Wetlands (2022) 42: 51
https://doi.org/10.1007/s13157-022-01572-4

PEATLANDS

Plant functional types drive Peat Quality differences

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Received: 17 January 2022 / Accepted: 24 May 2022 / Published online: 9 June 2022

Abstract

Peatlands contain enormous carbon stocks, but the stability of this carbon is variable. Peatlands can vary in tree cover from completely open to forested with associated differences in peat quality. Peat quality, or potential for mineralization, is a contributing factor affecting how the carbon balance of peatland ecosystems could change with climate or land use changes. We compared the peat quality of open peatlands dominated by *Sphagnum* mosses to forested, or silvic, peatlands dominated by black spruce and tamarack or northern white cedar to quantify the effects of different carbon sources on peat quality. We used Fourier-transform infrared spectrometry (FTIR) to analyze peat properties throughout the depth profile of 30 peat cores across the hemi-boreal Upper Great Lakes region. We found that tree cover was associated with differences in both surficial and deep peat quality. Silvic peat had lower peat quality than *Sphagnum* peat as shown by FTIR indices. *Sphagnum* peat also had significantly higher peat quality at the surface compared to at depth. However, silvic peat showed no significant difference with depth in any indices. Our results indicate that the dominant plant functional type is a strong driver of peat quality as we identified key differences between silvic and *Sphagnum* peatlands. These relatively local differences are similar in magnitude to those found across biomes comparing tropical swamps to boreal *Sphagnum* peatlands. This implies that the dominant plant functional type (e.g. tree, shrub, graminoid, or moss) may be more important to peat quality than species identity—or even latitude—in peatlands.

Keywords Peat · Peat quality · Fourier-transform infrared spectrometry · Carbon · Silvic peat

Introduction

Peatlands are critical long-term carbon (C) sinks with estimates ranging from 545 to 1055 Pg C (Nichols and Peteet 2019). The C storage function of peatlands primarily occurs through the production, accumulation, and storage of C-rich peat, formed when plant production is in excess of decomposition. Peatland environments are broadly unfavorable for decomposition, primarily due to inundation (Bridgham and Richardson 2003), and in northern peatlands low temperatures also reduce the rate of decomposition. However, there is concern that the C sink provided by peatlands could weaken or reverse owing to climate change or land conversion, releasing C stored in peat (Goldstein et al. 2020).

Peat differs in decomposition rates based on its quality and environment (Moore et al. 2007; Leifeld et al. 2012; Hribljan et al. 2017). Herein, peat quality refers to the content of organic molecules such as carbohydrates compared to phenolics or aromatics. It has been shown that higher carbohydrate content in peat is related to greater potential for mineralization across a broad range of peatland ecosystems across latitudes (Normand et al. 2021; Verbeke et al. 2022). While environmental factors (e.g. temperature, water table position) are cardinal factors controlling rates of decomposition, an evaluation of changes in peat quality with changes in the dominant vegetation cover within the same ecoregion is less well understood.

Vegetation provides the organic material available for decomposition and conversion to peat. The predominance of different types of vegetation in different ecosystems should therefore result in differing peat characteristics, with the magnitude of the difference corresponding with the vegetation type and level of dominance over biomass input. One

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common input for peat formation in boreal and hemi-boreal peatlands are peat mosses in the *Sphagnum* genus (Crum and Buck 1988). *Sphagnum* moss-dominated peatlands may produce peat that is chemically and physically different from tree-dominated peatlands, which produce silvic peat (Durig et al. 1988). However, these different initial producers of peat substrates are not the sole cause of differences in peat physical properties (Laiho 2006). Unstable components are preferentially consumed during decomposition, leaving behind waste products and more stable components, reducing peat quality, and increasing its resistance to mineralization. In this way, past decomposition is a major driver of current peat quality (cf., Grover and Baldock 2012). Yet, differences in peat inputs likely result in peat with different quality, even after significant decomposition has occurred.

Peatlands are often delineated by their vegetation communities, hydrology and electrochemistry (Vitt & Chee 1990), and these factors relate to peat biochemical properties and consequently to C cycling, as discussed above. Numerous studies (cf., Blodau et al. 2007) have used mesocosms or incubations to compare the C cycling response of different peat types to changes in environmental conditions, including temperature (Updegraff et al. 1995), hydrology (Updegraff et al. 2001; Keller et al. 2004), and nutrient loading (Keller et al. 2006). Moreover, recent work has highlighted the importance of peat carbohydrate content (peat quality) in determining mineralization potential across a wide range of peatland types (Normand et al. 2021). However, how these changes in peat quality vary with different cover types in the same ecoregion, or with depth in the peat profile, have not been well investigated for hemi-boreal peatlands.

We investigated changes in quality of silvic peat (*Thuja occidentalis* derived or *Picea mariana/Larix laricina* derived) and *Sphagnum* moss peat across the entire depth profile within the same region of the southern extent of the boreal biome. To evaluate peat quality, we elected to use Fourier-transform infrared spectrometry, as it is an established method for evaluating peat quality (Hribljan et al. 2017; Hodgkins et al. 2018; Flanagan et al. 2020; Verbeke et al. 2022). While studies already exist comparing peat quality throughout depth across latitudes as a proxy for climate (Hodgkins et al. 2018; Normand et al. 2021; Verbeke et al. 2022), we elected to make our comparison within one region to reduce confounding effects relating to climate. We hypothesized that the silvic peat is significantly lower in quality than *Sphagnum* peat, having a lower carbohydrate content, following the findings of Bridgham et al. 1998. We expect that this difference will be most apparent near the surface and will decrease, but not disappear completely, with depth due to the action of decomposers.

Methods

Sample Locations.

We sampled peatlands across the Upper Peninsula of Michigan, northern Wisconsin, and northern Minnesota (Fig. 1). The boreal zone of North America is typically considered to reach its southernmost extent along the north shore of Lake Superior, with a hemi-boreal zone that encompasses the Upper Peninsula of Michigan, a small part of northern Wisconsin, and much of northern Minnesota

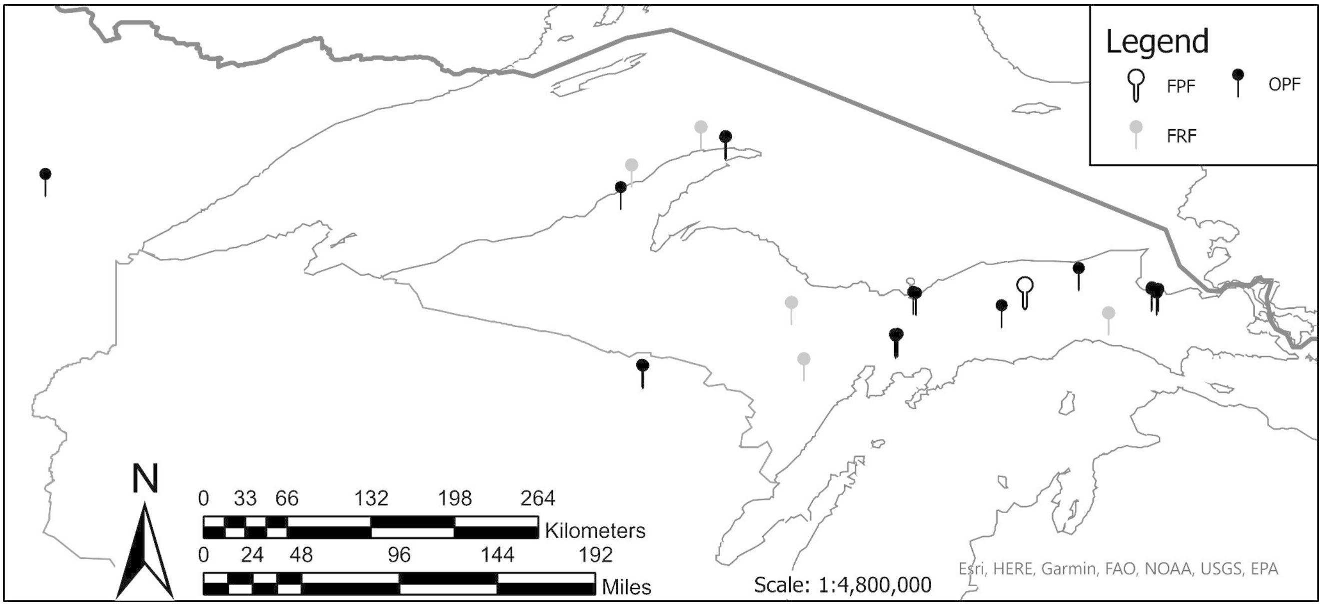

Fig. 1 Map showing the location and ecotype of our 30 sample sites (some site clusters overlap at this scale). The legend indicates forested poor-fens (FPF), open poor-fens (OPF) and forested rich-fens (FRF)

(Langor et al. 2014). Our sampling locations were all within this hemi-boreal zone. All sites also fell within the Northern Forests (I) > Mixed Wood Shield (II) > Northern Lakes and Forests (III) Ecoregion as defined by the US EPA (U.S. Environmental Protection Agency, 2013). This ecoregion is described as "humid continental, marked by warm summers and severe winters, with no pronounced dry season," with a mean annual temperature ranging from ~ 2 °C to ~ 6 °C, and mean annual precipitation ranging from 500 to 960 mm (Wiken et al. 2011).

The peatlands studied are best described as fens. Both poor fens and rich fens are common within the hemi-boreal region. These fens are extensive and may be isolated, coastal, or part of large upland-peatland complexes (Bourgeau-Chavez et al. 2017, see Fig. 10). The poor fens sampled for this study are dominated by *Sphagnum* (L.) mosses with additional typical species being black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), tamarack (*Larix laricina* (Du Roi) K. Koch), sedges (*Carex* spp., mostly *C. oligosperma* L. and *Eriophorum vaginatum* L.), Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), bog rosemary (*Andromeda polifolia* L.), leatherleaf (*Chamaedaphne calyculata* L.), etc. (Kost et al. 2007). The forested rich fens that we sampled are silvic and dominated by northern white cedar (*Thuja occidentalis* L.) with presence of balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), and hemlock (*Tsuga canadensis* L.) with a sparse understory due to heavy shading and deer herbivory (Kost et al. 2007). The forested poor fen site is unique in that densely forested peatlands with low pH are not common in this region. It follows the same pattern of the poor fens, but with much higher canopy cover that is dominated by black spruce and tamarack with additional bog birch (*Betula pumila* L.). This site was included as it offered a unique opportunity to investigate the effects of woody spruce vegetation in poor fens, which contrasts with the cedar dominating the forested rich fen sites.

Field Sampling.

We collected 30 peat cores from across the Upper Peninsula of Michigan, northern Wisconsin, and northern Minnesota. Thirteen cores were collected in 2012 for a related study (Chimner et al. 2014) and were stored dried and ground until analyzed for this project. We collected 17 new peat cores using methodology consistent with Chimner et al. 2014. At each poor fen site, a sharpened PVC tube was inserted into precut peat to a depth of 50 cm. The surficial peat was carefully removed from the tube, cut into 10 cm depth increments, and stored in sealed plastic bags. We then used a Russian peat corer with a sharp cutting edge (Aquatic Research Instruments, Hope, ID, USA) to core the remaining deeper peat in 50 cm segments. Pieces of decomposing wood and roots presented no issue due to the combination of the cutting edge and their fragility. We stored peat segments in PVC and wrapped in plastic. We avoided coring in laggs or ecotones to obtain samples representative of the ecotype. Peat samples were transported at ambient temperature and stored in a freezer immediately upon return to the lab, usually within hours of extraction.

Sample Processing.

In the lab, we cut the still-frozen peat into ~ 2 cm increments with a hand saw and dried them to constant weight in an oven at 60 °C. Samples were weighed to measure bulk density. Samples were then ground and homogenized using a Wiley mill equipped with a 40-mesh screen. This resulted in a powdered sample with a maximum particle size of 425 microns. A subsample of each ~ 2 cm peat increment was combusted at 500 °C for 12 h to obtain % organic matter by mass.

Spectrometry.

We used Fourier-transform infrared spectrometry (FTIR) to analyze the peat quality throughout the depth profile for each core. We prepared samples for FTIR by mixing milled peat with FTIR-grade KBr to 10% sample by mass. We dried samples at 60º C for > 24 h before subjecting them to diffuse reflectance FTIR (DRIFT) using a Thermo Scientific Nicolet iS5 spectrometer with an iD Foundation – Diffuse accessory (Thermo Fisher Scientific, Ann Arbor, MI). We produced spectra of the 400–4000 cm^{-1} range with resolution of 4 cm^{-1} and a data interval of 0.5 cm^{-1} by averaging 64 scans. We used ultrapure N^2 purge and automatic background correction to minimize the interference of humidity and to improve spectral fidelity.

We used custom code written in Python 3.0 to baseline correct and standardize the spectra to compare relative peak heights, rather than absolute data, which was variable due to sample properties, dilution factors, and atmospheric conditions during spectrometry. We used several indices previously applied to evaluating peat properties (Hribljan et al. 2017; Flanagan et al. 2020). These included two substrate quality indices, a lignin index, and a humification index (cf., Table 1). These indexes are derived mainly from wavenumber peaks associated with either relatively high quality biomolecules (e.g., polysaccharides ~ 1060) or low quality biomolecules (e.g., lignin-like components, ~ 1730; Artz et al. 2008 and references therein). The carbonyl/lignin ratio (C/L index) (1725/1620) is an index of the humification of fulvic acids (Kalbitz et al. 1999). The lipid/polysaccharide ratio (L/P index) (2920/1060) measures the peat composition, representing mainly waxes vs. cellulose and hemicellulose (Hribljan et al. 2017). The lignin index (1265, 1515, 1620) simply averages three lignin peaks on the FTIR spectra, and represents lignin content (Hribljan et al. 2017). The humification index (1630/1030) compares aromatics to carbohydrates, and indicates level of biochemical stability (the

Table 1 The PCA loading matrix for the surface two 25 cm peat depth bins (0–25 cm and 25–50 cm). This loading matrix corresponds with the PCA presented in Fig. 2

Index	PC1	PC2
Carbonyl/Lignin Index	-0.89264	0.37118
Lipid/Polysaccharide Index	0.80110	0.59471
Lignin Index	0.90839	-0.20728
Humification Index	0.98427	0.04389

inverse of peat quality) (Flanagan et al. 2020). It is important to note that all these FTIR indices represent the relative, not absolute, abundance of different biomolecules in peat. We consider the C/L index positively related to peat quality, the lignin and humification indices negatively related to peat quality, and the L/P index related to botanical origin. The Python script and further index details are available in the supplemental.

Statistics.

We binned vertical profile data into 25-cm depth increments to average out small-scale peat heterogeneity. Sample bins 0–25 and 25–50 cm were considered surface samples for our purposes and all deeper bins were considered deep. When samples would have crossed bin boundaries they were included only in the upper bin. Due to these considerations, bins were not entirely uniform in number of samples included or mean depth due to missing samples or imperfect division of subsamples.

We used principal components analysis (PCA) of index results to identify 3 groups of samples *a posteriori*, open poor fens, OPF, forested poor fens, FPF, and forested rich fens, FRF. Open sites were characterized by a lack of tree cover, either devoid of trees or with sparse, stunted trees. Open poor fens possess *Sphagnum* peat. Forested sites were characterized by dense stands of high stature trees. These were primarily black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in the FPF and northern white cedar (*Thuja occidentalis*) in the FRFs. The FRFs possess silvic peat. The forested poor fen was a relatively rare site which is shown as an example of an intermediate between *Sphagnum* and silvic peat. By using these group divisions, we focused on tree cover as the most impactful difference in vegetation inputs. We produced separate surficial (0–50 cm) and full (0 cm - base) PCAs to focus on the differences in contemporary ecosystems (surface peat) and the properties of peat profiles overall.

Initial analysis of each FTIR index indicated that some were not normally distributed. Therefore, we used nonparametric mean separation to compare across peat types but within peat depth categories, and within peat types but across peat depth categories. We elected to use nonparametric statistics, which do not require equal variance or normality, in all cases for the sake of consistency (Fujiwara et al. 2014). We used Welch's ANOVA for means testing before proceeding to perform all pairs comparisons via Steel-Dwass method in JMP v14. We considered means and pairs significantly different at α = 0.05.

Results

Ordination of peat quality was conducted using principal components analysis, which arranges peat samples based on similarity.

Surficial PCA.

Principal components ordination of surface peat samples (0–25 cm and 25–50 cm) resulted in principal component one explaining 80.8% of the variance (Fig. 2). Component two explained 13.4%. Component one was driven by the humification, lignin, carbonyl/lignin (C/L) and lipid/polysaccharide (L/P) substrate quality indices, in order of importance (Table 1). Component two was mainly composed of the L/P substrate quality index, with lesser contributions from the C/L quality index and the lignin index.

The principal components ordination of surface peat samples delineated three distinct groups (Fig. 2; Table 1). There was a distinct separation between the OPFs, in one group, and the FPF and FRF sites, in two other groups, similarly positioned along the axis of component 1. Component 1 was reflective of the relative degree of tree cover and was associated with both humification and lignin. Component 2

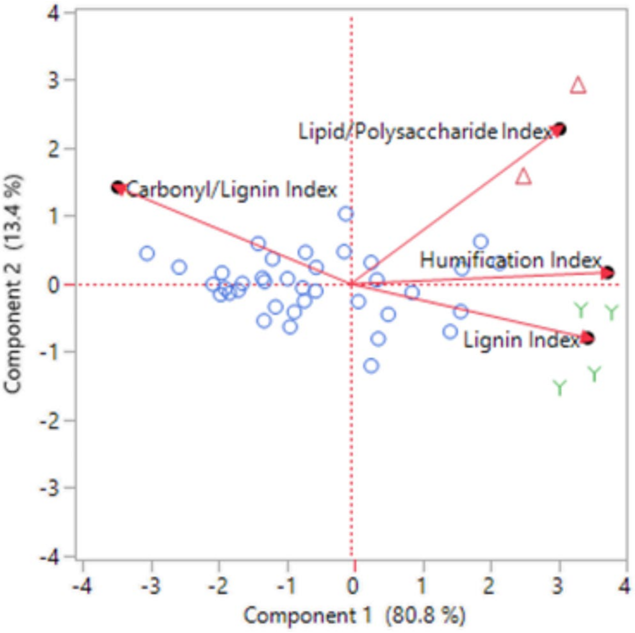

Fig. 2 The PCA chart and loading vectors, indicating the distribution of peat types for surface peat samples (0–25 cm and 25–50 cm). Symbols indicate distinct groups of samples, circles (○) indicate open poor fen (OPF) samples, triangles (Δ) indicate forested poor fen (FPF) samples, and Y-shapes indicate forested rich fen (FRF) samples. Component loadings are available in Table 1

separated sites by lignin and other subtle variances in peat quality, namely the lipid/polysaccharide ratio. The forested rich fens and the poor fens that we sampled appeared similar, only separated slightly by their positions on axis 2.

Whole Core PCA.

The PCA of all peat depths binned into 25 cm depth intervals produced a similar output to the surface peat analysis (Fig. 3; Table 2). The major loadings remained the same, but there was more of a balance between components 1 and 2, which explained 64.8 and 26.1% of the variance, respectively. In this PCA there were only two separate groups of samples that can be clearly differentiated, rich fens and poor fens, including the forested poor fen. Notably, there was less separation in quality indices across peat types. Near surface samples in the poor fen had negative loadings on component 1, while deeper peat samples clustered more around the center of the plot. Conversely, the position of cedar samples in the ordination space did not change much with depth.

Significance Testing.

Our three groupings showed distinctive differences in peat qualities (Fig. 4). Open poor fens showed significant differences between peat depth bins, with their surface samples being significantly higher than their deep peat on the carbonyl/lignin index, and significantly lower than their deep peat on the lipid/polysaccharide, lignin, and humification indices. In comparison, the FPF and FRFs showed no significant difference with depth in any indices. Open poor fens also differed significantly within depth classes from the other peat types; they were significantly higher than FRFs in C/L index and lower in L/P, lignin, and humification indices. Open poor fens were significantly lower in L/P indices and humification indices than FPF at depth (Fig. 4). These results are reiterated in a continuous, unbinned, manner in Fig. 5, which showed a continuous mean and confidence interval for each ecotype for each index (Fig. 5). Notably, most changes with depth, within ecotype and index, occurred between 25 and 75 cm.

Table 2 The PCA loading matrix for all 25 cm peat depth bins. This loading matrix corresponds with the PCA presented in Fig. 3

Index	PC1	PC2
Carbonyl/Lignin Index	-0.82702	0.43058
Lipid/Polysaccharide Index	0.61040	0.78067
Lignin Index	0.79239	-0.43708
Humification Index	0.95214	0.23727

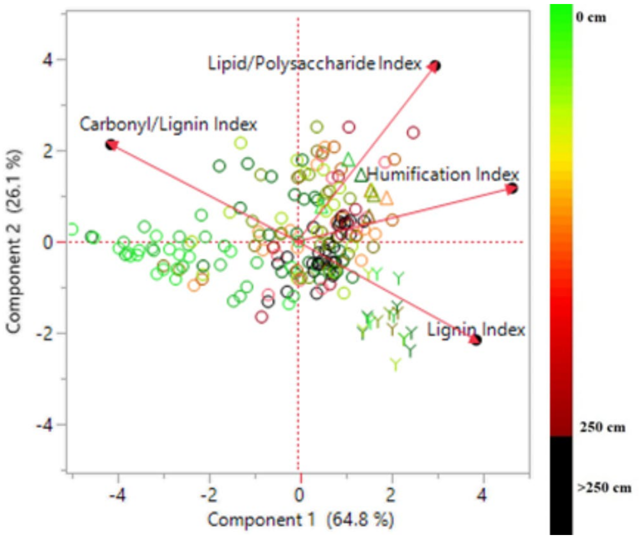

Fig. 3 The PCA chart and loading vectors, indicating the distribution of peat types for all 25 cm peat depth bins. Colors indicate depth, surface samples being light green and transitioning with increasing depth to dark red at 225 cm bins while all bins 250 cm and deeper are black. Circles indicate open poor fen samples (OPF), triangles indicate forested poor fen (FPF) samples, and Y-shapes indicate forested rich fen (FRF) samples. Component loadings are available in Table 2

Discussion

We quantified changes in peat chemistry that occurred with differences in tree cover and the depth patterns in common types of hemi-boreal peatlands. We found that rich fen silvic peat was lower in quality throughout the depth profile than the peat of open poor fens by all of our metrics. Extensive tree cover was associated with low peat quality at the surface, and more homogeneity across the depth profile. As peat depth increased, peat became more humified, and the distinction between the open poor fens and the forested poor fen declined, though they still differed in L/P and humification indices. These findings suggest that forested rich fen silvic peat is lower in quality both at the surface and at depth than poor fen peat, even in the presently silvic forested poor fen.

We also saw the tendency of peat to humify with age and depth. Humification causes concentration of stable molecular peat components by the preferential consumption of unstable molecules and therefore humification confers some resistance to further degradation. Our observations of high surface humification in forested peatlands support our hypotheses and match observations of high surficial decomposition in cedar peatlands using the von Post decomposition scale (Kolka et al. 2016) and labile C pool estimates (Bridgham et al. 1998). The forested sites, FPF and FRF, both had little ground cover vegetation due to shading from the canopy. In contrast to the open fens, which were covered in a carpet of live moss, the peat in forested fens was largely exposed muck not covered by litter. As a result, both FPF and FRF sites had surface peats that received mainly tree litter and little moss litter in contrast to the OPFs. This limited surficial vegetation also contributes to the relative homogeneity with depth in FPF and FRF peat in contrast

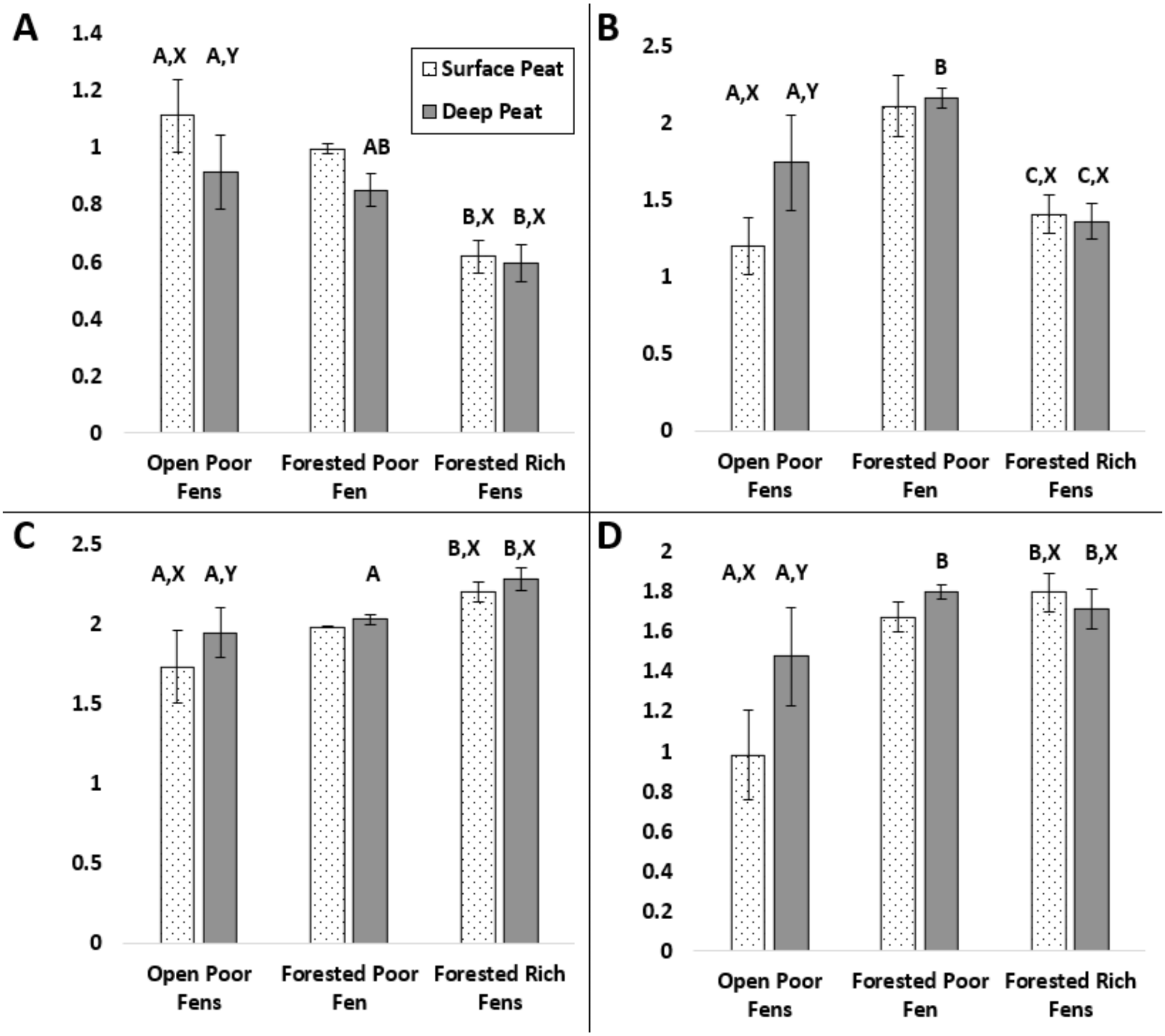

Fig. 4 Bar charts indicating the significant differences in peat qualities between peat types within depth bins (A, B, C) and between surface and deep peat bins within the same peat type (X, Y). Error bars indicate standard deviation. (A) Carbonyl/Lignin Index (B) Lipid/Polysaccharide Index (C) Lignin Index (D) Humification Index. Difference codes are not present between depths for the FPF or between peats for the FPF surface samples due to insufficient sample size

to the OPFs. Another factor that may drive the higher surficial humification observed in forested compared to open fens is the typically lower water table necessary to support trees. The interacting factors of water level and vegetation both likely contribute to driving the differences we observed among fen ecotypes. For example, earlier exploration with FTIR of German peat has shown that a higher and more stable water table was coincident with more aliphatic compounds (Heller et al. 2015).

The open poor fens showed equivalent or greater differences with depth as observed between peatland classes. This is reflective of the large difference in peat quality between the surface samples of the poor fens, which we observed to be fibric to hemic and their deeper peat samples, which we observed to be hemic to sapric. The gradual increase in humification with depth in OPFs, which never reaches parity with humification in other silvic peats, may indicate that in OPFs the decomposition process is slower and overall peat quality is higher.

We established that there are distinct differences in peat properties which vary with tree cover, even within the same region. The trends are similar to those found by Hodgkins et al. 2018, who investigated peat properties across latitudes. Their low latitude peatlands, particularly

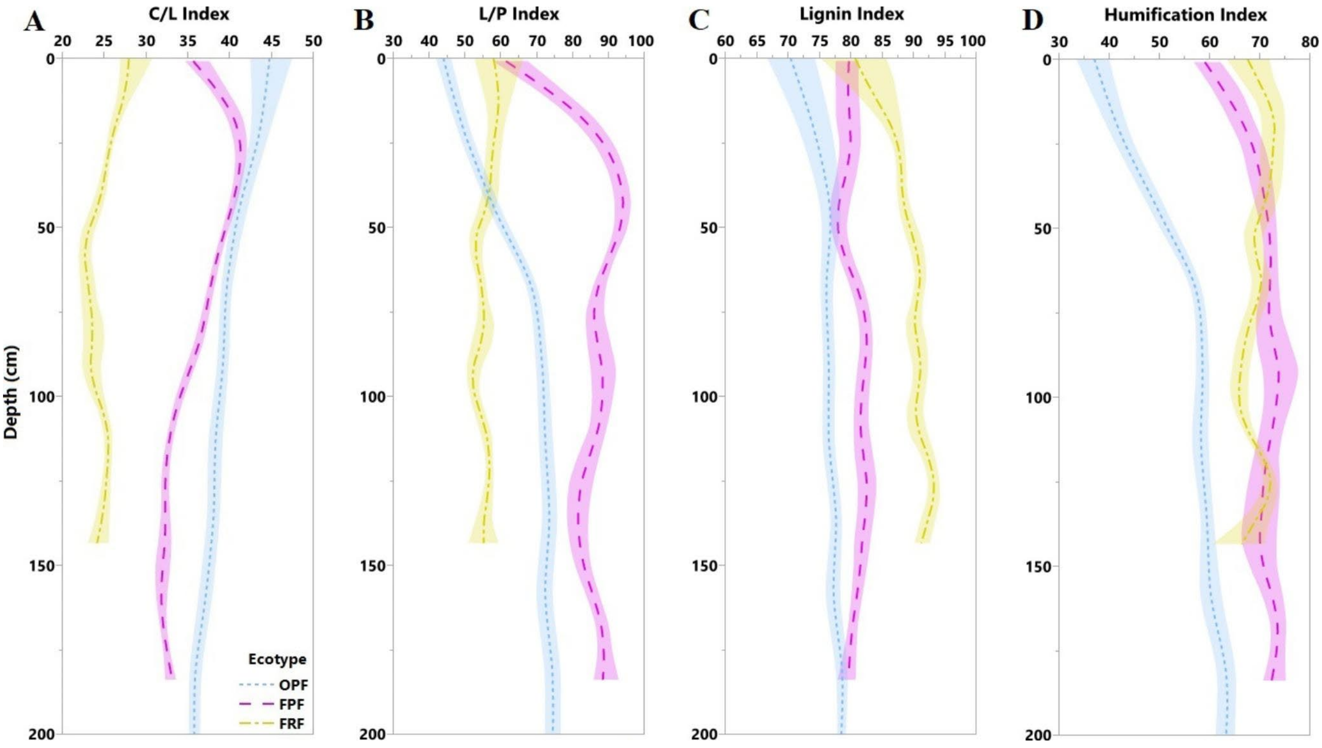

Fig. 5 Figure illustrating the relationship of each index with each ecotype and depth. All indices were multiplied by 40 for clarity. Trends for open poor fens (OPF; which extend to 500 cm) were truncated to 200 cm depth to highlight differences among the three sites. Dotted lines indicate means, colored zones indicate 95% confidence intervals. OPF = open poor fens, FPF = forested poor fen, FRF = forested rich fens

the shrub-dominated American Pocosin sites and tree-dominated tropical Bruneian Mendaram sites resembled our FRF sites, with lower peat quality at the surface, which decreased little with depth. Meanwhile, their *Sphagnum*-dominated high latitude peatlands were much like our poor fen peatlands, with higher relative peat quality at the surface, with decreasing peat quality at depth. These similarities make sense, as the sites selected by Hodgkins et al. had a covariance of vegetation with latitude: their high latitude peat was from sites similar to our poor fens, and their sites became increasingly tree dominated with decreasing latitude, similar to our FRFs. Another recent study by Verbeke et al. (2022) replicated the latitudinal gradient and explicitly attempted to separate the effects of latitude and vegetation. They reported increases in peat quality associated with increasing latitude even when vegetation effects were removed. Treed peatlands producing silvic peat appear to follow similar trends with depth in vastly different latitudes. Open *Sphagnum* and cushion plant peatlands of Patagonia also follow similar patterns of humification as our OPFs (Broder et al. 2012). This implies that the dominant plant functional type (e.g. tree, shrub, graminoid, or moss) may be more important to peat quality than species identity—or even latitude—in peatlands.

Conclusions

We found silvic peat in FRFs to be generally of lower quality than *Sphagnum* peat in poor fens, particularly at the surface. Peat in all systems converges in quality at greater depths, or greater age, but FRFs were the most similar across depths while open poor fens were the most dissimilar across depths, indicating a slower degradation process in poor fens than rich fens. We found that the patterns in peat quality observations with depth were comparable to previously published patterns in equivalent peat types regardless of location; silvic peat followed the same pattern of high surface humification that does not change much with depth in Brunei as we observed in Michigan, and moss peat followed the same pattern of low surface humification with gradual increase with depth in Patagonia as in Michigan. Michigan OPFs will likely be more impacted by climate change perturbations to temperature and water table, particularly seasonal perturbations, because their surficial peat quality is higher than FRFs. Differences in the plant functional types providing peat inputs, in this case trees and mosses, drive significant differences in peat quality throughout the peat column. Silvic peat was lower quality than moss derived peat, which has implications for C cycling and resilience to disturbance.

Acknowledgements We thank Sam Kurkowski and Andrew Robertson for all of their help with FTIR analyses, and Kate Heckman for her expertise. We additionally thank two anonymous reviewers for their constructive feedback, which contributed to greatly improving the manuscript.

Author contributions: All authors contributed to the conception of this study. Rodney Chimner and Evan Kane funded the study. Dominic Uhelski led material preparation, data collection, and analysis. Dominic Uhelski wrote the first draft, all authors contributed to editing previous drafts of the manuscript. All authors read and approved the final manuscript.

Funding: We acknowledge the support and funding that we received from the USDA Forest Service, Hiawatha National Forest, and in-kind support from the USDA Forest Service, Northern Research Station. Funding from the National Institute of Food and Agriculture, USDA, McIntire-Stennis program, MTU graduate school, and the Ecosystem Science Center (MTU) also supported this study.

Data Availability The datasets generated during and/or analyzed during the current study are available from the Pangaea data repository (https://doi.org/10.1594/PANGAEA.942942). In the event that data is inaccessible from Pangaea, it will be made available by the corresponding author upon reasonable request.

Declarations

Competing Interests: The authors have no relevant financial or non-financial interests to disclose.

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