# Effects of permafrost aggradation on peat properties as determined from a pan-arctic synthesis of plant macrofossils

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**Key Points**

- Permafrost aggradation history in peatlands was examined using plant macrofossil records
- Peat properties may reflect permafrost aggradation, especially nitrogen content
- Ecosystem succession in permafrost peatlands is highly dynamic and not uni-directional

## Abstract

Permafrost dynamics play an important role in high-latitude peatland carbon balance and are key to understanding the future response of soil carbon stocks. Permafrost aggradation can control the magnitude of the carbon feedback in peatlands through effects on peat properties. We compiled peatland plant macrofossil records for the northern permafrost zone (515 cores from 280 sites) and classified samples by vegetation type and environmental class (fen, bog, tundra and boreal permafrost, thawed permafrost). We examined differences in peat properties (bulk density, carbon (C), nitrogen (N) and organic matter content, C/N ratio) and C accumulation rates among vegetation types and environmental classes. Consequences of permafrost aggradation differed between boreal and tundra biomes, including differences in vegetation composition, C/N ratios, and N content. The vegetation composition of tundra permafrost peatlands was similar to permafrost-free fens, while boreal permafrost peatlands more closely resembled permafrost-free bogs. Nitrogen content in boreal permafrost and thawed permafrost peatlands was significantly lower than in permafrost-free bogs despite similar vegetation types (0.9% versus 1.5% N). Median long-term C accumulation rates were higher in fens (23 g C $m^{-2}$ $y^{-1}$) than in permafrost-free bogs (18 g C $m^{-2}$ $y^{-1}$), and were lowest in boreal permafrost peatlands (14 g C $m^{-2}$ $y^{-1}$). The plant macrofossil record demonstrated transitions from fens to bogs to permafrost peatlands, bogs to fens, permafrost aggradation within fens, and permafrost thaw and re-aggradation. Using data synthesis, we've identified predominant peatland successional pathways, changes in vegetation type, peat properties, and C accumulation rates associated with permafrost aggradation.

## 1 Introduction

Northern peatlands are one of the largest stocks of soil carbon (C) within the permafrost zone, storing nearly 30% of the 1035 ± 150 Pg C found in the top 3m of soils in the permafrost zone [*Hugelius et al.*, 2014]. Permafrost presence in the northern high latitudes has significant ramifications for the future of the peatland C stock as high latitudes warm [*Tarnocai*, 2006]. Permafrost aggradation in peatlands results in protection of soil organic matter from decomposition, as well as changes to soil hydrology that result in altered carbon exchange and increased vulnerability to wildfire [*Camill et al.*, 2009; *Turetsky et al.*, 2011]. Permafrost thaw can increase the decomposition of previously frozen soil organic matter and the release of greenhouse gases to the atmosphere including carbon dioxide, methane, and nitrous oxide [*Goulden et al.*, 1998; *Marushchak et al.*, 2011; *Schuur et al.*, 2009; *Turetsky et al.*, 2002]. In addition to soil temperature and moisture, the amount of C released during decomposition depends on peat composition and degree of decomposition at the time of permafrost aggradation [e.g. *Kuhry and Vitt*, 1996; *Sannel and Kuhry*, 2009; *Treat et al.*, 2014; *Vardy et al.*, 2000]. Therefore, understanding the history of permafrost aggradation and thaw in peatlands is important to understanding future climate feedbacks. However, determining the history of permafrost aggradation within peatlands still remains difficult due to a lack of distinct permafrost-specific plant indicator species [*Camill et al.*, 2009; *Oksanen and Väliranta*, 2006; *Sannel and Kuhry*, 2008]. Using changes in plant macrofossil *assemblages* and the presence of physical indicators such as cryostructures, charcoal, and highly humified peats, we synthesize peatland records with known permafrost history to examine how peat properties and carbon accumulation rates change with permafrost aggradation in boreal and tundra peatlands.

Permafrost aggradation in peatlands can alter hydrology, thus affecting vegetation composition, productivity, and decomposition, ultimately altering C accumulation rates. In boreal regions, permafrost aggradation and subsequent frost heave result in an elevated peatland surface that is drier than the surrounding unfrozen fens and bogs [*Bhiry et al.*, 2007; *Zoltai and Tarnocai*, 1975]. Drier surface conditions alter vegetation composition, increase the likelihood of wildfire [*Camill et al.*, 2009], increase the decomposition of surface peat [*Lamarre et al.*, 2012; *Turetsky et al.*, 2007] and ultimately result in lower C accumulation rates in boreal permafrost peatland environments than permafrost-free peatlands [*Camill et al.*, 2009; *Oksanen et al.*, 2001; *Robinson and Moore*, 2000; *Sannel and Kuhry*, 2009]. In tundra regions, permafrost aggradation also alters soil hydrology. Water infiltration is limited by permafrost presence, leading to saturated soils and subsequent wetland development [*Tarnocai and Zoltai*, 1988]. Ice-wedge development within polygonal peatlands results in microtopographical vegetation differences between the polygon wet centers with herbaceous vegetation and dry rims with woody vegetation [*Ellis and Rochefort*, 2004; *Mackay*, 1990; *Tarnocai and Zoltai*, 1988]. In contrast with boreal permafrost peatlands, simultaneous permafrost aggradation and peat deposition (i.e., syngenetic permafrost aggradation) in tundra and continuous permafrost regions can result in the assimilation of relatively undecomposed material into permafrost peat and relatively high rates of

C accumulation [*O'Donnell et al.*, 2012; *Sannel and Kuhry*, 2009; *Treat et al.*, 2014; *Vardy et al.*, 1997].

Permafrost thaw is associated with increased productivity, higher methane emissions, and higher rates of C accumulation [*Camill et al.*, 2001; *Robinson and Moore*, 2000; *Turetsky et al.*, 2007]. However, peat in permafrost thaw features is relatively young and more easily decomposed than other types of peat [*Jorgenson et al.*, 2013; *Payette et al.*, 2004; *Turetsky*, 2004], which may lower rates of long-term C accumulation as this peat decomposes. Despite high C accumulation rates following permafrost thaw, the net C loss from the former permafrost plateau can persist for decades to millennia [*O'Donnell et al.*, 2012].

Permafrost aggradation and thaw have been linked to a range of local and regional factors. Climate, both spatially and temporally, plays a role in permafrost aggradation. Permafrost aggradation can occur in regions where mean annual temperatures are lower than 0ºC. Late-Holocene Neoglacial cooling and Little Ice Age [820 - 150 cal yr BP; *Irvine et al.*, 2012] cooling resulted in wide-spread permafrost aggradation in many regions of Canada and Europe [*Halsey et al.*, 1995; *Hugelius et al.*, 2012; *Oksanen et al.*, 2003]. Additional factors affecting permafrost aggradation include the colonization of peatland surfaces by *Sphagnum* species (spp.), microtopography, tree and shrub cover, snow cover duration and depth, and disturbance [*Allard and Seguin*, 1987; *Camill*, 2000; 2005; *Johansson et al.*, 2006; *Payette et al.*, 2004; *Seppälä*, 2011; *Zoltai and Tarnocai*, 1975]. These factors cause changes in the soil thermal regime and result in decreased thermal conductivity during the summer or increased exposure to cold winter temperatures [*Halsey et al.*, 1995; *Oksanen et al.*, 2003; *Seppälä*, 1994; 2011; *Zoltai*, 1993; 1995; *Zoltai and Tarnocai*, 1975]. Permafrost thaw in peatlands can be associated both with climate and local factors such as disturbance, wildfire, and increased snow cover [*Camill*, 2005; *Johansson et al.*, 2006; *Payette et al.*, 2004; *Zoltai*, 1993].

Plant macrofossils can be used in conjunction with other physical indicators to determine the timing of transitions among peatland environmental classes, including transitions among fens, bogs, aggradation of permafrost, and thawing of permafrost (Figure 2). Transitions from brown moss (i.e., non-*Sphagnum* mosses such as Amblystegiaceae and Calliergonoideae sub-families) and Cyperaceae-dominated peat to *Sphagnum*-dominated peat is commonly associated with ombrotrophy and the fen-to-bog transition [*Vitt*, 2006], although *Sphagnum* alone cannot be used as a primary indicator of ombrotrophy because of the wide-range in nutrient status of *Sphagnum* species [*Laine et al.*, 2011]. Permafrost aggradation can result in plant macrofossil shifts to species tolerant of dry conditions, such as lichens, feather mosses, and dwarf shrubs [*Camill et al.*, 2009; *Oksanen et al.*, 2001; *Oksanen and Väliranta*, 2006; *Zoltai and Tarnocai*, 1975]. Permafrost aggradation that is concurrent with peat accumulation (syngenetic permafrost) can be indicated either by cryostructures or intermixing of mineral sediments and basal peat [*Kanevskiy et al.*, 2014; *Washburn*, 1979; *Zoltai*, 1995]. Changes in peat chemistry or peat properties, such as C/N ratios, have been used to aid in the identification of permafrost aggradation within a core [e.g. *Sannel and Kuhry*, 2009], but it is unknown whether permafrost widely affects peat properties. An abrupt transition from dry hummock bog species to wet fen or bog species can be used to indicate permafrost thaw [*Camill et al.*, 2009; *Jones et al.*, 2013; *Myers-Smith et al.*, 2008; *Nicholson et al.*, 1996; *Oksanen et al.*, 2001; *Robinson and Moore*, 2000; *Zoltai*, 1993; 1995]. Plant macrofossil records show repeated cycles of permafrost aggradation and thaw over the past several thousand years [*Jorgenson et al.*, 2013; *Kuhry*, 2008; *Oksanen et al.*, 2001; 2003; *Sannel and Kuhry*, 2008; *Zoltai*, 1993] in some records, but it is unclear how widespread these aggradation-degradation cycles are. These transitions sometimes contained a charcoal layer between the permafrost and thaw layers indicating wildfire in boreal permafrost peatlands that removed the insulating surface organic matter and, subsequently, resulted in thaw [*Kuhry*, 2008; *Oksanen et al.*, 2001; 2003; *Sannel and Kuhry*, 2008; *Zoltai*, 1993].

The objectives for this study were to first determine if a combination of plant macrofossil assemblages and peat properties can be used to identify permafrost aggradation and degradation based on a compilation of circumboreal/arctic peat cores. If these proxies can be used for permafrost history, then 1) determine to what degree permafrost aggradation and degradation impact carbon accumulation rates, 2) determine the frequency of transitions among peatland environmental classes and frequency of freeze/thaw cycles in Holocene peat cores, and 3) improve conceptual models of peatland succession by incorporating permafrost aggradation and thaw. We compiled existing plant macrofossil records from the boreal and tundra permafrost zone along with associated peat properties (carbon (C), nitrogen (N), carbon to nitrogen ratio (C/N), organic matter content (OM), bulk density, and C accumulation rates). To the best of our knowledge, a large-scale integrative comparison of peat properties and C accumulation rates among peatlands with permafrost has not yet been undertaken. In this study, we hypothesized that:

1) Environmental conditions associated with permafrost aggradation affect peat properties and C accumulation rates. Drying in boreal peatlands associated with permafrost aggradation increases decomposition, thereby decreasing C/N ratios and C accumulation rates. In tundra peatlands, syngenetic permafrost aggradation decreases decomposition through the freezing of relatively undecomposed organic matter, thereby increasing C/N ratios and C accumulation rates.
2) Repeated events of permafrost aggradation and thaw are more common in boreal regions than tundra regions.

## 2 Methods

### 2.1 Data compilation

We compiled records of plant macrofossils, radiocarbon dates, lithologies, and peat properties from cores collected within or adjacent to the contemporary northern permafrost zone. We identified studies using: 1) Web of Science search with the terms peatland, boreal, tundra, permafrost, carbon, macrofossil, and/or Holocene; 2) contributions of published and unpublished data, and 3) references from published studies. We included studies that contained data on peat properties (e.g., bulk density, C, N, organic matter content) and/or chronologic information in addition to information about lithology, macrofossil information, or stratigraphy for the entire peat record. We extracted depth information, peat properties, chronology, plant macrofossil data, and data interpretation from publicly available data, contributions, and published studies. Data were extracted from figures using a data extraction tool (PlotDigitizer; http://plotdigitizer.sourceforge.net/). Bulk density was measured on dry soils for 515 cores using gravimetric methods (Table S1). Organic matter content was measured using the loss-on-ignition technique at combustion temperatures ≥ 550°C for the 446 cores that reported values (Table S1). Total carbon and nitrogen were measured on bulk samples using elemental combustion analyzers for the 93 cores (%C) and 80 cores (%N) that reported data (Table S1). Total C and N data are reported per gram dry weight of sample for easy comparison with other studies. The C/N ratio is calculated on a mass basis. We excluded mineral soils from analysis based either on a %C cutoff (< 20% C by dry mass), organic matter cutoff (< 65% OM), or lithology descriptions (sand, silt, clay).

In this study, peat properties are presented for 517 cores from 280 pan-arctic permafrost zone sites with and without permafrost (Figure 1; Table S1). Fifty-three cores without permafrost were also included from a previous synthesis effort focused on northern hemisphere non-permafrost peatlands [*Loisel et al.*, 2014].

## 2.2 Vegetation type and environmental classification

Each sampling depth of each peat core was classified in two different categories, dominant vegetation type and environmental class, using plant macrofossil composition and/or lithology. Vegetation type was categorized using the dominant macrofossil component (> 35%) or the dominant description in the lithology. The categories for vegetation type included brown moss [*Tuittila et al.*, 2013], feather moss [*Tuittila et al.*, 2013], herbaceous (grasses, forbs, *Equisetum,* Cyperaceae), lichen, ligneous (shrubs, trees, rootlets), limnic (gyttja, organic rich silt, silty peat), *Sphagnum* spp.*,* or amorphous (no discernable dominant macrofossil type due to decomposition). A grouped "*Sphagnum*" vegetation type was used because *Sphagnum* functional types [hummock, lawn, hollow; *Laine et al.*, 2011; *Tuittila et al.*, 2013] were more similar to each other than to other vegetation types (Table S2).

Samples were also classified as one of six environmental classes using the macrofossil assemblages (Figure 2): fens [*Group*, 1988; *Zoltai and Vitt*, 1995], bogs [*Group*, 1988; *Zoltai and Vitt*, 1995], tundra permafrost peatlands, boreal permafrost peatlands, thawed permafrost (including collapse scar fens, bogs, and thaw ponds), and open water (ponds, pools, marshes, lakes, swamps, that all precede peat deposition). Boreal permafrost peatlands included fens and bogs with permafrost in the peat, palsas, and peat plateaus. Tundra permafrost peatlands included high center polygons, low center polygons, and tundra sites with organic soil horizons greater than 30 cm, where organic soil was defined by bulk organic C content of > 20%. We used authors' interpretation of their own cores to classify the macrofossil assemblages unless it strongly deviated from our criteria for classification (Figure 2). When authors did not make a classification and sufficient information was available, we used plant macrofossil assemblages, specific species composition information (e.g. *Sphagnum riparium* vs. *Sphagnum fuscum*) or taxonomic section, and other physical evidence from the depth interval in the environmental class determination (Figure 2) to classify the macrofossil assemblages. Because the threshold of detail was lower for the vegetation type classification than the environmental classification, there are more samples for the vegetation type category (n=10,647) than for environmental class (n=8778). Occasionally, macrofossil composition from a sample indicated conditions found either in a dry bog or a boreal peat plateau; in these situations, we conservatively classified these samples as "bog" [*Camill et al.*, 2009]. Polygonal peat plateaus occur in both boreal and tundra vegetation zones [*Zoltai et al.*, 1988] and were partitioned using the delineation of tundra and boreal permafrost peatlands from maps of vegetation zones [*Olson et al.*, 2001]. "Permafrost aggradation" refers to the moment of the transition towards peatland vegetation characteristically found in permafrost peatlands in the plant macrofossil assemblages rather than the distinction between the seasonally thawed soil active layer and the permafrost layers.

## 2.3 Carbon accumulation rates

Apparent C accumulation rates were calculated using dry bulk density, carbon content (%C), and peat accumulation rates based on depth and dating constraints (radiocarbon dates, $^{210}$Pb radiogenic dates, tephras) for each depth interval within a core. These apparent C accumulation rates are not necessarily reflective of rates of C accumulation at the time of deposition due to subsequent decomposition [*Frolking et al.*, 2014]. In the case of permafrost thaw, C losses from formerly frozen peat plateaus (boreal permafrost class) can exceed the high rates of C accumulation in the permafrost thaw class and thus result in a net C loss [*O'Donnell et al.*, 2012]. A single peat accumulation rate was calculated between each adjacent set of calibrated radiocarbon dates (linear interpolation) [*Reimer et al.*, 2013]. Carbon accumulation rates for each depth interval within a core were then calculated using the carbon density of the depth interval and the peat accumulation rate. To calculate C density for cores missing bulk density, we estimated (or gap-filled) bulk density measurements using mean bulk density for each vegetation type (Table 1), which was a better predictor of bulk density than age or depth ($F = 850$, $P < 0.0001$). To calculate C density for cores missing C content (Table S1), C content was calculated from organic matter content (% LOI, if available) using an empirical relationship from our dataset for the vegetation type (Table 1, n = 3380). For the amorphous vegetation type, we used the mean %C values from *Loisel et al.* [2014]. Bulk density was not filled for boreal or tundra permafrost soils for depths greater than 50 cm due to error arising from variable ice content. Estimated bulk density and C content were used for the calculation of C density for C accumulation rates but gap-filled data points (n= 416) were excluded from the analysis of peat properties (Table S5, S6). These efforts resulted in a record of C accumulation rates from 147 cores across 80 sites; however, many of these cores had poorly constrained peat accumulation rates due to low frequency or sporadic dating of peat horizons. We set a minimum threshold of one date per thousand years (Loisel et al., 2014), which resulted in 80 cores from 40 sites and represents an additional 48 cores within the pan-arctic permafrost and boreal regions from the previous synthesis effort (Loisel et al., 2014). Median C accumulation rates are calculated based on samples older than ca. 1000 cal. y BP to minimize the artifact of mixing peat that is stabilized in the catotelm versus undergoing continued decomposition in the acrotelm, whereas recent median C accumulation rates are calculated from samples < 1000 y age.

## 2.4 Statistical analysis

Means and standard errors are presented for most physical peat properties. Median C accumulation rates are presented due to the presence of outliers that met the chronologic control thresholds but exceeded known rates of productivity [> 200 g C m-2 y-1; Table S3, S4; e.g. *Sannel and Kuhry*, 2009]. The C accumulation rates were not normally distributed; median rates, 1$^{st}$ and 3$^{rd}$ quantiles (Q1 = 25%, Q3= 75% percentiles) of the C accumulation rates are reported, while the natural log-transformed data were used in the statistical analysis to improve normality. Mixed-effects modeling was used to test for statistical differences in peat properties and C accumulation rates among vegetation types and environmental classes. Core, age, and depth were included as random effects for both dependent variables. Vegetation type was included as an additional random effect in the analysis for differences among environmental classes to account for effects of vegetation type. Mixed-effects modeling was necessary because of the bias introduced from having multiple samples from the same core, to account for the effects of peat depth and age resulting from physical and decomposition processes, and to account for differences in vegetation types within the environmental classes. We implemented the mixed effects model using the lmer command from the lme4 package [*Bates*, 2010] for R statistical software [R Core Development *Team*, 2008]. Models were selected using Akaike's Information

Criterion (AIC) and $Chi^2$ test. Differences among samples were determined from 95% confidence intervals.

## 3 Results

### 3.1 Peat properties

Peat properties (organic matter content, C, N, and C/N mass ratios) differed significantly among different vegetation types (Table 1). Organic matter content was generally > 85% per gram dry weight across all vegetation types, with the exception of limnic peat, which was 77 ± 7% (sd) organic matter (Table 1; $P < 0.0001$). The mean C content of organic matter was 49.5% and did not differ significantly among vegetation types (Table 1). Bulk C content was generally greater than 42% C per gram dry mass except in limnic peat (39%) and amorphous peat (37%; Table 1; $P < 0.0001$). The mean N content of organic matter ranged from 1.0 ± 0.5% in *Sphagnum* vegetation types to 2.2 ± 1.0% in limnic peat, with a mean of 1.6 ± 0.9% among all vegetation types. N content was significantly higher in herbaceous peat (1.8 ± 0.7% per gram dry mass) than in *Sphagnum*-dominated peat (0.9 ± 0.4%; Table 1; $P < 0.0001$). Differences in bulk density among vegetation types were not statistically significant after accounting for differences among cores, depths, and ages using mixed effects modeling (Table 1). The C/N ratio was lowest in the amorphous peat (30) and limnic peat present at the initial stages of peat formation in many cores (31) and was approximately double in *Sphagnum* and lichen-dominated vegetation types (62; Table 1; $P < 0.0001$), likely reflecting the differences in initial C/N ratios among taxa and decomposition effects.

Peat properties differed significantly among different environmental classes even after accounting for differences in vegetation types (Table 2). The C/N ratio was significantly higher in boreal permafrost peatlands (67) and thawed permafrost peatlands (53) than all other environmental classes, and 40 – 80% higher than the C/N of bogs (Table 2; Figure 5a; $P < 0.0001$). C/N remained higher in boreal permafrost and permafrost thaw environmental classes with age (Figure 5a). Organic matter content was greatest in bogs (97%) but similar among all other types (91%) except for the open water environmental class (74%; Table 2; $P < 0.0001$). Mean C content in organic matter was lowest in thawed permafrost (47 ± 2%), followed by boreal and tundra permafrost (48%), bogs (49 ± 4%), and fens (51 ± 5%). Mean N content in organic matter was lowest in thawed permafrost (0.8 ± 0.3%), followed by boreal permafrost (0.9 ± 0.9%), bogs (1.1 ± 0.4%), tundra permafrost (1.7 ± 0.8%), and fens (2.4 ± 1.1%). Bulk C content was significantly higher in bogs, fens, and boreal permafrost environmental classes (mean: 47%, respectively) than in other tundra permafrost and thawed permafrost (Table 2; $P < 0.0001$). Bulk N differed significantly among environmental classes (Table 2; Figure 5b). N contents in fens were higher than all other classes (1.9 ± 0.7%), followed by bogs (1.6 ± 0.7%). N contents in tundra permafrost were significantly lower (1.4 ± 0.6%), but were still significantly larger than boreal permafrost and thawed permafrost environmental classes (0.9 ± 0.4%; Table 2; Figure 5b; $P < 0.0001$). Low N in boreal permafrost and thawed permafrost environmental classes persisted with age (Figure 5b). Bulk density did not differ significantly among environmental classes (Table 2).

## 3.2 Ecosystem dynamics in permafrost peatlands

The relative frequency of the dominant peat vegetation type varied between boreal and tundra permafrost environmental classes (Figure 3). Ligneous vegetation types were common in boreal and tundra permafrost environmental classes (20% and 25%, respectively), although macrofossils from trees were common in boreal permafrost, whereas ericaceous shrubs were common in tundra permafrost. *Sphagnum* was the primary vegetation type found in the boreal permafrost ecosystems (> 50%), while it was less common in tundra permafrost ecosystems (< 30%; Figure 3). Herbaceous (23%) and brown mosses (12%; including species from both tundra hummocks and wet depressions) vegetation types were the other common components of tundra permafrost ecosystems.

Our interpretation of environmental class based on plant macrofossil assemblages (Figure 2) showed that permafrost aggraded in 72% of boreal cores and 97% of tundra cores, based on our assumption of permafrost-free conditions when macrofossil assemblages were ambiguous. Twenty-five percent of cores with permafrost layers in the boreal zone showed evidence of permafrost thaw (Figure 4), based on an abrupt transition to herbaceous and *Sphagnum* species tolerant of wetter conditions (Figure 2). Subsequent permafrost re-aggradation occurred in 21% of these cores. A maximum of 18% of tundra cores showed evidence of permafrost thaw based on the increase in species indicative of wetter conditions in previously dry conditions, but more than half of these re-aggraded permafrost (62%; Figure 4).

Using environmental classifications obtained from the macrofossil assemblages (Figure 2), a majority of cores showed transitions among the different environmental classes (Figure 4). Open water preceded peat accumulation in 30% of all cores; of these cores, 85% subsequently transitioned to fens while 6% transitioned directly to bogs and 9% aggraded syngenetic permafrost (permafrost aggradation concurrent with peat accumulation). The later occurred nearly exclusively in drained thaw lake basins. The majority (nearly 80%) of all cores were characterized by fen vegetation at some depth within the core (Figure 4). Of these fen sites, 55% transitioned to permafrost-free bogs, 38% aggraded permafrost, and 7% remained fens. Aggradation of permafrost in fens was more common in tundra than boreal biomes (24% and 14%, respectively). A bog stage was present in 51% of cores. Permafrost aggraded in 54% of bog cores, while 31% of bog cores transitioned back to fens, and the final 15% remained permafrost-free bogs.

## 3.3 Peat and carbon accumulation rates

In addition to differences in peat properties among vegetation types, rates of C accumulation also differed among vegetation types (Figure 6b; Chi$^2$ = 2300, df = 6, $P < 0.0001$). Median rates of C accumulation were greatest in brown moss (median = 32.7, Q1 = 23.3, Q3 = 41.2 g C m$^{-2}$ y$^{-1}$) and limnic peat (median = 52.2, Q1 = 45, Q3 = 82 g C m$^{-2}$ y$^{-1}$). Ligneous (median = 15.5, Q1 = 12.4, Q3 = 24.9 g C m$^{-2}$ y$^{-1}$), *Sphagnum* (median = 16.7, Q1 = 11.6, Q3 = 24.9 g C m$^{-2}$ y$^{-1}$), herbaceous (median = 19.1, Q1 = 13.6, Q3 = 27.3 g C m$^{-2}$ y$^{-1}$), and amorphous vegetation types (median = 20.8, Q1 = 16.0, Q3 = 26.1 g C m$^{-2}$ y$^{-1}$) had lower median C accumulation rates than brown moss and limnic vegetation types.

Rates of C accumulation varied significantly among environmental classes throughout the Holocene after accounting for differences in vegetation type (Figure 6a; Chi$^2$ = 80, df = 2, $P < 0.0001$). Median rates of C accumulation were greatest in the open water stage (median = 27.3, Q1 = 23.8, Q3 = 34.1 g C m$^{-2}$ y$^{-1}$) and in permafrost tundra environmental classes (median = 108, Q1 = 14.9, Q3 = 111.0 g C m$^{-2}$ y$^{-1}$), but both values represented a limited number of cores for the open water stage (n = 6) and permafrost tundra (n = 3). The median rates of C accumulation were greater in fens (median = 23.2, Q1 = 15.1, Q3 = 35.5 g C $m^{-2}$ $y^{-1}$) than bogs (median = 17.7, Q1 = 11.6, Q3 = 26.8 g C $m^{-2}$ $y^{-1}$), and lower still for the boreal permafrost environmental classes (median = 14.2, Q1 = 9.5, Q3 = 19.8 g C $m^{-2}$ $y^{-1}$). Median rates of recent C accumulation (ages < 1000 years) were highest in the permafrost thaw (median = 33, Q1 = 17, Q3 = 64 g C $m^{-2}$ $y^{-1}$) and boreal permafrost environmental classes (median = 33, Q1 = 20, Q3 = 65 g C $m^{-2}$ $y^{-1}$). Including recent peat accumulation, median vertical peat growth rates were greatest in the permafrost thaw peat class (0.9 mm $y^{-1}$), followed by the boreal permafrost peat class (0.8 mm $y^{-1}$). Fen and bog classes had similar rates of vertical peat accumulation of 0.5 mm $y^{-1}$, while the open water and tundra permafrost classes were slightly less (both 0.4 mm $y^{-1}$).

# 4 Discussion

## 4.1 Broad patterns in permafrost peatland ecosystem dynamics

Using plant macrofossils for environmental classification should not rely on a single species, since vegetation types overlap among among different environmental classifications (Figure 3). For example, the transition to *Sphagnum*-dominated peat is commonly associated with ombotrophic transition to bogs [*Vitt*, 2006] but can also be associated with the oligotophic conditions found in fens. Distinguishing between these two environmental classes can be accomplished by identifying *Sphagnum* species (spp.) to the section level [*Laine et al.*, 2011], or using the macrofossil vegetation assemblage as a whole. Similarly, individual species found in present-day permafrost peatlands, such as *Sphagnum fuscum* and *Picea mariana*, are also found in dry, unfrozen bogs [*Camill et al.*, 2009]. Therefore, it is important to carefully consider the vegetation assemblage, including moss species, as a whole and the regional context [*Oksanen et al.*, 2001; 2003; *Oksanen and Väliranta*, 2006; *Sannel and Kuhry*, 2008]. Supplemental indicators of environmental transitions, such as changes in peat properties, would be helpful to better elucidate the history of permafrost aggradation and thaw at sites within the permafrost zone.

Peatlands in the high-latitude permafrost zone did not show straightforward successional trajectories from fens to bogs to permafrost peatlands. First, not all fens transitioned to bogs.

While the majority transitioned to bogs (55%), over 10% remained permafrost-free fens for the entire macrofossil record, including sites from the discontinuous permafrost regions of Eurasia that ranged from ca. 5000 – 9000 years in age [*Andreev et al.*, 2004; *Hugelius et al.*, 2012; *Mäkilä and Moisanen*, 2007; *Oksanen*, 2006] and Western Canada that ranged from ca. 1300 – 10,300 years in age [*Kettles et al.*, 2003; *Robinson*, 2006; *Yu et al.*, 2014]. Persistent fen conditions are related to the regional hydrologic dynamics, such as groundwater input, precipitation, throughflow, and input from adjacent water bodies, combined with catchment topography [*Glaser et al.*, 2004; *Nicholson and Vitt*, 1990; *Quinton et al.*, 2003; *Zoltai and Johnson*, 1985]. Changes in regional hydrology can also result in transitions from bog to fen [*Hájková et al.*, 2012; *Van Bellen et al.*, 2013], which occurred in 16% of all cores [*Camill et al.*, 2009; *Kettles et al.*, 2003; *Van Bellen et al.*, 2013]. Second, permafrost aggraded in 35% of fens as shown by the beginning transitions to more ligneous vegetation associated with the development of polygons, which means that many sites with permafrost were never bogs. In tundra regions, permafrost underlies low-center polygons with brown mosses, *Carex* spp., and *Eriophorum* spp. [Figure 2, 3; *Tarnocai and Zoltai*, 1988]. In Fennoscandia and boreal Canada, aapa mires, string fens, and earth hummocks contain permafrost under ridges or hummocks [*Luoto and Seppälä*, 2002; *Mäkilä and Moisanen*, 2007; *Oksanen*, 2006; *Seppälä*, 1998; *Zoltai et al.*, 1988].

Throughout the Holocene, permafrost aggradation and thaw were common processes in boreal and tundra peatlands within the permafrost zone. Permafrost aggradation occurred in ~ 70% of boreal and 97% of tundra cores that we analyzed from the modern permafrost zone. While *Sphagnum* moss presence has been cited as a factor promoting permafrost aggradation within bog hummocks, especially in more southern permafrost regions [*Camill et al.*, 2009; *Zoltai*, 1995; *Zoltai and Tarnocai*, 1975], *Sphagnum* presence was not required for permafrost formation at higher latitudes in our study and was less common in tundra permafrost than boreal permafrost (Figure 3). Permafrost thaw occurred in 25% of boreal and 12% of tundra cores. Most of the permafrost thaw in the tundra occurred in the discontinuous permafrost zone, and, following thaw, more cores in tundra re-aggraded permafrost than in boreal zones (62% in tundra vs. 21% in boreal; Figure 4). Repeated cycles of permafrost aggradation and thaw have previously been described at two sites in Western Canada in the isolated permafrost zone [*Zoltai*, 1993]. However, in this compilation of records, cyclical permafrost aggradation of more than two aggradation/thaw events was limited to a few additional sites located in Western Canada [nb. *Bauer and Vitt*, 2011 sampled same peatland complex as Zoltai (1993); *Kuhry*, 2008] and two Eurasian sites [*Oksanen et al.*, 2001; 2003]. Single events of permafrost thaw followed by permafrost re-aggradation were more common in this study zone (16 additional sites). While it appears that the cyclical pattern of multiple permafrost thaw and re-aggradation events was rare in peatlands within the permafrost zone, material from thawed areas may be poorly preserved and best identified using techniques such as chemical biomarkers [*Ronkainen et al.*, 2015].

## 4.2 Peat properties in high-latitude wetlands

The peat properties described in this study are in general agreement with the trends found by previous studies. Organic matter content in this study agreed well with previously reported values [*Bauer et al.*, 2006; *Loisel et al.*, 2014]. The mean carbon content of organic matter in this study (49.5 ± 5.1% (sd), n = 739) was slightly higher than the 49.2% reported by Loisel et al. [2014], but nearly identical to other values reported for North America [*Gorham*, 1991], Western Canada [*Vitt et al.*, 2000], and Siberia [*Sheng et al.*, 2004]. Median C accumulation rates were within the range reported by *Gorham et al.* [2003], *Yu et al.* [2009], and *Loisel et al.* [2014].

There were large differences in the C/N ratio between our data and previous syntheses, with much lower mean C/N ratios in this study (41) compared to *Loisel et al*. [2014] (55), likely due to many fewer *Sphagnum* peat samples in this study. The C/N ratio in bogs was greater than in fens, similar to findings for a large number of peatlands in temperate and boreal Ontario, Canada [*Wang et al.*, 2015], and consistent with higher C/N in *Sphagnum* peat compared to other peat types [*Loisel et al*., 2014]. The N contents for *Sphagnum*, herbaceous and woody/ligneous peats were moderately higher (5 – 24%) relative to mean values reported by *Loisel et al.* [2014]. This study encompassed a much larger number of permafrost peat samples than that of *Loisel et al.* [2014], who focused on the northern peatland domain as a whole.

## 4.3 Effects of permafrost aggradation on peat properties

The effects of permafrost aggradation on peat properties is somewhat difficult to discern because peat properties differed significantly between boreal and tundra permafrost environmental classes. The boreal permafrost environmental class had higher organic matter content (92 and 72%, respectively), higher C/N ratios (67 and 34, respectively; Figure 5a), but significantly lower N content (0.9 and 1.4%, respectively; Table 2; Figure 5b) and lower rates of C accumulation compared with tundra permafrost (median: 14 and 108 g C $m^{-2}$ $y^{-1}$ for boreal and tundra permafrost, respectively),. This could reflect differences in vegetation type (Figure 3; Table 1)[*Kuhry and Vitt*, 1996] or more frequent disturbance (wildfire) in boreal than tundra regions that results in C and N loss from soils [*Harden et al.*, 2002; *Mack et al.*, 2011].

The history of permafrost aggradation can be difficult to distinguish using vegetation types alone because of the similarity among vegetation types, even with additional information from considering plant macrofossil assemblages. However, if we compare the permafrost environmental classes to the other classes with similar vegetation and nutrient status (Figure 3), differences emerge that may be attributed to permafrost presence. Both permafrost-free fens and tundra permafrost had a high abundance of herbaceous peat. Ligneous and *Sphagnum* peat were more abundant in tundra permafrost classes than in permafrost-free fens (Figure 3), likely resulting from microtopography created by permafrost aggradation and polygon formation [*de Klerk et al.*, 2011]. Both boreal permafrost peatlands and permafrost-free bogs had a high abundance of *Sphagnum* peat, but again, ligneous peat was more abundant in boreal permafrost class (Figure 3). Based on this analysis, ligneous peat appears to be more prevalent in permafrost environmental classes than the comparable permafrost-free environmental classes.

Permafrost aggradation affects peat properties such as C/N ratios, nitrogen content, and organic matter content when permafrost peatlands are compared to permafrost-free peatlands with similar vegetation. Compared to permafrost-free fens, tundra permafrost peatlands had higher C/N ratios (34 versus 29; Figure 5a), lower N content (1.4% vs. 1.9%, Figure 5b), and a higher occurrence of intermixed mineral sediments (Figure 3). When compared to permafrost-free bogs, boreal permafrost environmental classes had higher C/N ratios (67 versus 37; Figure 5a) but significantly lower N content (0.9% versus 1.6%; Figure 5b).

Higher C/N ratios in the permafrost environmental classes than permafrost-free environmental classes may reflect the initial botanical composition of the vegetation types, differences in degree of decomposition, or differences in the peat N content. Vegetation differences between tundra permafrost and permafrost-free fens, such as higher abundance of *Sphagnum* peat (C/N = 62) and ligneous peat (32), could explain the higher mean C/N in tundra permafrost (34) than permafrost free-fens (27). Using the composition of vegetation types among environmental classes (Figure

3) and mean C/N ratios for those vegetation types (Table 1), we predict higher C/N ratios for tundra permafrost (41) than fens (36) based on vegetation differences. Accordingly, due to the higher frequency of *Sphagnum* peat in bogs (Figure 3), we predict that C/N ratios in bogs should be higher than the boreal permafrost environmental class (bog = 57 and boreal permafrost = 49), but this is not the case (bog = 37 and boreal permafrost = 67). Decomposition lowers C/N ratios in peat [*Kuhry and Vitt*, 1996]. Higher C/N ratios in permafrost peats than permafrost-free peats, especially in older peat (Figure 5a), might reflect a lack of decomposition related to the cold temperatures found in permafrost. Relatively high C/N throughout the record in boreal permafrost environmental classes (Figure 5a) suggests limited decomposition of boreal permafrost peats throughout the Holocene, whereas C/N ratios in the bog environmental class decreases in older samples, indicating a legacy of decomposition.

Nitrogen contents were also lower in tundra and boreal permafrost than their permafrost-free counterparts and may be attributable to disturbance losses, denitrification, or storage in the undecomposed, frozen organic matter in permafrost. Nitrogen could be lost from permafrost ecosystems as $N_2O$ from denitrification [*Marushchak et al.*, 2011; *Repo et al.*, 2009] or N could be lost during wildfire from both boreal permafrost peatlands [relatively common; *Harden et al.*, 2002] and tundra permafrost ecosystems [relatively uncommon; *Mack et al.*, 2011]. Permafrost presence and the resulting N storage in frozen organic matter may result in N limitation, resulting in N resorption into tissues prior to litterfall, reduced rates of decomposition and positive feedbacks to low nitrogen concentration in permafrost peats [*Aerts et al.*, 1999; *Harden et al.*, 2012; *Shaver and Chapin*, 1991; *Vitousek*, 1982], whereas N can be remineralized from greater depths in permafrost-free peats. Similarly, permafrost aggradation and shifts in hydrology associated with uplift can further increase the isolation of the peat surface from hydrologic sources of N. Alternatively, relatively low N content in boreal and tundra permafrost peatlands could reflect the relatively undecomposed peat material compared to similar peatlands without permafrost, as indicated by the C/N ratios (Figure 5a). Finally, differential amounts of nitrogen fixation among the peat classes may also be reflected in the peat N contents [e.g. *Berg et al.*, 2013; *Harden et al.*, 2002; *Larmola et al.*, 2014; *Vile et al.*, 2014]. Using the synthesis approach, we are unable to directly evaluate these mechanisms, although the differences in C/N ratios among environmental classes support the hypothesis of limited decomposition in permafrost peats.

### 4.4 Effects of permafrost aggradation on apparent C accumulation rates

Permafrost aggradation and thaw changes C accumulation rates (Figure 6a) as well as peat properties (Table 2). Boreal and tundra permafrost peatlands had significantly different rates of C accumulation, but the magnitude of change associated with permafrost aggradation also differed when compared to environmental classes with similar vegetation types but without permafrost. Greater C accumulation rates occurred in tundra permafrost than fen environmental classes, while C accumulation rates were lower in boreal permafrost than bog environmental classes. In the short-term, recent C accumulation rates increased following permafrost thaw, although C is also simultaneously lost from deeper soils. At several sites included in this study, syngenetic permafrost aggradation limited decomposition and resulted in high C accumulation rates at depth [*O'Donnell et al.*, 2012; *Sannel and Kuhry*, 2009; *Vardy et al.*, 2000]. This may have been a factor in the relatively high rates of C accumulation observed in tundra permafrost peat classes compared to fens.

### 4.5 Limitations to reconstructing ecosystem and climate dynamics

Reconstruction of ecosystem dynamics requires more detailed macrofossil analysis than is common in many descriptions of core lithologies. Using the lithology or vegetation type to determine the environmental classification can be problematic because of the frequent presence of *Sphagnum* peat among different environmental classes (Figure 3). Therefore, the transition to *Sphagnum*-dominated peat cannot be used as a proxy for the fen-bog transition without consideration to the other common indicators of ombotrophy [*Laine et al.*, 2011]. The environmental classification in this study uses plant macrofossil assemblages along with other physical and biological indicators rather than simply the surface vegetation or vegetation type, which can be ambiguous and change through time [Figure 4; *Yu et al.*, 2013].

Determining the timing of permafrost aggradation can require multiple lines of evidence. Using temporal changes in the plant macrofossil composition and shifts in assemblages is the most widespread and reliable but requires caution due to overlapping habitats among species. Several common macrofossils are found in multiple environmental classes and make discerning the onset of permafrost aggradation difficult [*Camill et al.*, 2009; *Oksanen*, 2006; *Oksanen et al.*, 2001; *Sannel and Kuhry*, 2008]. In addition to plant macrofossil composition, previous studies have used several techniques to infer permafrost aggradation, including testate amoeba [*Jones et al.*, 2013; *Lamarre et al.*, 2012; *Swindles et al.*, 2015], changes in physical and chemical properties including charcoal presence [*Camill et al.*, 2009; *de Klerk et al.*, 2011; *Oksanen*, 2006; *Oksanen et al.*, 2001; *Sannel and Kuhry*, 2008; *Tarnocai and Zoltai*, 1988; *Zoltai*, 1993], and analysis of cryostructures [*Kanevskiy et al.*, 2014; *O'Donnell et al.*, 2012; *Vardy et al.*, 1997]. We propose that N content could be used as an additional proxy of permafrost aggradation. Our analyses show significantly lower N content in peat deposited following permafrost aggradation; these differences persist over time (Figure 5b). Using > 3000 measurements from 90 peat profiles across the pan-arctic, N content in boreal permafrost and tundra permafrost environmental classes was significantly lower than in permafrost-free peats with similar vegetation (Figure 5b). While C/N ratios showed similar trends, the variability in N content was smaller than variability in C/N ratios, making this metric more useful (Figure 5). Other promising chemical and biological analyses that warrant further exploration and might help to discern permafrost history within high latitude peatland peat core profiles include stable C and N isotopes, lipid biomarker extraction, testate amoeaba, orabatid mites and ancient DNA extraction [*Andersson et al.*, 2011; *Andersson et al.*, 2012; *Lamarre et al.*, 2012; *Markkula*, 2014; *Parducci et al.*, 2014; *Ronkainen et al.*, 2014; *Routh et al.*, 2014; *Swindles et al.*, 2015].

The interpretation of climate dynamics from peatland records of permafrost aggradation and thaw is difficult due to the combination of autogenic processes, local factors and regional climate. Regional differences in climate, glacial history, and geomorphology affect peatland development and permafrost history [*Ellis and Rochefort*, 2004; *Nicholson et al.*, 1996]. For example, the history of two arctic regions differs greatly. Peat in many tundra permafrost peatlands in Western Canada accumulated during warmer and wetter climatic conditions [e.g. *Tarnocai and Zoltai*, 1988; *Zoltai*, 1995], while in regions of Alaska and Siberia, the thawing of massive Pleistocene ice wedges in loess sediments has resulted in thermokarst lakes and subsequent, on-going peat accumulation [*Jones et al.*, 2012; *Kanevskiy et al.*, 2014; *O'Donnell et al.*, 2012; *Walter Anthony et al.*, 2014]. Ideally, multiple proxies, such as diatoms, pollen, testate amoeba, or chemical analyses, and multiple sites could be used to support site-specific processes versus regional climate influences. The approach of synthesizing macrofossils records used in this study offers great promise for future studies with the goal of understanding historical permafrost dynamics across the high-latitude permafrost zone.

## 5 Conclusions

Ecological and hydrological changes associated with permafrost aggradation in peatlands altered vegetation types as well as carbon and nitrogen cycling, and ultimately affected peat properties, ecosystem productivity, decomposition, and net carbon balance. Using the frequency of vegetation types and common successional transitions among environmental classes, we found that boreal permafrost peats were most similar to permafrost-free bogs, while tundra permafrost peats were most similar to permafrost-free fens. Using this comparison, permafrost aggradation reduced peat N content relative to their permafrost-free counterparts (Figure 5b), although the exact mechanism remains unclear and should be explored with further research. This would enable the use of N as a supplementary indicator of permafrost aggradation. Permafrost aggradation also increased C accumulation rates in boreal permafrost peat relative to permafrost-free bogs due to slightly higher rates of C accumulation in the surface peat that may have been related to the presence of relatively undecomposed organic matter, which is supported by the relatively high C/N ratios (Figure 5a). Finally, the interactions between permafrost aggradation, productivity, decomposition, disturbance and nitrogen illustrated here warrant further research.

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Table 1. Mean peat properties, standard deviation (sd), and number of samples (n) among vegetation types, including C/N ratio, carbon (%C), nitrogen (%N), organic matter (%OM), carbon content in organic matter (%) and bulk density. Vegetation types were determined from the dominant plant macrofossil (>30%). Different superscript letters indicate significantly different means among groups ($P < 0.05$).

| Vegetation type | C/N ratio | | | %C | | | %N | | | % OM | | | Carbon content in organic matter (%) | | | Bulk density (g cm$^{-3}$) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | mean | sd | n | mean | sd | n | mean | sd | n | mean | sd | n | mean | sd | n | mean | sd | n |
| Amorphous | $30^{c}$ | 15 | 118 | $36.5^{d}$ | 10.7 | 119 | $1.47^{bc}$ | 0.73 | 118 | $86.2^{e}$ | 9.4 | 258 | 59.4 | 9.5 | 20 | 0.153 | 0.075 | 382 |
| Brown Moss | $40^{b}$ | 19 | 106 | $44.1^{ab}$ | 8.1 | 145 | $1.32^{cd}$ | 0.64 | 106 | $91.6^{c}$ | 4.9 | 979 | 50.1 | 3.5 | 79 | 0.111 | 0.046 | 1008 |
| Feather Moss | $36^{abc}$ | 15 | 3 | $46.8^{ab}$ | 1.8 | 6 | $1.43^{abcd}$ | 0.47 | 3 | $92.5^{abcde}$ | 11.5 | 6 | 48.6 | 3.5 | 5 | 0.160 | 0.060 | 6 |
| Herbaceous | $29^{c}$ | 16 | 323 | $44.5^{b}$ | 8.5 | 406 | $1.77^{a}$ | 0.71 | 406 | $90.6^{d}$ | 6.1 | 2905 | 51.4 | 4.2 | 218 | 0.123 | 0.051 | 3033 |
| Lichen | $62^{a}$ | 22 | 13 | $47.3^{ab}$ | 4.9 | 13 | $0.89^{de}$ | 0.47 | 13 | $94.0^{abcde}$ | 4.2 | 2 | 53.0 | | 1 | 0.062 | 0.045 | 13 |
| Ligneous | $32^{bc}$ | 16 | 180 | $42.1^{b}$ | 8.6 | 204 | $1.47^{bc}$ | 0.55 | 180 | $93.2^{b}$ | 6.0 | 972 | 49.7 | 3.9 | 90 | 0.124 | 0.070 | 1060 |
| Limnic | $31^{c}$ | 21 | 20 | $39.4^{c}$ | 8.2 | 25 | $1.76^{ab}$ | 0.88 | 20 | $76.5^{f}$ | 6.7 | 99 | 57.1 | 11.1 | 2 | 0.168 | 0.100 | 121 |
| *Sphagnum** | $62^{a}$ | 28 | 612 | $45.4^{a}$ | 4.6 | 691 | $0.88^{de}$ | 0.40 | 612 | $95.7^{a}$ | 4.3 | 3243 | 47.8 | 3.9 | 276 | 0.083 | 0.045 | 3664 |
| All samples | 41 | 26 | 2778 | 45.6 | 6.3 | 3012 | 1.48 | 0.72 | 2779 | 92.4 | 6.4 | 9161 | 49.5 | 5.1 | 739 | 0.110 | 0.063 | 11,029 |
| Chi$^{2}$ (df =7) | 12,994 | | | 7465 | | | 3385 | | | 2818 | | | 12 | | | 0 | | |
| *P* | < 0.0001 | | | < 0.0001 | | | < 0.0001 | | | < 0.0001 | | | 0.11 | | | 1 | | |

* Means for different Sphagnum groups (hummock, hollow, lawn) can be found in Table S2.

Table 2. Mean peat properties, standard deviation (sd), and number of samples (n) among environmental classifications, including C/N ratio, carbon (%C), nitrogen (%N), organic matter (% OM), and bulk density for different environmental classes. Environmental classification was determined from the plant macrofossil records. Different superscript letters indicate significantly different means among groups ($P < 0.05$).

| Environmental class | C/N ratio | | | %C | | | %N | | | % OM | | | Bulk density (g cm$^{-3}$) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | mean | sd | n | mean | sd | n | mean | sd | n | mean | sd | n | mean | sd | n |
| Open water | $18^{abc}$ | 3 | 2 | $34.5^{ab}$ | 10.1 | 2 | $2.0^{abcd}$ | 0.90 | 2 | $74.0^{d}$ | 6.2 | 8 | 0.243 | 0.124 | 11 |
| Fen | $29^{c}$ | 15 | 1082 | $46.5^{a}$ | 5.9 | 1217 | $1.89^{a}$ | 0.66 | 1076 | $91.8^{bc}$ | 6.8 | 2603 | 0.120 | 0.058 | 3369 |
| Bog | $37^{c}$ | 19 | 733 | $47.0^{a}$ | 4.2 | 783 | $1.55^{b}$ | 0.66 | 732 | $96.6^{a}$ | 3.7 | 1825 | 0.094 | 0.050 | 2482 |
| Permafrost: boreal | $67^{a}$ | 33 | 576 | $46.7^{a}$ | 5.3 | 594 | $0.88^{cd}$ | 0.45 | 576 | $92.4^{b}$ | 7.9 | 348 | 0.109 | 0.079 | 913 |
| Permafrost: tundra | $34^{bc}$ | 18 | 273 | $39.5^{b}$ | 9.0 | 290 | $1.35^{c}$ | 0.55 | 273 | $91.3^{c}$ | 8.3 | 390 | 0.165 | 0.214 | 384 |
| Permafrost thaw: boreal | $53^{b}$ | 23 | 211 | $42.0^{b}$ | 6.3 | 219 | $0.93^{d}$ | 0.40 | 212 | $92.5^{b}$ | 5.2 | 196 | 0.089 | 0.072 | 422 |
| Chi$^{2}$ (df = 5) | 192 | | | 154 | | | 105 | | | 208 | | | 0 | | |

Figure 1. The locations of sites included in this synthesis of peat properties across the permafrost zones [*Brown et al.*, 1998, revised 2001]. Sites included in the analysis of peat properties (PeatProp, circles), carbon accumulation (C acc.; squares), peat properties and carbon accumulation (PP + C acc.; triangles), or ecosystem transitions (black crosses). Sites included in previous analysis by Loisel *et al*. [2014] are indicated by an interior black dot; original sites are indicated within the legend (orig.). Labels indicate the site number and correspond with additional site information in Table S1.

Figure 2. Schematic diagrams showing relationships between peatland classes used in this study and macrofossil assemblages, taxonomic examples, and other physical indicators used to interpret peatland classes for boreal zone ecosystems (A) and tundra zone ecosystems (B).

[1] Open water peatland classes included ponds, pools, marshes, swamps and first-generation thermokarst lakes formed in upland, un-glaciated terrain that later accumulate sufficient organic matter to meet the peatland criteria (> 30cm) [e.g. *Jones et al.*, 2012; *Walter Anthony et al.*, 2014].

[2] Fen in the boreal zone included minerotrophic rich fens, mesotrophic fens, and oligotrophic poor fens [*Group*, 1988].

[3] Permafrost: boreal included permafrost bogs, palsas, peat plateaus, aapa mires with permafrost, and polygonal peat plateaus within the boreal zone [*Camill et al.*, 2009; *Group*, 1988; *Oksanen and Väliranta*, 2006; *Sannel and Kuhry*, 2009; *Zoltai and Tarnocai*, 1975].

[4] Permafrost thaw included collapse scar bogs, collapse scar fens, and thaw ponds within peatland complexes [*Camill et al.*, 2009; *Oksanen and Väliranta*, 2006; *Robinson and Moore*, 2000; *Zoltai*, 1993] but excludes first-generation thermokarst lakes formed in upland, un-glaciated terrain.

[5] Fens in the tundra zone included rich fens, mesotrophic fens and poor fens and are well described by *Tarnocai and Zoltai* [1988]. Here, tundra fens include fens without permafrost in the organic soil. However, in the continuous permafrost zone, permafrost was likely present in the underlying mineral soils.

[6] Permafrost tundra includes high-center polygons, low-center polygons, tundra with more than 30 cm of organic soil, and polygonal peat plateaus. In polygons, the plant macrofossil assemblages reflect vegetation differences that are generally controlled by microtopography and relative water table position [*de Klerk et al.*, 2011; *Ellis and Rochefort*, 2004; *Nicholson et al.*, 1996; *Vardy et al.*, 1997]. Microtopography and polygonal patterns develop over many centuries with ice wedge and permafrost aggradation [*Mackay*, 1990]. In this case, permafrost aggradation refers to the occurrence of permafrost within the organic soil rather than underlying mineral soil. Permafrost thaw in

polygons results in a deepening of wedges and troughs, which resemble the earlier sedge meadow communities [*Jorgenson et al.*, 2006] but may contain more inter-mixed mineral soil [*de Klerk et al.*, 2011].

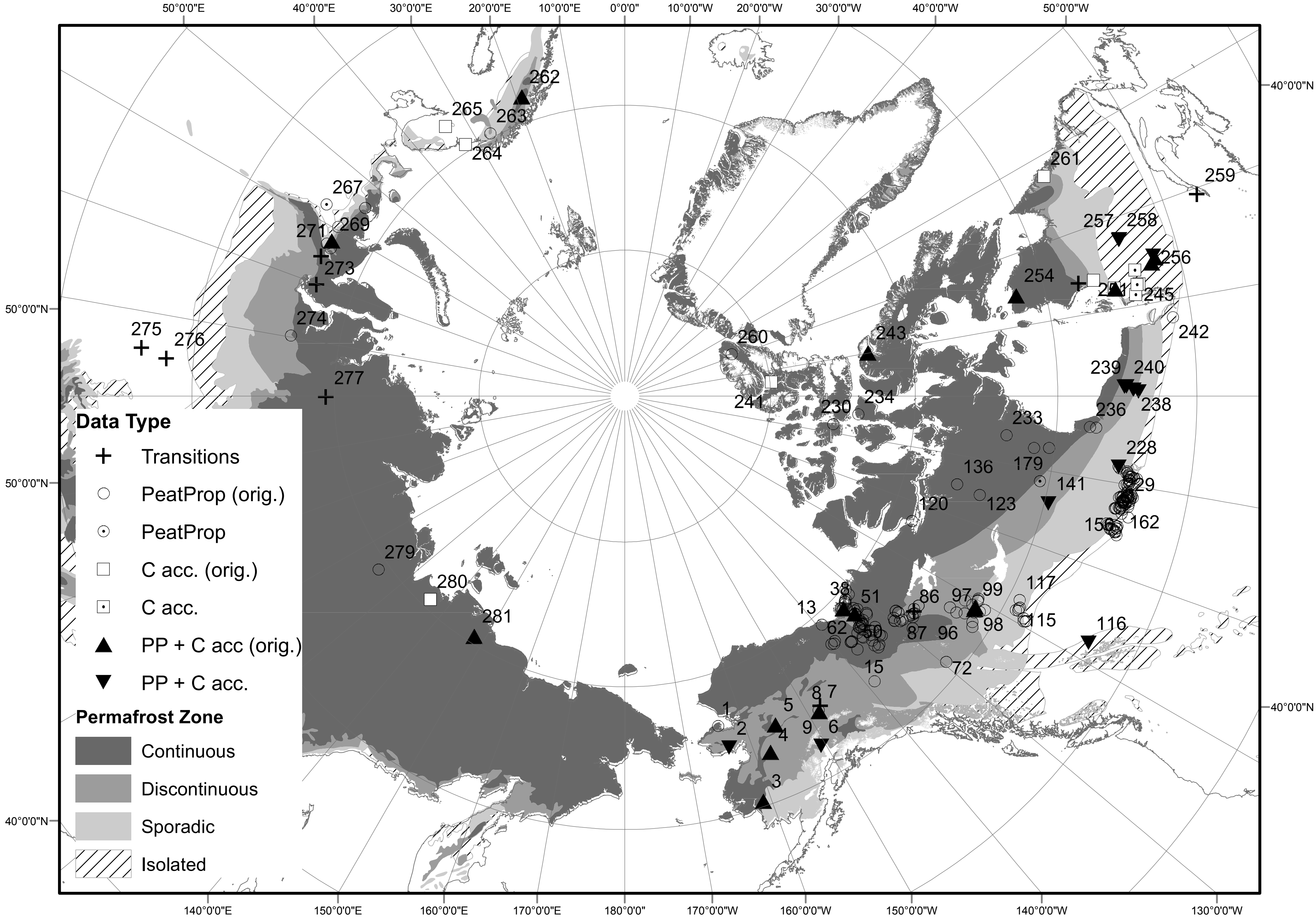
Figure 3. The relative composition of vegetation types among the environmental classifications. The order of bars from left to right follows the order of the legend. The vegetation type of samples were classified using the dominant species, which generally represented > 30% of the sample count.

Figure 4. The relative frequency of transitions among environmental classifications and frequency of environmental class occurrence based on macrofossil records in peat cores within the permafrost region. The thickness of the arrows is proportional to the frequency of transitions between environmental classes. The relative frequency of the environmental classes was determined relative to the total number of cores (fens, bogs) and number of cores in each region (boreal, tundra) and is labeled beneath each environmental class (number of cores in environmental class / number of cores per region). The percentage of cores that transitioned among environmental classes was considered relative to the number of cores in each initial environmental class. Shading represents permafrost aggradation.

Figure 5. Mean values of (a) C/N ratio and (b) nitrogen content (% dry mass) for each environmental classification during the Holocene for non-permafrost and permafrost (PF) sites for the past 1000 cal. y BP (< 1000) and earlier time periods (>1000). Error bars represent standard error. Open water is excluded due to insufficient data with associated time periods (n=0).

Figure 6. Median long-term apparent rate of C accumulation (LARCA) among a) environmental classes and b) vegetation types during the Holocene for the past 1000 years (< 1000) and before (> 1000). Error bars represent first and third quantiles. PF = permafrost. Rates met the most stringent dating criteria of one or more dates per thousand years and included 80 cores and 5754

measurements. Feathermoss and lichen are not shown because of the limited number of samples that met the dating criteria (≤ 3 samples among all cores).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PeatProp
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PP + C acc (orig.)
PP + C acc.
Permafrost Zone
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Discontinuous
Sporadic
Isolated
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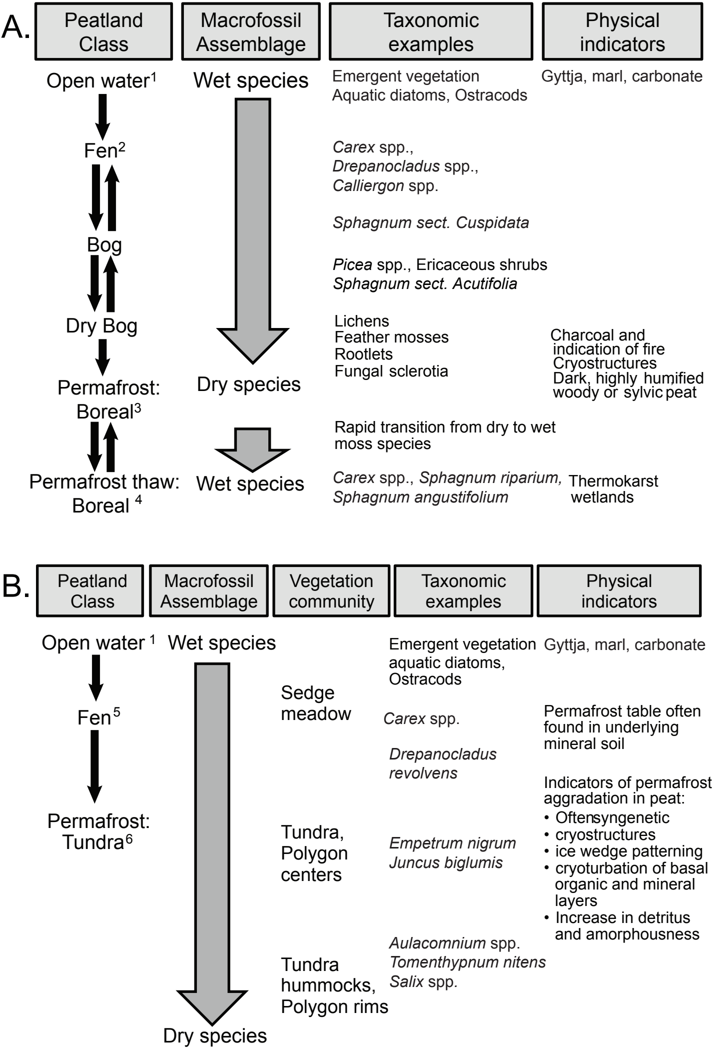
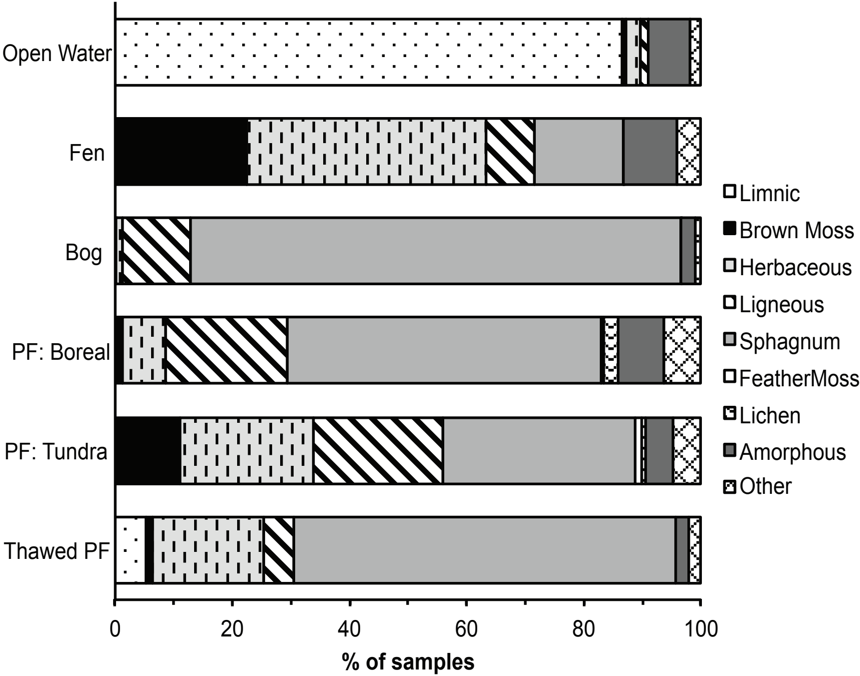
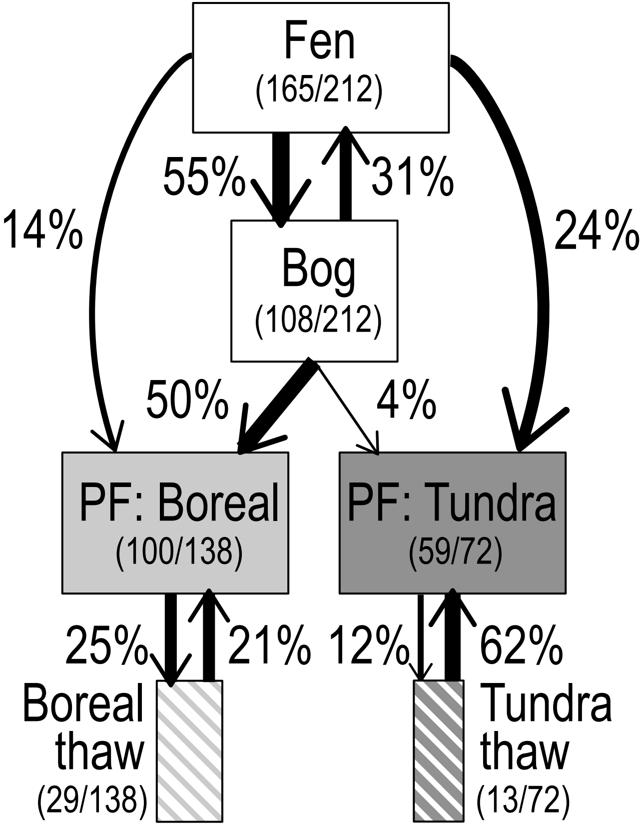
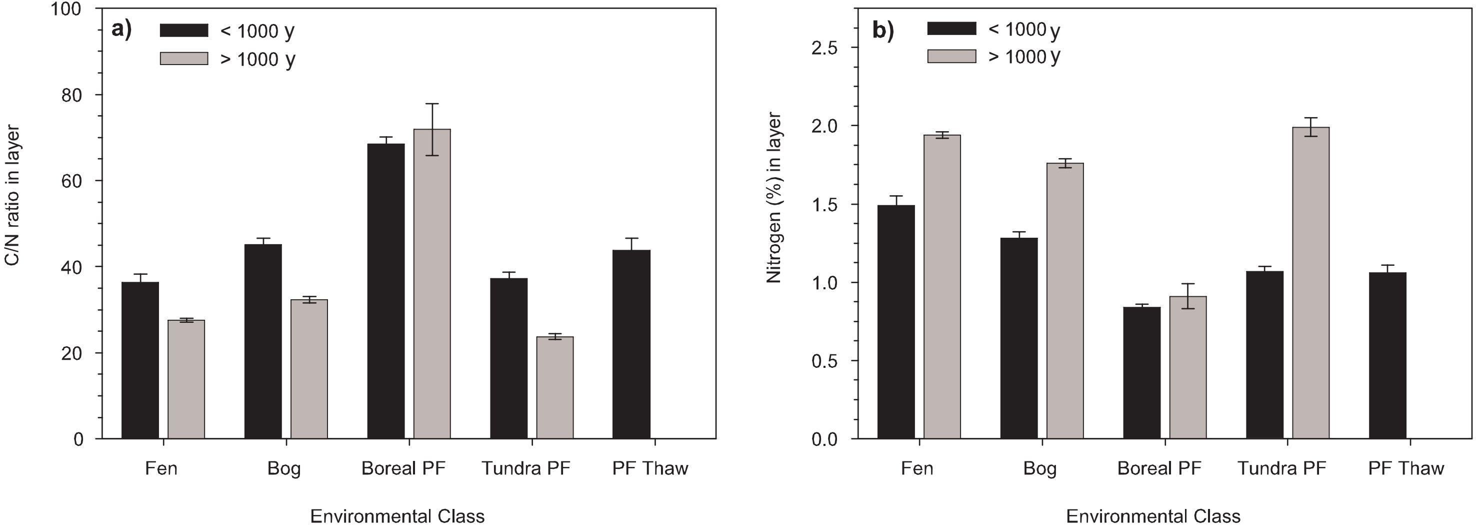
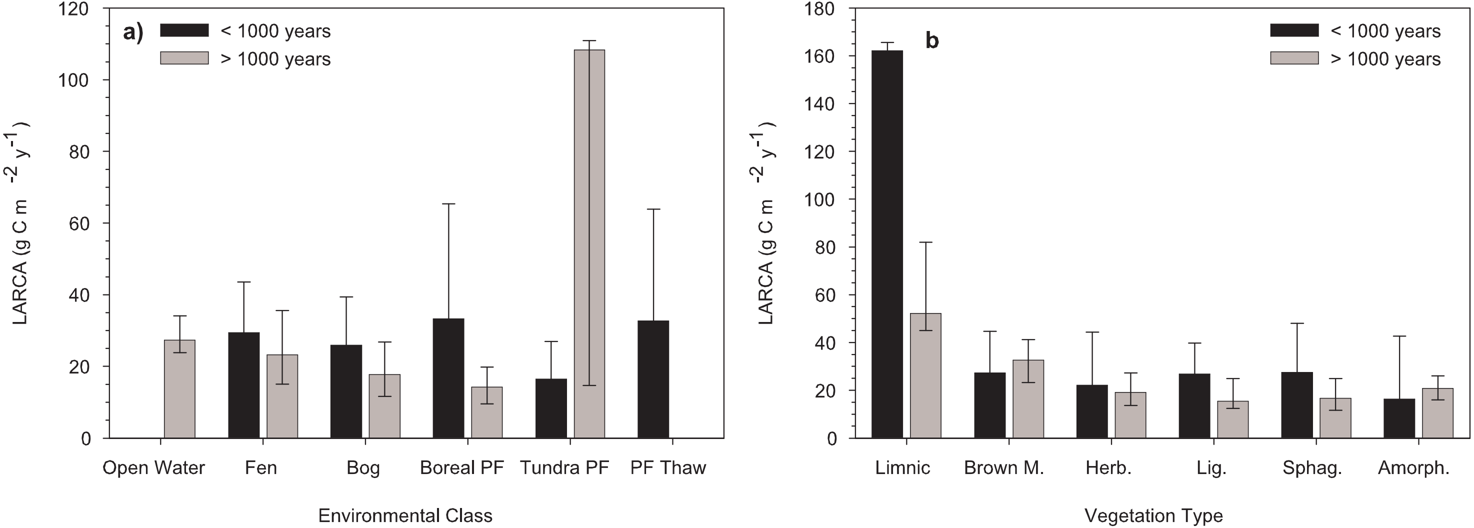
3


A.
Peatland Class
Macrofossil Assemblage
Taxonomic examples
Physical indicators
Open water1
Wet species
Emergent vegetation
Aquatic diatoms, Ostracods
Gyttja, marl, carbonate
Fen2
*Carex* spp., *Drepanocladus* spp., *Calliergon* spp.
*Sphagnum sect. Cuspidata*
Bog
*Picea* spp., Ericaceous shrubs
*Sphagnum sect. Acutifolia*
Dry Bog
Lichens
Feather mosses
Rootlets
Fungal sclerotia
Charcoal and indication of fire
Cryostructures
Dark, highly humified woody or sylvic peat
Dry species
Permafrost: Boreal3
Rapid transition from dry to wet moss species
Permafrost thaw: Boreal 4
Wet species
*Carex* spp., *Sphagnum riparium*, *Sphagnum angustifolium*
Thermokarst wetlands
B.
Peatland Class
Macrofossil Assemblage
Vegetation community
Taxonomic examples
Physical indicators
Open water 1
Wet species
Emergent vegetation aquatic diatoms, Ostracods
Gyttja, marl, carbonate
Fen 5
Sedge meadow
*Carex* spp.
Permafrost table often found in underlying mineral soil
*Drepanocladus revolvens*
Indicators of permafrost aggradation in peat:
• Oftensyngenetic
• cryostructures
• ice wedge patterning
• cryoturbation of basal organic and mineral layers
• Increase in detritus and amorphousness
Permafrost: Tundra6
Tundra, Polygon centers
*Empetrum nigrum*
*Juncus biglumis*
Tundra hummocks, Polygon rims
*Aulacomnium* spp.
*Tomenthypnum nitens*
*Salix* spp.
Dry species


Open Water
Fen
Bog
PF: Boreal
PF: Tundra
Thawed PF
Limnic
Brown Moss
Herbaceous
Ligneous
Sphagnum
FeatherMoss
Lichen
Amorphous
Other
0
20
40
60
80
100
% of samples


Fen
(165/212)
55%
31%
14%
24%
Bog
(108/212)
50%
4%
PF: Boreal
(100/138)
PF: Tundra
(59/72)
25%
21%
12%
62%
Boreal thaw
(29/138)
Tundra thaw
(13/72)


a)
< 1000 y
> 1000 y
C/N ratio in layer
0
20
40
60
80
100
Fen
Bog
Boreal PF
Tundra PF
PF Thaw
Environmental Class
b)
< 1000 y
> 1000 y
Nitrogen (%) in layer
0.0
0.5
1.0
1.5
2.0
2.5
Fen
Bog
Boreal PF
Tundra PF
PF Thaw
Environmental Class


a)
< 1000 years
> 1000 years
LARCA (g C m$^{-2}$ y$^{-1}$)
0
20
40
60
80
100
120
Open Water
Fen
Bog
Boreal PF
Tundra PF
PF Thaw
Environmental Class
b
< 1000 years
> 1000 years
LARCA (g C m$^{-2}$ y$^{-1}$)
0
20
40
60
80
100
120
140
160
180
Limnic
Brown M.
Herb.
Lig.
Sphag.
Amorph.
Vegetation Type