peat depth can be related to surface environmental gradients such as fen versus bog vegetation [*Glaser et al.*, 1990; *Thormann et al.*, 1999]; However, a complex array of geomorphic, hydrological and biological factors influences peat accumulation rate and total peat depth [*Clymo et al.*, 1998; *Glaser et al.*, 1990; *Rydin and Jeglum*, 2006], and depth in north temperate peatlands is notoriously difficult to predict from surface vegetation characteristics [*Curtis*, 1959; *Soper*, 1917].

[6] A better estimate of peat C stores requires enhanced understanding of peatland geomorphology with particular attention to the mode of peatland formation. There are two main means by which peatlands form: terrestrialization (i.e., the in-filling of lake basins) or paludification (i.e., the formation of peat on terrestrial sites) [*Rydin and Jeglum*, 2006; *Wieder and Vitt*, 2006]. Climate and physiographic setting interact to influence the location and mode of peatland formation [*Glaser et al.*, 1997; *Seppälä*, 2005; *Soper*, 1917]. Paludification is a favored process of peatland origin where a positive water balance is maintained due to climatic and/or local hydrologic and soil conditions. Such areas are found throughout much of the boreal zone and also in some north temperate regions such as the lowlands of glacial Lake Agassiz in Minnesota [*Soper*, 1917]. Terrestrialization requires the prior presence of lakes, which are common in kettle-hole depressions on glacial moraines, till plains, and pitted outwash plains. These geomorphic features are widespread across formerly glaciated regions of the boreal and north temperate climatic zones [e.g., *Seppälä*, 2005]. As a result of this combination of factors, paludified peatlands are extensive in the boreal zone and comprise the bulk of the global peat pool [*Gorham*, 1991; *Seppälä*, 2005; *Vitt*, 2006], although boreal peatlands form by terrestrialization in regions where lakes are common [*Kuhry and Turunen*, 2006; *Seppälä*, 2005]. In temperate regions, peatlands are commonly formed primarily by terrestrialization [*Anderson et al.*, 2003; *Koster*, 2005; *Kratz and Dewitt*, 1986].

[7] At a given location, the method of peat formation is often not apparent from the surface vegetation [*Anderson et al.*, 2003; *Klinger*, 1996; *Soper*, 1917]. However, the implications of this difference are substantial in terms of local C storage, because the peat depth distribution is very different between terrestrialized and paludified peatlands. Paludified areas typically have a relatively consistent peat depth of up to a few meters, although depths as much as 8 m are possible [*Glaser and Janssens*, 1986]. In contrast, infilled lake basins contain a wide range of depths within the same basin, and may form organic deposits to a maximum depth of 10 m or more depending upon the lake bathymetry [e.g., *Huels*, 1915; *Kratz and Dewitt*, 1986]. In this context it is important to note that under terrestrialized peatlands, in addition to peat there is commonly a soft layer of organic lacustrine sediment known as gytjja, which underlies the peat and may be up to several meters deep. In the NHLD and surrounding regions, the picture is complicated because both major pathways of peat formation have been active, and many wetlands in northern Wisconsin have developed at sites that are former lake basins [e.g., *Kratz and Dewitt*, 1986; *Kratz*, 1988].

[8] This study was undertaken to augment understanding of environmental controls and correlates to peat depth, and also to fill in the knowledge gap regarding peat C stores in the NHLD region. In particular, we were interested in models of peat depth that use available remotely sensed data. To address these issues, we asked three questions: (1) How spatially variable is peat depth within and among peatlands of the NHLD? (2) To what degree can peat depth and volume be predicted from available field and/or remotely sensed spatial data? (3) How much C is stored in peatlands of the NHLD?

2. Study Region and Site Selection

[9] The Northern Highlands Lake District (Figure 1) is one of the most lake-rich regions of the world [*Magnuson et al.*, 2006]. This region of ~7000 km^2 consists of a mosaic of lakes and wetlands interspersed in a mixed forest landscape with minimal agriculture and development. The surface morphometry of the region was structured by the last deglaciation 10000–15000 years b.p. [*Attig*, 1985; *Martin*, 1965], which produced a pitted sandy outwash landscape [*Curtis*, 1959]. Depressions (pits) in the low-relief (total range 450–580 m asl) sandy terrain were formed by melting ice blocks, and many subsequently filled with water giving rise to numerous lakes. Over time many of these depressions have accumulated organic and mineral material. About 7000 open water bodies, the majority of which are <1 ha in size, cover 13% of the surface area. A similar number (ca. 8000) of discrete peatlands cover an additional 20% of the surface area [*Natural Resources Conservation Service* (*NRCS*), 2008], and are also dominated by areally small units (median size ca. 2 ha). The majority of the peatlands are forested, commonly with black spruce (*Pinus mariana*) and tamarack (*Larix laricina*), although a smaller number are dominated by northern white cedar (*Thuja occidentalis*). Upland forests comprise most of the rest of the landscape (62% by area), and include mature northern mesic hardwoods (*Acer* spp., *Tilia americana, Betula alleghaniensis*, *Fraxinus* spp.) and younger aspen (*Populus tremuloides*), with smaller coverage of xeric softwoods and hardwoods [*Desai et al.*, 2008]. The magnitude of landscape C storage is not well known, particularly in the peatlands, because the depth profiles and underlying morphometry of the peatlands are not well characterized. Notably, studies of several small nonforested peatlands revealed that the peatlands had formed from the infilling of small lakes, giving rise to a characteristic lake-like morphometry, grading from shallow peat at the edges to deep peat (>5 m) in the center underlain by up to a few

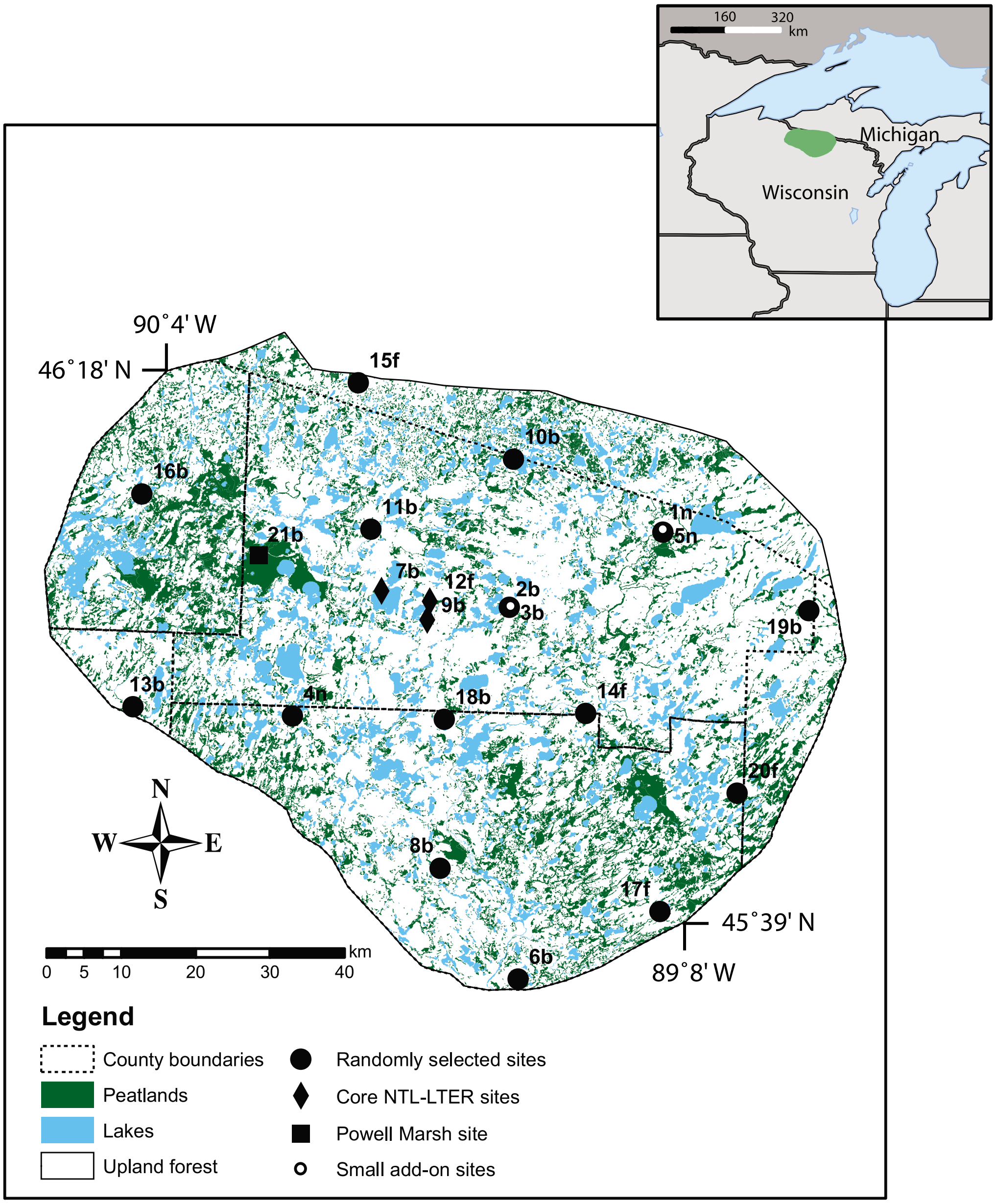

Figure 1. Location of Northern Highlands Lake District (NHLD) study region in north central Wisconsin and Michigan, United States (inset), and location of 21 study sites (labeled by site ID, see Table 1) within the NHLD.

meters of remnant organic lake sediment [*Kratz and Dewitt*, 1986].

[10] We sampled 21 of the 8035 discrete peatlands (Table 1 and Figure 1) in the NHLD. The majority of the sites (15 of 21) were selected randomly from a 10 km grid overlain on a peat soils map [*NRCS*, 2008], to establish good spatial coverage over the region (Figure 1). At two of these locations, the sample sites were so small that they required only a half day to complete sampling, and on these 2 days, we also sampled the next nearest discrete peatland as a separate site (sites 1n and 2b). Three additional sites (Crystal Bog (9b), Trout Bog (7b) and Allequash Wetland (12f)) were chosen because of their location adjacent to well studied lakes in the North Temperate Lakes LTER research program [*Magnuson et al.*, 2006], and one site (21b) was chosen at the center of Powell Marsh, the largest contiguous peatland complex in the region.

3. Methods

3.1. Field Sampling

3.1.1. Sampling Design

[11] At each location, the extent of the peatland basin was examined visually using the soils map and a long axis was defined as the longest linear stretch of peat, while a short axis was defined perpendicular to the long axis. The sample area of a given site was defined as the entire peatland basin (“full basin site,” N = 11) if the length of the long axis was 800 m or less. For larger peatlands, the site was defined as an area with width 150–200 m and length 400–600 m

Table 1. Location and Description of 21 Peatland Sites Sampled During Summer 2008, Ordered by Whole Basin Area

Site ID[a]	Longitude (W)	Latitude (N)	Wetland Plant Community Type[b]	Surface Pore Water pH	Whole Basin Area[c] (ha)	Sample Area[d] (ha)	Full Basin Site[e]
1n	89°11′57″	46°7′36″	sedge or fresh (wet) meadow	na	0.6	0.4	x
2b	89°27′37″	46°1′42″	coniferous bog	3.91	0.8	0.8	x
3b	89°27′45″	46°1′37″	coniferous bog	3.91	1.0	1.0	x
4n	89°49′56″	45°53′12″	coniferous bog	na	2.2	2.2	x
5n	89°11′58″	46°7′24″	sedge or fresh (wet) meadow	na	2.3	2.3	x
6b	89°25′40″	45°34′39″	coniferous bog	3.73	5.0	5.0	x
7b	89°41′8″	46°2′30″	coniferous bog	3.72	5.2	5.2	x
8b	89°34′6″	45°42′31″	sedge meadow, open bog	4.09	5.2	5.2	x
9b	89°36′15″	46°0′31″	open bog	3.70	8.7	8.7	x
10b	89°27′47″	46°12′22″	coniferous bog	3.82	22.9	7.8	
11b	89°42′27″	46°6′58″	coniferous bog	3.60	26.6	24.6	x
12f	89°36′5″	46°1′51″	sedge meadow, open bog	5.54	40.8	26.6	x
13b	90°6′32″	45°53′26″	open bog	3.69	72.0	5.2	
14f	89°19′27″	45°54′5″	sedge meadow, alder thicket	5.72	85.9	3.4	
15f	89°44′17″	46°17′33″	coniferous (cedar) swamp	6.38	87.9	9.8	
16b	90°6′30″	46°8′55″	coniferous bog, open bog	4.23	231.2	7.9	
17f	89°11′10″	45°39′51″	open bog, coniferous bog	5.95	232.8	6.1	
18b	89°34′10″	45°53′20″	coniferous bog, open bog	3.93	256.0	20.4	
19b	88°56′31″	46°1′59″	coniferous bog	3.66	352.0	4.7	
20f	89°3′30″	45°48′35″	alder thicket, coniferous bog	5.29	658.7	8.9	
21b	89°54′6″	46°4′47″	open bog	3.81	5108.9	8.5	

[a]Letters refer to classification based solely on surface pore water pH: b, bog (pH < 4.25); f, fen (ph > 5.25); n, no pH measurement due to low water table.
[b]Classification system of *Eggers and Reed* [1997]; see section 4 for more details.
[c]Total area of contiguous peat soil encompassing the site, based on NRCS soils map.
[d]Area defined by the extent of peat depth measurements.
[e]Sample area/whole basin area >0.5 is full basin site. All others are partial basin sites.

("partial basin site," N = 10) extending outward from one edge of the peatland and if possible crossing the entire short axis. Peat depth was measured throughout the area on a regular grid at intervals varying from 20–90 m depending upon the size of the site. In addition, vegetation was surveyed and peat pore water chemistry was sampled at 3 plots located at 25%, 50% and 75% of the length of the long axis of the sampling area. Peat cores were taken at the same plots for a subset of 5 sites described below, and slope at the upland-peatland interface at the edge of the site was also measured for all 11 full basin sites and 4 of the 10 partial basin sites. Further details of field sampling follow.

3.1.2. Peat Depth

[12] The depth of organic sediment (primarily peat) was measured to depth of contact with mineral surface (typically sand) throughout the sampling area using a stainless steel peat depth probe (PDP) on a regular grid at intervals varying from 20–90 m. Two different versions of the PDP were used, and intercalibrated to ensure consistency. The first consisted of 6′ (1.83 m) sections of 3/8″ (0.95 cm) diameter threaded steel rod, connected with hex-shaped coupling nuts. The second was a custom-made version with the same general design including length and diameter of sections, but consisted of a smooth stainless steel surface and contained an inset male and female threading system to avoid the protruding coupling nuts. The PDP was used only to determine depth to refusal and was not equipped to collect samples; thus it could not differentiate between peat and soft organic lacustrine sediment. In nearly all cases, the person using the PDP could feel contact with sand (typical glacial sediments) at depth to refusal.

3.1.3. Peat Cores

[13] Peat cores were taken at 13 different locations, including the central plot for site 4n and each of the 3 plots for sites 7b, 9b, 12f, and 21b. At each core location, samples were taken using a Russian-style corer (50 cm length × 5 cm diameter) [*Jowsey*, 1966; *Kratz and Dewitt*, 1986] at depths of 0.5, 1.0, 2.0, 4.0 and 6.0 m, up to the maximum depth (peat-sand interface). We examined peat color and degree of decomposition using the von Post scale [*von Post*, 1916] in the field. Particular attention was paid to the presence/absence of gyttja at the peat-sand interface. Gyttja is a dark olive-green algae-derived gelatinous lacustrine sediment, which indicates the former presence of a clear-water lake at a given site [*Hansen*, 1959].

[14] For each core sample (N = 45), a central 10 cm section was preserved and used to measure moisture content, bulk density, and organic matter (OM) content in the laboratory. The 10 cm section was halved vertically, and one half (between 50 and 150 g wet weight) was used for measurement of wet bulk density ($\rho_w = m_w/V$; where m_w = wet weight and V = volume measured by water displacement). The other half was used to measure mass loss by oven-drying at 55°C until the mass was stable (typically 5–10 days, measurement precision ± 0.1 g). Volumetric moisture content was calculated as $(m_w - m_d)/V$ and bulk density (ρ_b) as m_d/V where m_d = dry weight, m_w = wet weight, and V = volume calculated as m_w/ρ_w. From the dried sample, a 1–3 g homogenized subsample was ashed in a muffle furnace at 440°C for 8 h to determine ash-free dry weight ($m_{af} = m_d - m_{ash}$; precision ± 0.01 g), and OM content (OM%) was calculated as m_{af}/m_d. Finally, OM density (ρ_{OM}) was calculated as $\rho_b \cdot$OM%.

[15] For each of the 13 core locations, we estimated the total mass of OM by summing the product of ρ_{OM} and volume over all measurement intervals. To estimate a continuous vertical distribution, ρ_{OM} was interpolated linearly by depth between measurement points. The 0.25–0.5 m

interval was assigned the same ρ_{OM} as the 0.5 m value, while the 0–0.25 m surface interval was assigned a ρ_{OM} of half of that measured at 0.5 m, to account for the lower bulk density in living/recently dead *Sphagnum* in the acrotelm. The deepest measured ρ_{OM} value was extrapolated down to a depth of 0.25 m above the base of the core, and the basal 25 cm of the core was assigned a ρ_{OM} of 46 kg m^{-3}. This is equivalent to the mean value measured for gyttja, to account for the fact that the peat is grading into lower-OM gyttja and/or sand at the interface with glacial till. Vertically averaged mean ρ_{OM} was calculated as the total mass of OM in the core divided by the total core volume.

3.1.4. Edge Slope in the Field

[16] Because many peatlands in this region formed from in-filling of lakes, we hypothesized that local geomorphology, specifically slope at the peatland margin (peatland-upland interface), might be a good indicator of peatland depth. At a subset of 15 sites (including all 11 full basin sites) we measured slope at the peatland-upland interface (Edge Slope in the Field, ESF). At full basin sites, ESF readings were taken at 8 peatland-upland interface locations distributed evenly around the edge of the site. At partial basin sites, measurements were only taken at those site edges that were adjacent to upland, resulting in fewer than 8 locations at each site. At each location, a Suunto clinometer was used to measure slope (%) from the peatland-upland interface oriented up the steepest upland slope at a distance of 5 m, 10 m, 20 m and 30 m, and these four values were averaged to give a single slope value for each location. The precision of individual measurements was ±0.3% slope (mean SD of replicate measurements). The values used for statistical analysis were site mean (ESF_{mean}) and maximum (ESF_{max}) of location slopes.

3.1.5. Vegetation

[17] We hypothesized that the surface vegetation characteristics might be related to peat depth, either directly (due to differential contributions of plant species to decomposition rates and water-holding capacity), or indirectly by responding to local environmental characteristics (e.g., water table, groundwater flow) that also influence peat formation. Vegetation was surveyed following a modification of the U.S. Forest Service Forest Inventory and Analysis (FIA) protocol [*Johnson et al.*, 2008; *U.S. Department of Agriculture* (*USDA*), 2007]. At each plot, a circular sampling area with 7.3 m radius was laid out, with 3 linear transects extending from the center to the perimeter at 0, 120 and 240 degrees from compass north. Within the circular plot, all trees with diameter at breast height (DBH) of 2.5 to 4.9 cm were counted as saplings and their species recorded, while species and DBH were recorded for all trees with DBH $\geq$ 5 cm. Basal area for each tree species in units of m^2 ha^{-1} was calculated by summing the DBH of all individual trees and normalizing by plot area. The mean height and intersection length of each of 4 categories of shrub (alder, bog birch, ericaceous or tree seedling) were recorded for woody vegetation of height >50 cm (but DBH < 2.5 cm) that intersected any of the linear transects. Shrub percent cover was estimated for each category by dividing the intercepted length by the total transect length. Coarse woody debris (CWD) with length >1 m that intersected any of the linear transects with diameter >5 cm was tallied; small end diameter (down to 5 cm), large end diameter, and length of each piece of CWD was recorded and used to calculate volume as described by *Waddell* [2002]. Finally, three ground-layer quadrats (1 m^2) were laid out, 1 each adjacent to the 3 linear transects spanning a distance of 4 to 5 m from the center point. Within each quadrat, percent cover was recorded for each of 8 commonly occurring ground cover types: bare ground, ericaceous shrubs, ferns, forbs, graminoids, *Sphagnum* mosses, other mosses, and other woody vegetation (tree seedlings). Values for the 3 quadrats were averaged to give a plot mean cover of each ground cover type.

3.1.6. Water Table Depth and Peat Pore Water Chemistry

[18] At the center of each plot, a soil pit was dug to a depth of ca. 10 cm below the water table, up to a maximum of 75 cm. The pit was covered and allowed to equilibrate for at least 1 h and until the water level change was <1 mm per minute. Water table depth (WT) was measured as vertical distance to the water table from the gently compressed peat surface. pH of the water was measured using an Orion 266 portable waterproof pH meter, and conductivity was measured using an Oakton CON 11 conductivity and TDS meter. A water sample for chemical analyses (Table 2, chemical variables) was collected from the pit and stored cool and dark in a prerinsed 1 L polycarbonate bottle until return to the laboratory in the evening.

3.2. Laboratory Analyses

[19] In the laboratory, water samples were filtered through a Whatman GF/D glass fiber prefilter followed by a Geotech 0.45 μm cellulose acetate filter. Samples for total nitrogen (TN) and total phosphorus (TP) were preserved by acidification (1% v/v ultrapure HCl), samples for ammonium (NH_4^+) and nitrate (NO_3^-) were frozen until analysis, and samples for dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and absorbance were refrigerated until analysis. DOC and DIC were measured with a carbon analyzer (TOC-V; Shimadzu Scientific Instruments, Columbia, MD, United States). NH_4^+ and NO_3^- were measured with a segmented flow auto-analyzer (Astoria 2; Astoria-Pacific, Inc., Clackamas, OR, United States), while TN and TP were measured on the same auto-analyzer after persulfate digestion to NO_3^- and PO_4^{3-}, respectively. Dissolved organic nitrogen (DON) was calculated as TN - (NH_4^+ + NO_3^-), N/C was calculated as DON/DOC (mass ratio), and P/C was calculated as TP/DOC (mass ratio). Optical absorbance was measured in a 1 cm quartz cuvette on a scan of wavelengths (λ) from 200 to 800 nm, using a DU 800 Spectrophotometer (Beckman Coulter, Fullerton, CA, United States). Absorbance values were converted to absorption coefficients (a_λ) and corrected for scattering due to particles [*Zhang and Qin*, 2007]. Spectral slope was calculated as -1000 times the slope of ln(a_λ) versus λ using the wavelength range 280–500 nm. Specific UV absorbance at 254 nm ($SUVA_{254}$) was calculated as a_{254}/DOC (units m^2 g^{-1}).

3.3. Spatial Data

[20] Spatial data for each site including land cover, soil type, slope parameters, and distance to nearest water feature (Table 3) were extracted from map layers using ArcGIS 9.1 (Environmental Systems Research Institute, Inc., Redlands,

Table 2. Summary of Environmental Variables Measured in the Field

Description	Abbreviation	N	Units	Median (Minimum – Maximum)	Transform[a]
Mean edge slope	ESF_{mean}	15	% slope	17 (0–35)	
Maximum edge slope	ESF_{max}	15	% slope	20 (2–42)	
Sum of basal area of all trees >5 cm DBH[b]	BasalArea	21	m^2 ha^{-1}	10 (0–45)	
Balsam fir basal area[c]	ABBA_BA	21	m^2 ha^{-1}	0.0 (0.0–5.7)	log (x + 1)
Maple spp. basal area	ACSP_BA	21	m^2 ha^{-1}	0.0 (0.0–6.3)	log (x + 1)
Birch spp. basal area	BESP_BA	21	m^2 ha^{-1}	0.0 (0.0–1.3)	log (x + 1)
Tamarack basal area	LALA_BA	21	m^2 ha^{-1}	0 (0–25)	log (x + 1)
Black spruce basal area	PIMA_BA	21	m^2 ha^{-1}	3 (0–28)	log (x + 1)
White pine basal area	PIST_BA	21	m^2 ha^{-1}	0.0 (0.0–3.2)	log (x + 1)
Basal area of standing dead trees	dead_BA	21	m^2 ha^{-1}	0.5 (0.0–5.9)	log (x + 1)
Volume of coarse woody debris	CWD	20	m^3 ha^{-1}	3.2 (0.0–33.0)	
Total cover of woody shrubs >0.5 m height	SHRUB	21	% cover	8.1 (0.0–54.4)	log (x + 1)
Alder shrub cover	ALIN_SHRUB	21	% cover	0.0 (0.0–42.5)	log (x + 1)
Bog birch shrub cover	BEPU_SHRUB	21	% cover	0.0 (0.0–19.4)	log (x + 1)
Ericaceous shrub cover	ERIC_SHRUB	21	% cover	0.0 (0.0–9.1)	log (x + 1)
Tree seedling (DBH < 2.5 cm) shrub cover	SEEDLING_SHRUB	21	% cover	3.7 (0.0–23.7)	log (x + 1)
Bare ground	BARE	21	% cover	3 (0–44)	arcsin (sqrt p)
Ericaceous shrubs	ERIC	21	% cover	26 (0–78)	arcsin (sqrt p)
Ferns	FERN	21	% cover	0 (0–16)	arcsin (sqrt p)
Forbs	FORB	21	% cover	7 (0–40)	arcsin (sqrt p)
Graminoids	GRAM	21	% cover	21 (1–96)	arcsin (sqrt p)
Mosses other than *Sphagnum*	MOSS	21	% cover	1 (0–34)	arcsin (sqrt p)
Woody plants other than ericaceous shrubs	WOODY	21	% cover	11 (0–29)	arcsin (sqrt p)
Sphagnum spp.	SPHAGNUM	21	% cover	65 (0–100)	arcsin (sqrt p)
Water table depth below peat surface	WT	21	cm	20 (0–100)	
Specific conductivity, corrected for H^+ ion	K_{corr}	18	mS cm^{-1}	27 (12–271)	log (x + 1)
pH	pH	18	pH units	3.9 (3.6–6.4)	
Dissolved inorganic carbon	DIC	17	mg L^{-1}	10 (3–33)	log (x + 1)
Dissolved organic carbon	DOC	17	mg L^{-1}	57 (16–101)	
Ammonium	NH4	17	μg-N L^{-1}	181 (43–2291)	log (x + 1)
Nitrate	NO3	17	μg-N L^{-1}	20 (10–33)	log (x + 1)
Total phosphorus	TP	17	μg L^{-1}	45 (23–97)	
Dissolved organic nitrogen	DON	17	μg L^{-1}	1803 (693–2854)	
DON/DOC	N/C	17	mass ratio	0.034 (0.021–0.093)	log (x + 1)
TP/DOC	P/C	17	mass ratio	0.0009 (0.0004–0.0034)	log (x + 1)
Absorbance at 254 nm	a_{254}	17	m^{-1}	596 (167–1162)	
Spectral slope (280–500 nm)	SpectralS	17	μm^{-1}	16 (14–20)	
Specific ultraviolet absorbance (a_{254}/DOC)	$SUVA_{254}$	17	m^2 g^{-1} C	10 (8–12)	

[a]Transformation applied prior to use in statistical analyses.
[b]Includes rare trees and standing dead.
[c]Individual tree species/genera were only included in the statistical analyses (and in Table 2) if they were commonly found, i.e., were present at 4 or more of the 21 sites.

Table 3. Summary of Spatial Variables Extracted From a GIS for the 21 Sites, With Site Median Values

Description	Abbreviation	Units	Median (Minimum – Maximum)	Transform[a]
Area of whole basin	Area	ha	27 (1–5109)	log (x)
Mean altitude	Alt	m	498 (475–518)	
Mean slope of sample area	Slope	% slope	1.7 (0.1–5.8)	
Percent of soils classified as acidic, NRCS soils map	Acid_soils	% area	100 (0–100)	arcsin (sqrt p)
Developed area (including road margins), NLCD land cover map	Developed	% area	0 (0–60)	arcsin (sqrt p)
Deciduous forest, NLCD land cover map	DecForest	% area	0 (0–55)	arcsin (sqrt p)
Coniferous forest, NLCD land cover map	ConForest	% area	1 (0–55)	arcsin (sqrt p)
Mixed forest, NLCD land cover map	MixForest	% area	7 (0–45)	arcsin (sqrt p)
Woody wetlands, NLCD land cover map	WoodyWetlands	% area	56 (0–100)	arcsin (sqrt p)
Emergent (open) wetlands, NLCD land cover map	EmergentWetlands	% area	0 (0–86)	arcsin (sqrt p)
Distance to nearest stream[b]	Stream_dist	m	788 (13–1946)	
Distance to edge of nearest lake[c]	Lake_dist	m	631 (10–1670)	
Presence of bog lake within 500 m of site[d]	Boglake	binary	0 (0–1)	
Presence of stream entering/exiting peatland within 500 m of site	Stream_conn	binary	0 (0–1)	
90th percentile of upland slope at edge of whole basin	ES_{90}	% slope	9 (0–21)	

[a]Transformation applied prior to use in statistical analyses.
[b]Distance (m) from center of site to the nearest stream or river.
[c]Distance (m) from center of site to nearest lake edge, where a lake is defined as a surface water body of >1 ha in area and not fully surrounded by peatlands.
[d]Bog lake defined as surface water body of >0.1 ha in area, fully surrounded by the same peatland as that containing the site, and within 500 m of the site center.

CA, United States). Data sources used were: National Land Cover Data (NLCD 2001) map [*Homer et al.*, 2004], Natural Resources Conservation Service (NRCS) soils map [*NRCS*, 2008], and a 30 m grid cell size digital elevation model (DEM) from the United States Geological Survey (USGS) national elevation data set (http://seamless.usgs.gov/, accessed 27 October 2008).

[21] For each site, the proportions of all land cover types were calculated from the NLCD 2001 map (Table 3). The NRCS soils map was used to classify the peats as either "acidic" (Beseman, Dawson, Greenwood or Loxley soil series, pH $\leq$ 4) or "nonacidic" (Carbondale, Cathro, Lupton, Markey or Seelyeville soil series, pH 6 $-$ 8), and calculate the proportion of acidic soils for each site. Mean elevation and slope were calculated from the DEM, with slope being calculated for each grid cell as the maximum % slope between the given cell and its neighbors. Additionally, slope at the peatland-upland interface (Edge Slope, ES) was determined for each site. To obtain this value, using ArcGIS we created a 50 m buffer around each discrete site-containing peatland (defined as a contiguous area of peat soils based on NRCS soils map), and analyzed the distribution of slope values within the buffer. Areas within the buffer containing peat soils or water are excluded from the analysis. For statistical analyses we use the 90th percentile of that distribution (ES_{90}) for each site, which gives an indication of the steepness of the hillslopes at the peatland edge. Calculation of other spatial parameters is described in Table 3.

3.4. Statistical Analyses and Upscaling

3.4.1. Interpolation of Peat Depth and Volume

[22] The average peat depth for each site was calculated using interpolation in the Surfer 8 program (Golden Software, Golden, CO, United States). The peat depths, measured with the PDP, and the peatland edges (assumed depth = 0) identified from NRCS soils maps in GIS, were combined to create a data set containing every known depth within a given site. In instances where the depth exceeded our abilities to measure it (depth > ca. 15 m), the maximum measured depth was used at that point. This set of data was interpolated using Triangulation and Linear Interpolation in Surfer 8. The resulting grid file was a raster of all depths within the sampling area, with 1 m^2 cell size (horizontal resolution of 1 m). The edges of the site were digitized and the excess data beyond the NRCS peatland boundaries were removed. The resulting raster included only depth data from within the wetland boundaries. The planar surface area of the sites was calculated, and the volume of the total amount of peat present was calculated using Surfer 8's trapezoidal rule. The average peat depth was then found by dividing the total volume of peat by the planar surface area.

3.4.2. Statistical Analyses

[23] A variance components analysis (SAS v. 9.1, SAS Institute Inc., Cary, NC, United States) was used to partition the variance in peat depth between among-site and within-site variability. Other statistical analyses were performed at the site level, using R (v. 2.80). For field vegetation and chemistry parameters, we used the mean of the three plots to give an average site value. Field measurements and GIS-derived remotely sensed spatial data were regressed against mean peat depth for the 21 sites using univariate regression and multiple linear regression (MLR). We defined three sets of variables for use in analyses: (1) field variables (2) spatial variables (3) field + spatial variables. For MLR analysis, missing field data were gap-filled using the mean value for the given parameter from the other sites. The regression analysis was repeated for the subset of full basin sites only (N = 11).

[24] The all-subsets regression routine (regsubsets function in leaps package, R version 2.80) was used to test all potential univariate and MLR models for each of the three sets of individual predictor variables. For each set of predictor variables, the Akaike Information Criterion (AIC) was used to select the best model(s) including 1, 2 and 3 predictor variables. We report all models that met all of the following criteria: (1) model significant at the p = 0.05 level; (2) does not contain cocorrelated explanatory variables ($p < 0.05$ based on correlation matrix); (3) within 2 AIC units of the best qualifying model in the same set and with the same number of variables; (4) AIC value better than all of the qualifying models with fewer predictor variables in the same set.

3.4.3. Upscaling to Estimate Size of Regional Peat C Pool

[25] We estimated mean peat depth for the peatlands of the NHLD region by two different methods, after which total regional peat C was also estimated. For all calculations, a bootstrapping procedure (R v. 2.80) with 10,000 iterations was used to estimate uncertainty (95% CI) in the regional totals. Method 1: assuming that the 21 sites we sampled were representative of the region as a whole, we used the mean depth (±SD) to define a normal distribution, from which values were randomly drawn and assigned to each of the 8035 discrete peatlands in the region. Method 2: using the best regression model relating remotely sensed spatial variables to mean peat depth, we calculated mean peat depth for all (N = 8035) discrete peatlands in the NHLD region. Here, values were drawn at random from a normal distribution describing the prediction interval of the regression model at a given value of the predictor variable(s). Assumptions and uncertainty of this approach are further described in sections 4 and 5.

[26] Mean peat depth values were converted to an estimate of the regional carbon pool (CP) using equation (1), which includes notation based on *Sheng et al.* [2004]. Regional mean carbon density (CD) was calculated by dividing CP by the total area of peatlands in the region (1259 km^2). A bootstrapping procedure with 10,000 iterations was applied to equation (1), and the resulting distribution was used to estimate uncertainty (reported as 95% CI) in the regional carbon pool size and carbon density based on uncertainty in peat depth, OM density, and the C content of peat OM.

$$CP = R\sum_{i=1}^{n} \rho_{OM}\overline{D}_i A_i \qquad (1)$$

where CP is the mass of total carbon pool, R is the C content of OM, ρ_{OM} is the organic matter density of peat (kg-OM m^{-3}), n is the number of peatlands, $\overline{D_i}$ is the mean depth of peatland *i* (m), and A_i is the surface area of peatland *i* (m^2).

[27] Following the approach of *Vitt et al.* [2000], for upscaling we used OM density (ρ_{OM}, the product of peat

Table 4. Summary of Peat Depth Measurements

Site ID	N	Spacing (m)	Median Depth (m)	Mean Depth[a] (m)	Maximum Depth (m)	Peat Volume[a] ($\times10^4$ m^3)
1n	34	10	0.1	0.1	0.6	0.1
2b	23	20	1.5	2.4	9.1	1.8
3b	29	25	0.1	0.8	4.6	0.8
4n	20	35	0.8	0.9	2.7	1.8
5n	95	20	0.2	0.2	1.0	0.5
6b	72	30	0.5	0.9	8.2	4.2
7b	74	20	3.6	2.4	9.4	10.8
8b	54	30	1.3	1.6	5.6	7.9
9b	44	50	2.8	4.0	10.1	32.6
10b	42	45	2.3	1.3	7.2	9.1
11b	72	50	0.4	1.9	7.1	45.1
12f	49	70	4.0	5.1	14.3	124.3
13b	33	50	2.4	2.7	5.9	13.0
14f	25	40	0.0	1.8	7.6	6.0
15f	42	50	1.5	1.4	3.2	13.2
16b	23	45	3.7	3.3	10.4	25.0
17f	33	45	1.4	1.6	4.9	9.1
18b	24	90	3.3	3.3	14.6	63.5
19b	39	30	0.5	0.8	2.4	3.4
20f	31	50	1.5	1.3	4.9	10.6
21b	44	50	2.4	2.5	2.7	19.1

[a]Mean depth and total volume for the sample area were calculated using interpolated peat depths (SURFER 8.0 program).

bulk density and OM content) in combination with the C content of peat OM. We used the mean (±SE) of 45 peat core samples from 13 locations in this study to estimate the regional mean (±uncertainty in regional mean) ρ_{OM}. We also explored the impact of accounting for depth-dependent variation in ρ_{OM}. A value of 52 ± 1% was used for the regional mean and uncertainty in carbon content of OM, based on extensive studies of Canadian peatlands with thousands of cores analyzed [*Bauer et al.*, 2006; *Gorham*, 1991; *Vitt et al.*, 2000]. We assumed no error in the peatland surface area based on NRCS maps.

4. Results

4.1. General Site Characteristics

[28] Wetland vegetation and water chemistry varied substantially among our sites (Tables 1 and 2). Of the 21 sites, 13 had low pH (~4) and specific conductivity indicative of ombrotrophic bog conditions, while 5 sites had higher pH (5 – 7) and specific conductivity indicative of minerotrophic fen conditions with substantial groundwater contribution [*Glaser et al.*, 1990; *Rydin and Jeglum*, 2006]. Pore water dissolved organic carbon (DOC) concentration ranged from 16–101 mg L^{-1}, and most other chemical analytes also varied considerably among sites (Table 2). The remaining 3 sites had water tables >75 cm depth at all plots, and at these sites we were unable to retrieve water samples for chemistry analyses.

[29] Twelve of the 21 sites were forested (tree basal area >5 m^2 ha^{-1}; Table 2). The most common tree species were *Larix laricina* and *Picea mariana*, while other tree species/genera found at 4 or more sites were *Abies balsamea*, *Acer* spp., *Betula* spp., and *Pinus strobus*. Tree species/genera found at fewer than 4 sites (not included in the statistical analyses) included *Alnus incana*, *Fraxinus nigra*, *Pinus resinosa*, and *Thuja occidentalis*. Surface vegetation could be represented by wetland plant community type (Table 1) using the organizational framework of *Eggers and Reed* [1997] for Wisconsin and Minnesota wetlands. Sedge meadow/fresh (wet) meadow sites were characterized by a lack of trees, nearly continuous graminoid cover and very low ericaceous shrub and *Sphagnum* cover (means both <10%). These sites ranged widely in their chemistry, with one low pH, two high pH, and two low water table sites (Table 1). Coniferous bog sites, characterized by an overstory of *Larix laricina* and *Picea mariana*, had nearly continuous *Sphagnum* cover and low graminoid cover (mean <10%), with a mean ericaceous shrub cover of about 30%. The most common ericaceous shrubs were *Chamaedaphne calyculata*, *Andromeda polifolia*, *Ledum groenlandicum*, *Kalmia polifolia*, *and Vaccinium* spp. Open bog sites lacked or had low density of trees, but were otherwise similar to coniferous bog sites with continuous *Sphagnum* cover, low graminoid cover (mean about 30%) and intermediate ericaceous shrub cover (mean about 50%). Of the 14 sites characterized primarily by bog vegetation, 12 had mean pore water pH < 4.25, one had a deep water table precluding pH measurements, and one had a higher pH indicative of groundwater inputs (Table 1). Two of the 21 sites included plots classified as Alder Thickets [*Eggers and Reed*, 1997], which varied in their ground cover but were characterized by >50% cover of *Alnus incana* shrubs and relatively high pore water pH (5.26–5.74). Last, one site was a Coniferous (Cedar) Swamp with an overstory of *Thuja occidentalis* and ground cover quite distinct from the other sites, including substantial cover of forbs, non-*Sphagnum* mosses and tree seedlings as well as graminoids and bare ground. Water chemistry of this site was also distinct from the others, with a high mean pore water pH of 6.4. Some sites contained a mixture of wetland plant community types (Table 1), resulting in large among-plot variation in vegetation and chemistry characteristics. For statistical analyses, mean site values were used.

4.2. Spatial Variability of Peat Depth

[30] In total, 902 peat depth measurements were made at the 21 sites (Table 4). Site mean depths ranged from 0.1 to 5.1 m with a mean of 1.9 ± 1.3 (SD), while the maximum depth recorded was 14.6 m (Table 4). Two of the sites were shallow throughout (<1 m), while most sites had a distribution of depths ranging from 0 at the edges to 2–10 m toward the center of the peatland (Figures 2 and 3). The exception to this pattern was the site in the center of the >5000 ha expanse of Powell Marsh (21b), in which peat depth ranged only from 2.0 to 2.7 m. Aside from this site, there was no clear difference between partial or full basin sites in terms of mean depth, maximum depth or depth distribution, and 16 of the 21 sites were skewed toward shallow depths (median < mean depth, see Figure 3). Within-site variation was higher than among-site variation in peat depth. Of the total variance in the 902 depth data points, based on a variance components analysis 29% was attributed to among-site differences, while 71% was attributed to within-site variability.

[31] Mean/maximum depth ratios give information about basin shape, and have been often used to characterize lakes [*Hutchinson*, 1957]. We evaluated the depth ratios of our peat sites to determine the plausibility that they formed via direct in-filling of lakes. The total range of mean/maximum depth ratios for the 21 peatland sites was 0.11–0.90, with 17

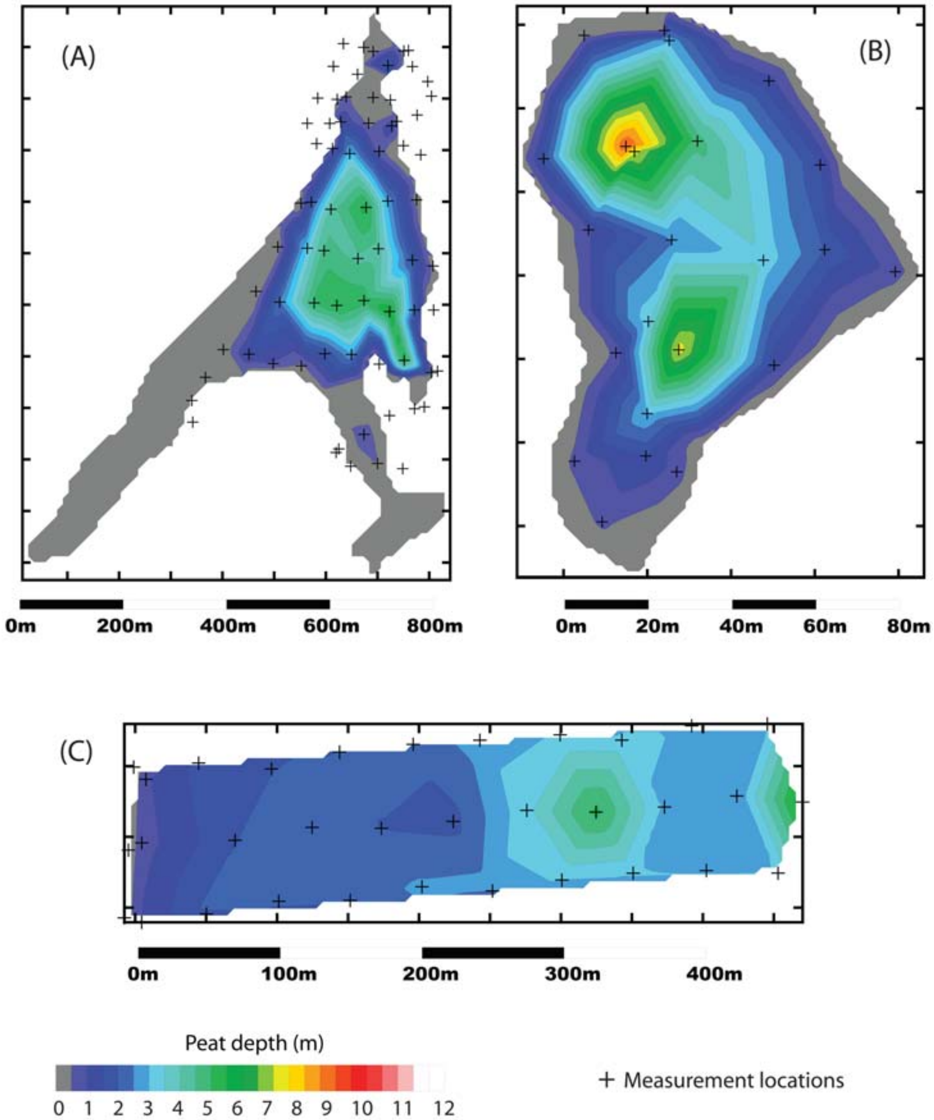

Figure 2. Examples of peat depth sampling design and interpolated depth contours for (a) a medium/shallow depth full basin site (11b), (b) a deep full basin site (2b), and (c) a medium/shallow depth partial basin site (13b) at which the peatland extends further to the south, east, and north.

of the sites between 0.23 and 0.45. This range overlaps with the low end of the 0.33–0.5 range of depth ratios typical of glacially formed lakes such as kettle-holes [*Carpenter*, 1983; *Hutchinson*, 1957], and with the low end of the 0.27–0.60 range observed for 90% of the lakes of the region [*Wisconsin Department of Natural Resources* (*WDNR*), 2005].

4.3. Peat Core Characteristics

[32] The 13 core locations ranged in peat depth from 1.5 to 9.1 m. Of the 45 samples, 40 were peat based on analysis of color and texture in the field, while 4 of the deep samples were gyttja (organic lake sediment), and one contained a mixture of peat and sand. Peat decomposition ranged from intermediate (mean von Post number of 5) for near-surface (0.5 m) samples to highly decomposed (mean von Post number of 8) at depths ≥4 m. The four deepest cores all had gyttja as their basal sediments: D_{gyttja} = 6.0–6.4 m (7b, plot A), D_{gyttja} = 6.0–8.6 m (9b, plot A), D_{gyttja} = 4.0–6.2 m (12f, plot A), and D_{gyttja} ~6.0–9.1 m (12f, plot B). None of the shallower core locations (≤5 m) contained gyttja. Peat cores taken at the Powell Marsh site (21b) revealed an underlying layer of silt and clay, corroborating the existence of a postglacial outwash plain or lake at that location [*Curtis*, 1959]. The last cored site (4n) was very shallow with a maximum peat depth of <3 m, and showed no evidence of remnant lacustrine sediments at the core location (depth 1.7 m).

[33] Bulk density increased and organic matter content decreased with depth in the cores. The samples which contained primarily peat (N = 40) had a moisture content of 93 ± 4% (SD) v/v, bulk density of 125 ± 40 kg m^{-3}, and organic matter content of 86 ± 13% w/w of dry matter, giving rise to an OM density (ρ_{OM}) of 105 ± 26 kg m^{-3}. When all 45 samples were considered, ρ_{OM} was 103 ± 34 kg m^{-3}

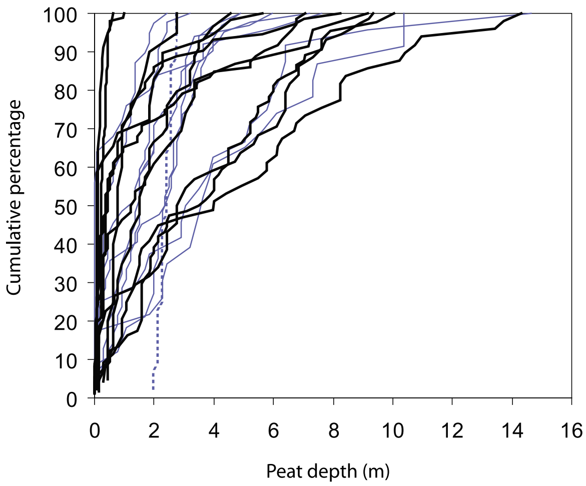

Figure 3. Cumulative frequency distribution of individual peat depth measurements for full basin sites (thick black lines) and partial basin sites (thin blue lines). All sites include both edge (shallow) measurements and center (deep) measurements, except for site 21b (dashed line), at which measurements were taken in the center of a large peatland expanse.

(SD) and decreased with depth: 124 ± 33 kg m^{-3} (SD, N = 13) at 0.5 m depth, 111 ± 23 kg m^{-3} (N = 13) at 1 m depth, 103 ± 22 kg m^{-3} (N = 10) at 2 m depth, and 58 ± 14 kg m^{-3} (N = 9) at 4–6 m depth. Basal lake sediments (gyttja) had a low ρ_{OM} (46 ± 8 kg m^{-3}, N = 4 pure gyttja samples) and contributed to the low sample ρ_{OM} at depth >4 m in some locations.

[34] For the 13 core locations, vertically averaged mean ρ_{OM} ranged from 54 kg m^{-3} for an 8.6 m deep highly fibrous, low density core in which the basal 2.5 m was gyttja (9b, Plot A), to 145 kg m^{-3} for a 1.7 m deep core at a relatively dry (WT > 75 cm) site with dense, compact peat (4n, Plot B). When aggregated by site, vertically averaged mean ρ_{OM} ranged from 79 kg m^{-3} (site 12f) to 145 kg m^{-3} (site 4n). Vertically averaged mean ρ_{OM} was negatively correlated with peat depth, both at the level of individual cores (ρ_{OM} = 122–6.6·D, R^2 = 0.55, N = 13) and at the site level where a logarithmic model best fit the data (equation (2)).

$$\rho_{OM} = 136 - 37.3 \cdot \ln(\overline{D}) R^2 = 0.95, N = 5 \qquad (2)$$

where ρ_{OM} is the vertically averaged OM density, and $\overline{D}$ is the basin mean peat depth (m) calculated from the grid of depth measurements. The nearly twofold range in ρ_{OM}, and particularly the correlation with depth, suggests the need to consider nonrandom variation in ρ_{OM} for the regional estimate of peat C.

4.4. Relating Site Mean Peat Depth to Environmental Variables

[35] Of the 38 variables measured in the field, only three were significantly (α = 0.05) correlated to site mean peat depth (Table 5 and Figure 4). Forb cover and WT were each negatively correlated with site mean peat depth, but only weakly (Adj. R^2 < 0.3). Maximum edge slope measured in the field (ESF_{max}) was positively correlated to mean peat depth (Adj. R^2 = 0.59).

[36] Multiple linear regression (MLR) analysis with the best combinations of two and three field parameters gave

Table 5. Results of MLR Analysis Relating Site Mean Peat Depth to Environmental Variables, Using the Set of All Sites[a]

Predictor Group	Model Fit: Variable	AIC	Adjusted R^2	p_{model}	Model: Intercept	β1	Var1	β2	Var2	β3	Var3
Field	1	−15.73	0.59	<0.001	0.05	0.087	ESF_{max}				
	1	−3.59	0.23	0.016	2.63	−0.018	WT				
	1	−1.54	0.15	0.046	2.72	−2.859	FORB				
	2	−21.45	0.68	<0.001	0.27	0.094	ESF_{max}	−1.814	dead_BA		
	2	−20.80	0.67	<0.001	0.44	0.087	ESF_{max}	−0.030	BasalArea		
	2	−19.67	0.66	<0.001	0.43	0.091	ESF_{max}	−0.811	PIMA_BA		
	3	−23.27	0.72	<0.001	0.82	0.087	ESF_{max}	−1.702	dead_BA	−1.472	FORB
	3	−22.40	0.71	<0.001	2.80	0.101	ESF_{max}	−1.981	dead_BA	−0.265	$SUVA_{254}$
	3	−22.28	0.71	<0.001	0.42	0.094	ESF_{max}	−2.032	dead_BA	−1.024	ALIN_SHRUB
	3	−22.14	0.71	<0.001	0.19	0.092	ESF_{max}	−0.046	BasalArea	2.114	MOSS
	3	−21.70	0.70	<0.001	0.23	0.093	ESF_{max}	−1.998	dead_BA	2.522	ERIC_SHRUB
Spatial	1	−1.37	0.14	0.051	1.06	0.096	ES_{90}				
	2	−4.72	0.30	0.016	21.31	0.117	ES_{90}	−0.041	Alt		
	3	−6.55	0.38	0.011	20.60	0.115	ES_{90}	−0.040	Alt	1.275	EmergentWetlands
Combined	2	−23.35	0.71	<0.001	−0.39	0.093	ESF_{max}	1.065	Stream_conn		
(field plus spatial)	2	−21.45	0.68	<0.001	0.27	0.094	ESF_{max}	−1.814	dead_BA		
	3	−26.14	0.76	<0.001	−0.03	0.095	ESF_{max}	0.906	Stream_conn	−0.605	PIMA_BA
	3	−25.91	0.75	<0.001	−0.03	0.092	ESF_{max}	0.844	Stream_conn	−0.021	BasalArea
	3	−25.23	0.75	<0.001	−0.13	0.096	ESF_{max}	0.793	Stream_conn	−1.181	dead_BA
	3	−25.23	0.75	<0.001	−0.11	0.092	ESF_{max}	0.931	Stream_conn	−0.582	LALA_BA
	3	−25.18	0.75	<0.001	−0.82	0.095	ESF_{max}	1.014	Stream_conn	0.688	GRAM
	3	−24.85	0.74	<0.001	−0.46	0.091	ESF_{max}	0.898	Stream_conn	0.821	EmergentWetlands
	3	−24.62	0.74	<0.001	−0.03	0.099	ESF_{max}	1.146	Stream_conn	−1.686	WOODY
	3	−24.54	0.74	<0.001	−0.26	0.103	ESF_{max}	1.031	Stream_conn	−0.152	Slope
	3	−24.26	0.73	<0.001	0.12	0.087	ESF_{max}	0.970	Stream_conn	−1.256	FORB
	3	−24.17	0.73	<0.001	0.23	0.092	ESF_{max}	1.108	Stream_conn	−0.012	TP

[a]N = 21. All significant univariate models and the best 2 and 3 variable models are listed for each group of predictor variables.

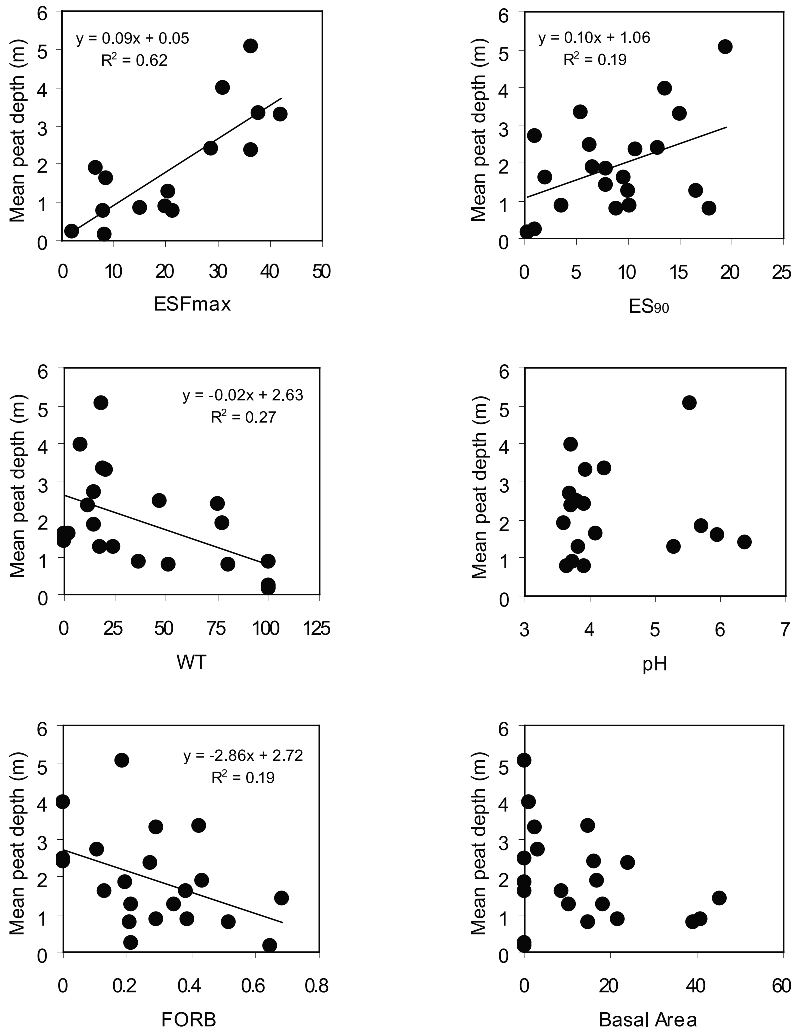

Figure 4. Examples of relationship between single environmental predictor variables and site mean peat depth, using all 21 sites. All of the variables that were significantly correlated with mean peat depth in univariate models are shown with best fit lines, and several additional variables are shown to illustrate their distributions. Variable descriptions, units, and transformations as in Tables 2 and 3.

models with adjusted R^2 of ~0.7 (Table 5). All of the best models included the variable ESF_{max} (maximum basin edge slope measured in the field). Total tree basal area, dead tree basal area and black spruce basal area were selected as secondary variables, all negatively correlated to peat depth. Several other field variables were selected as the third variable for one model, but added only slightly to the explanatory power (Table 5).

[37] Of the spatial parameters extracted from GIS layers (Table 3), only ES_{90} (90th percentile of basin edge slope calculated from the DEM) was correlated with peat depth in univariate regressions (Table 5), with an Adj. R^2 of ~0.2 (Table 5 and Figure 4). In MLR models with two or three spatial variables, Adj. R^2 ranged up to ~0.4 and ES_{90} was selected for all best models. In the multivariate models, altitude was negatively associated with peat depth, while emergent (open) wetlands land cover was positively associated with peat depth.

[38] MLR models of site mean peat depth using combinations of spatial and field data gave slightly higher adjusted R^2 than either variable group alone (Table 5). All best models included the variable ESF_{max}. The presence of a stream or river near the site (stream connectivity, Table 3), positively associated with peat depth, substantially improved the ESF_{max}-alone model and was also chosen for 11 of the 12 best MLR models. Several equivalent 3 variable models also included variables associated with forest cover or upland vegetation (all negatively correlated with peat depth), or emergent (open) wetland land cover and graminoid cover (both positively correlated with peat depth). These tertiary variables added only slightly to the model explanatory power relative to the 2-variable model with ESF_{max} + stream connectivity (Table 5).

[39] When only the full basin sites (N = 11) were considered, edge slope variables ESF_{max} and ES_{90} were again those most strongly correlated with peat depth

Table 6. Results of MLR Analysis Relating Site Mean Peat Depth to Environmental Variables, Using the Set of Full Basin Sites Only[a]

Predictor Group	Model Fit				Model				
	Variable	AIC	Adjusted R^2	p_{model}	Intercept	$\beta 1$	Var1	$\beta 2$	Var2
Field	1	−7.36	0.51	0.008	0.01	0.094	ESF_{max}		
	1	−4.79	0.38	0.022	8.07	−2.664	NH4		
	1	−4.59	0.37	0.025	3.25	−0.026	WT		
	2	−13.78	0.73	0.001	2.00	0.103	ESF_{max}	−0.035	DOC
	2	−13.77	0.73	0.002	5.00	0.076	ESF_{max}	−1.985	NH4
	2	−13.15	0.71	0.002	1.97	0.128	ESF_{max}	−0.051	TP
	2	−12.83	0.70	0.002	1.50	0.110	ESF_{max}	−0.003	a_{254}
	2	−12.02	0.68	0.004	0.42	0.104	ESF_{max}	−2.203	dead_BA
Spatial	1	−12.63	0.70	<0.001	0.07	0.219	ES_{90}		
	1	−5.50	0.42	0.018	5.08	−2.268	Acid_soils		
	1	−5.10	0.40	0.022	0.79	1.780	Area		
	2	−22.13	0.87	<0.001	1.21	0.223	ES_{90}	−2.785	MixForest
Combined (field plus spatial)	2	−25.24	0.90	<0.001	0.54	0.244	ES_{90}	−2.393	dead_BA

[a]N = 11. All significant univariate models and the best 2 variable models are listed for each group of predictor variables.

(Table 6). The DEM-derived variable ES_{90} was the strongest single predictor (Table 6), positively correlated with mean peat depth (equation (3) and Figure 5). The range of ES_{90} values found in these 11 sites (0.3–19.4) also represents well the range of ES_{90} for the NHLD region; 93% of the 8035 peatlands in the NHLD, representing 97% of the total peatland area, fall within this range. This relationship was subsequently used for regional upscaling as described below.

$$\overline{D} = 0.219 \cdot ES_{90} + 0.07 \quad \text{Adj. } R^2 = 0.70, N = 11 \qquad (3)$$

where $\overline{D}$ is the basin mean peat depth (m) and ES_{90} is the basin edge slope, 90th percentile.

[40] In the MLR models applied to the full basin sites only (N = 11), edge slope was again highly positively correlated to mean peat depth, with either ESF_{max} or ES_{90} selected for all of the best models (Table 6). MLR models with 2 variables represented a slight improvement over univariate models, including a spatial model utilizing ES_{90} and mixed forest land cover (negatively correlated with peat depth) with Adj. R^2 = 0.87 (Table 6).

4.5. Upscaling: Carbon Storage in Peatlands of the NHLD Region

[41] Making the assumption that the peat depths of the 21 sampled sites were representative of the distribution of depths for the region as a whole (method 1), we calculated a regional mean peat depth of 1.9 ± 0.3 m (95% C.I.). Then, using equation (1) we estimated a regional mean carbon density of 104 ± 19 kg-C m^{-2} in peat areas, and a total C pool size of 132 ± 24 Tg C. As an alternate approach (method 2), using the ES_{90} regression model developed on full basin peatlands (Figure 5 and equation (3)) and assuming that this relationship holds true for larger peatlands as well, mean depth was modeled for each of the 8035 peat basins in the NHLD region. By this method, estimates for individual peatlands ranged from 0.1 to 8.3 m, with 90% of the peatlands falling between 0.4 and 4.5 m. Areally averaged mean peat depth for the entire region was 2.1 m ± 0.2 m (95% C.I.), which gave an average value of 115 ± 17 kg-C m^{-2} in peat areas using equation (1). For the study region of 6397 km^2 with 20% peatlands by area, this is equal to a total C pool size of 144 ± 21 Tg C.

[42] The potential bias introduced by our treatment of ρ_{OM} as a normally distributed variable randomly assigned to individual peatlands was examined by substituting the depth-dependent modeled ρ_{OM} from equation (2) into equation (1), summed over all peatlands for the region. The resulting mean values for regional C pool size were 134 Tg C by method 1, and 145 Tg C by method 2, both within 2% of the values achieved by assuming the ρ_{OM} is unrelated to peatland depth. Thus we do not believe that our use of a mean value for this parameter has biased our

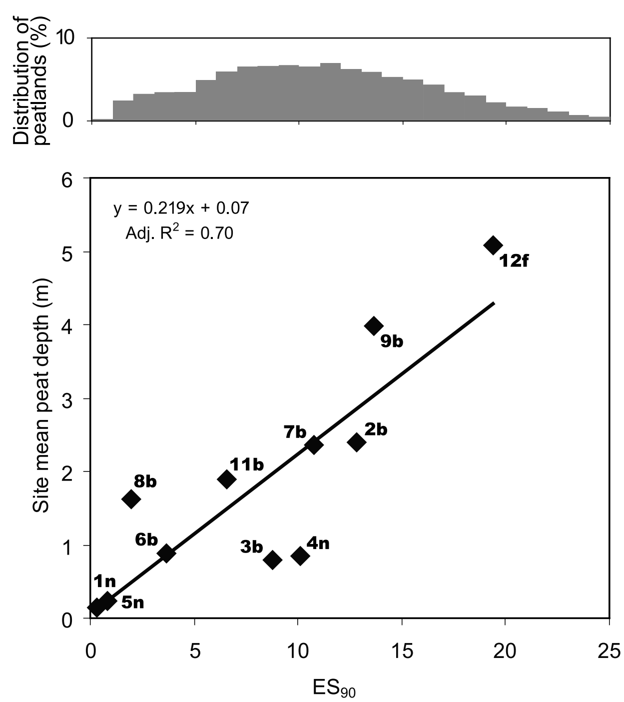

Figure 5. (bottom) ES_{90} (basin edge slope, 90th percentile) is strongly positively correlated with mean peat depth for the group of sites (labeled by site ID) where depth measurements were made over the full basin. (top) Of the 8035 peatlands in the NHLD region, 93% (covering 97% of the total peatland area) have ES_{90} values which fall within the range of our 11 measured sites.

regional estimate of pool size, in spite of the observation that ρ_{OM} varies with depth and from site to site.

[43] Our approach does not explicitly generate separate estimates for peat and basal organic lacustrine sediments (gyttja). However, we generated a rough estimate of the amount that gyttja likely contributes to the total by making the following assumptions: (1) Basal gyttja is currently found in peatland locations with deep holes. As an upper bound, we assume all of the depths >4 m contain gyttja, and as a lower bound, all of the depths >7 m (based on our core stratigraphy results and those of *Kratz and Dewitt* [1986]). (2) For a given peatland, the proportion of total peat volume contributed by peat below a certain depth can be described as a linear function of mean peatland depth as observed for our 21 peatlands (see Figure 3), i.e., $P_{D\,>\,4m} = 0.093\,\overline{D} - 0.053$ (R^2 = 0.67) and $P_{D\,>\,7m} = 0.032\,\overline{D} - 0.034$ (R^2 = 0.66). (3) Mean peatland depth can be estimated for all of the peatlands of the region using either methods 1 or 2 above. (4) The ρ_{OM} of gyttja is 46 ± 8 kg m^{-3} (based on our core results). Using this approach we calculated a regional mean depth of gyttja of 0.1–0.4 m averaged over all of the peatlands in the NHLD, and a total regional C pool of 5–18 Tg. Based on this estimate, organic lake sediments may contribute up to about 20% of the total NHLD peat volume, and 10% of what we have termed the total regional peat C pool.

[44] Uncertainty in the regional C pool size estimate was primarily due to uncertainty in mean peat depth, in spite of our field campaign and modeling effort. The coefficient of variation (CV) of the estimate of regional mean peat depth was 8% for method 1 and 5% for method 2, similar to the CV of regional mean OM density (6%) and greater than that attributed to C content of OM (2%), the other two main contributors to uncertainty in our C pool estimate. Although the two methods gave similar values for total regional C pool size, we favor and generally focus our discussion on the results of method 2, as this approach takes into account the geomorphometry-related among-basin variation in peat depth.

5. Discussion

5.1. Spatial Variation in Peat Depth and Implications for Historical Peat Formation in the NHLD

[45] At least 17 of the 21 study sites likely formed primarily by the infilling of lake basins (terrestrialization), based on the spatial distribution of peat depth, mean/maximum depth ratios, and lake sediment found in peat cores taken at a subset of 5 sites. The prevalence of terrestrialized sites explains the high within-site variability in peat depth, since most sites range in depth between 0 at the edges to 5–10 m at the center, often in the span of a few hundred meters or less. Those peatlands with mean depth to maximum depth ratios of 0.3–0.45 (N = 8) may have formed solely by terrestrialization of glaciated lake basins, whose depth ratios typically range from 0.3 to 0.5 [*Carpenter*, 1983; *Hutchinson*, 1957]. These sites had an average mean peat depth of 2.5 m, and an average maximum depth of 6.8 m. The remaining peatlands with slightly lower depth ratios (N = 12) likely formed by a combination of terrestrialization and paludification, giving rise to peat basin morphometry with a deep hole(s) and surrounding shallow paludified areas. These sites had a similar average maximum depth (6.7 m) as the first set of sites, but a shallower average mean depth (1.5 m) owing to extensive areas of shallow peat (<1 m) around the peatland perimeter. The combination of formation processes is consistent with *Klinger*'s [1996] model of bog formation, in which the lake edge forms a seed point from which peat grows both inward (terrestrialization) and outward (paludification). Our results suggest that it is likely that the majority of peatlands in the NHLD were formed at least in part by terrestrialization. The location and depth distribution of peat (and thereby the landscape C storage) can thus best be seen through the lens of glacial history, in which sandy outwash deposits and melting ice blocks [*Attig*, 1985] gave rise to the current landscape dotted with thousands of mostly small, shallow lakes and thousands of mostly small peatlands.

[46] Although there was a high degree of spatial variability in depth, and maximum depths up to 15 m, the estimated regional mean depth of 2.1 m for the NHLD aligns well with the estimated global mean depth of 2.3 m compiled by *Gorham* [1991]. The mean depth is also similar to the mean for peatlands in North America, which average 2.2 and 2.5 m for Canada and the United States, respectively [*Gorham*, 1991]. This similarity is a surprising result since the global estimates rely largely on measurements from peatlands in the boreal zone which formed primarily by paludification, while our north temperate study site included a large number of peatlands formed by terrestrialization. The similarity in depths may be a chance result dictated by the particular landforms in the NHLD region. Nonetheless the morphometry of the kettle lake basins formed by melting ice blocks in the NHLD are not atypical for pitted sandy outwash landscapes.

5.2. Environmental Predictors of Peat Depth

[47] Mean peatland depth was well predicted using a linear relationship with ground slope at the peatland-upland margin. This relationship was found using slope measurements made in the field (ESF_{max}), and those derived from a 30 m DEM (ES_{90}), opening the possibility to scale up to the entire region. ES_{90} also correlated well with ESF_{max} for the full basin sites (r = 0.85, p = 0.001, N = 11), suggesting that even in this relatively flat landscape, the 30 m resolution of the DEM provides a reasonable proxy for slope on the ground. Interestingly, the remotely derived ES_{90} parameter was more tightly correlated with peat depth than was the ESF_{max} measured in the field (Table 6). Our interpretation of this difference is that the remote-sensing based approach offers the advantage of complete coverage of the peatland-upland margin; while the accuracy of the field measurements was limited by a relatively small (N = 8) number of sampling points, thus may not always capture the important topographic features. Finer resolution elevation data (such as LIDAR) should improve the remote-sensing based relationship further. As DEM data are widely available and LIDAR data are becoming more so, a similar approach could be used for other regions that contain peatlands formed by terrestrialization.

[48] Our study is the first to our knowledge to quantify the link between local upland slope and peat depth in terrestrialized peatlands. Peat formation and depth are known to be related to local terrain [*Rydin and Jeglum*,

2006], and *Anderson et al.* [2003] noted in a study of several small New England peat basins that the basins with steeper sides tended to have deeper holes. However, other recent studies of regional variation in peat depth have not found a relationship with local slope [*Garnett et al.*, 2001] or variability in elevation [*Beilman et al.*, 2008]. *Beilman et al.* [2008] tested for the influence of variability in elevation in a study of peat depth in a 25,000 km^2 boreal region in western Canada, and hypothesized that more variable terrain would give rise to deeper peatlands, akin to what we saw in the current study. No relationship was found at the scale of their analysis (relating single depth measurements to terrain variability within 1 km or 5 km of the measurement). Most of the depth variation occurred at scales smaller than the measurement spacing, and the authors acknowledged that the fine-scale depth variation might be related to fine-scale topographic patterns not be detected by their sampling approach [*Beilman et al.*, 2008]. We found a similar partitioning of depth variability, with greater fine-scale (within-peatland) than broad-scale (among-peatland) variation in depth. Detection of this variation was made possible by our nested sampling design, with an average of ~45 measurements of depth made at each of 21 different peatlands.

[49] Variation in peat depth was not well correlated with vegetation or surficial pore water chemical properties in our study, suggesting a disconnect between surface hydrochemistry and vegetation and the underlying morphometry of the peatlands. Of particular note, there was no difference in peat depth between the forested and nonforested sites or between the sites with bog chemistry and those with fen chemistry. The geomorphic variation relating edge slope to basin depth was clearly the primary gradient in peat depth at the spatial scale of our study. Once that variation was accounted for, two other classes of variables further explained variation in peat depth: (1) tree basal area and related measures of forest cover, particularly upland forest (negatively related to peat depth); (2) indicators of wetness, including emergent (open) wetland cover, water table depth and stream connectedness (wetness positively related to peat depth). These relationships highlight the noted connection between hydrology, vegetation and peat formation [*Glaser et al.*, 1997; *Rydin and Jeglum*, 2006], but did not add substantial predictive power to our model of peat depth, and were not helpful in upscaling since most required detailed field measurements. Other studies have had mixed results on this topic, with some finding relationships between depth and surface characteristics to be weak or absent [*Beilman et al.*, 2008; *Curtis*, 1959], and others noting a relationship [*Emili et al.*, 2006; *Jeglum and He*, 1995; *Sims et al.*, 1982; *Thormann et al.*, 1999]. The differing results likely derive in part from differing spatial scale of the studies. For instance, covariation of peat depth and vegetation in a study of forested wetlands in Ontario, Canada was associated with fine-scale (within-basin) variation [*Jeglum and He*, 1995]. In our study, we compared vegetation among basins, thus did not pick up within-basin variation.

[50] The edge slope (ES_{90}) based model of peat depth may be a useful tool but still contains considerable uncertainty when used for upscaling. Notably, the strong relationship (equation (3) and Figure 5) between mean peat depth and ES_{90} only held true for the full basin sites, i.e., the smaller sites. There are two plausible explanations for this. First, edge slope and mean depth may only be related in small basins. Alternatively, the relationship is weak only because of our inability to characterize mean depth accurately for the larger (partial basin) sites. Without intensive sampling of larger sites, we cannot differentiate between these two potential issues, but both may play a role. Taking a conservative approach to the upscaling, we note that our largest full basin site was 41 ha in area. In the NHLD, 95% of the discrete peat bodies are 41 ha or smaller, but this accounts for only 27% of the surface area of peat in the region. In fact, one-third of the peat surface area in the NHLD is encompassed by the 10 largest peatland complexes, each exceeding 1000 ha (10 km^2). For these largest of peatlands, it is unlikely that the relationship between ES_{90} and mean peat depth strongly holds, thus other methods of upscaling depth should be considered. However, we found no relationship between peatland area and mean depth, suggesting that upscaling with the ES_{90} relationship (equation (3)) is unlikely to give a substantially biased estimate of the actual peat content of the region.

5.3. Magnitude and Uncertainty of Regional Peat C Storage

[51] Our results demonstrate that carbon stored in peat is the largest quantified pool of terrestrial fixed C in the NHLD region. The large contribution of peat to regional C storage has also been recently noted in other peat-containing regions across a range of northern climatic zones [*Beilman et al.*, 2008; *Garnett et al.*, 2001; *Sheng et al.*, 2004; *Weishampel et al.*, 2009]. Even covering only 20% of the NHLD, the mean depth of 2.1 ± 0.2 m and carbon density of 115 ± 17 kg-C m^{-2} (144 ± 21 Tg-C in total) is enough to make peat a larger regional store than the forested uplands. Upland soils cover 62% of the NHLD area and store on the order of 30–50 Tg-C based on a range of 8–12 kg-C m^{-2} [*Grigal et al.*, 1989; *Grigal and Ohmann*, 1992; *Martin and Bolstad*, 2005], while tree biomass in upland forests is estimated at 16–24 Tg-C based on a range of 4–6 kg-C m^{-2} [*Rhemtulla*, 2007; *Turner et al.*, 1995]. Other components of upland, wetland and lake ecosystems may also have sizable C storage, with lake sediments the most uncertain, and likely the largest, of the remaining pools. Based on surveys of glacially formed lakes in North America, estimates of regional mean lake sediment organic carbon accumulation rates vary from 15 to about 30 g-C m^{-2} yr^{-1} [*Campbell et al.*, 2000; *Dean and Gorham*, 1998; *Mulholland and Elwood*, 1982], i.e., about 150 to 300 kg-C m^{-2} assuming an average accumulation period of 10,000 years for the Holocene. For the NHLD, this would amount to a sizable regional storage of 125–250 Tg-C, on the same order as the storage in peatlands.

[52] Following this study the uncertainty in NHLD peat C storage is still about ±15% (95% CI), with equal contributions to uncertainty from peat depth and peat density. These two factors are typically the major sources of error in regional/large-scale estimates of peat C stocks, with uncertainty in peatland areal coverage also substantial in less well mapped regions [*Botch et al.*, 1995; *Clymo et al.*, 1998; *Gorham*, 1991; *Turunen et al.*, 2002; *Vasander and Kettunen*, 2006]. As demonstrated in this study, peat depth can be highly variable both within and among peatlands,

particularly in regions with peatland formation by both terrestrialization and paludification. Peat bulk density also varies considerably with depth and location/peatland type [*Lynn and Grossman*, 1974], but OM density is more consistent and useful for upscaling [*Lynn and Grossman*, 1974; *Vitt et al.*, 2000]. Our mean value of 103 ± 5 kg m^{-3} (SE) for OM density is similar to the value of 112 kg m^{-3} used by *Gorham* [1991] for global upscaling, the mean values of 94 and 105 kg m^{-3} estimated for wooded/shrubby fens and bogs/open fens, respectively, in western Canada [*Vitt et al.*, 2000], and the range of 90–105 kg m^{-3} observed at Fallison bog in the NHLD region [*Kratz and Dewitt*, 1986]. We found the use of a mean, depth-independent value for OM density did not bias our regional estimate of C storage, but OM density is still a notable contributor to uncertainty and future studies should incorporate this parameter in a rigorous way into C upscaling estimates.

5.4. Relevance for Peat C Pool Size Estimates in This and Other Regions

[53] In spite of recent advances in our study and others [e.g., *Beilman et al.*, 2008; *Turunen et al.*, 2002; *Vasander and Kettunen*, 2006] precise regional and global estimates of peat C stocks remain an elusive but important goal required for estimating potential climate change feedbacks via the terrestrial carbon cycle. For the NHLD region, our observation of the relationship between basin edge slope and mean peat depth for the NHLD represents a step forward in terms of C stock estimation. This DEM-based approach may also be useful in other regions that feature terrestrialized peatlands, i.e., the glacially shaped lake-rich regions common across certain areas of the boreal and north temperate zones. Many north temperate regions in particular contain peatlands formed primarily by terrestrialization rather than paludification [*Anderson et al.*, 2003] and thus may lend themselves to the DEM-based estimate of mean depth, given knowledge of regional geomorphology and proper local calibration. Lending some credence to this prospect, in a study of small peatlands in central New England peat basins with steeper sides were found to have deeper holes, illustrating the link between local landform and peatland morphometry [*Anderson et al.*, 2003]. It would be interesting to follow up on our study by comparing the relationship between basin edge slope and peatland depth within and among other lake districts such as those in Canada [*Dillon and Molot*, 1997; *Schindler et al.*, 1996], Scandinavia [*Seppälä*, 2005] and the UK [*Koster*, 2005]. Another area recommended for future research is the applicability to larger peatlands. We presume that the strength of the basin edge slope approach will be limited to smaller (terrestrialized) peatlands, but this limitation has not been well explored.

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