THE ENGINEERING OF PEATLAND FORM AND FUNCTION BY BEAVER (*Castor spp.)*

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ABSTRACT

Northern peatlands are significant contributors to global biogeochemical cycles. In Canada alone, peatlands cover over a tenth of the land surface and store over half of the country's terrestrial carbon. Their ability to function as a carbon sink is inextricably linked to hydrological conditions defined by an intricate web of feedbacks from numerous autogenic (internal) and allogenic (external) drivers. Research over the last forty years has been focused on understanding the importance of each driver, as such knowledge is necessary to foresee how these landscapes might respond climate change. However, one external driver - the activity of beaver (*Castor canadensis* in North America and *C. fiber* in Eurasia) - has received little attention, even though beaver have inhabited northern peatlands for many thousands of years. Identified as a keystone species and ecosystem engineer, beaver can alter the physical, hydrological, and biogeochemical function of landscapes on a scale comparable to that of humans. Thus, the primary goal of this dissertation was to enhance our understanding of how beaver activity alters peatland function and transforms these landscapes over time. To achieve this goal, the associated impacts of beaver activity were studied over numerous scales, mostly in the montane peatlands of Alberta, Canada, via the collection and analyses of field data comprised of different physiographic, hydrological and soil variables.

It was found that the activities of beaver have profound impacts on peatland landscapes. Beaver activity changes the physical appearance of peatlands, with the construction of berm-like dams that persist for long periods even after dams breach and/or are abandoned. Peat, excavated from the surrounding area, was a primary dam building material, and dams often extended far beyond the stream channel and inundated large surface areas. Peat excavation added complexity to the pond shape and bathymetry, but despite the physical complexity of beaver ponds, it was found that relationships between quickly measured field attributes allows for reliable estimates of surface water storage in these features.

In addition to storing large volumes of surface water, Beaver dams/ponds had significant impacts on hydrological processes in the peatlands studied. Just as in mineral soil environments, beaver ponds acted as sinks for mineral and organic sediments. Furthermore, a multi-year study in a Rocky Mountain fen, showed that the beaver dams connected the peatland to the stream, thereby raising and stabilizing shallow ground water tables within 150-m proximity. Such findings have implications for peat formation in affected areas because plant community and carbon sequestration are tightly linked to water table behavior.

Beaver ponds also had significant impacts on underlying soils. Regional sampling of peatland beaver meadows found they were depleted in organic matter. Deeper inspection of this phenomenon through multi-proxy analysis and paleo-reconstruction of peat cores revealed that beaver-meadow soils accumulated the least amount of peat over time compared to areas unaffected by beaver. This phenomenon is likely a result of sediment deposition, which increases the bulk density of peat bulk volumes and may enhance turnover and decomposition when ponds wash out. Unlike beaver ponds built in mineral soil environments, the peatland beaver ponds studied here were not associated with an accumulation of organic matter.

Overall, this research shows that beaver activity can alter the appearance of peatlands and exert control over processes fundamental to their function as a carbon sink. This activity leaves a legacy beyond cyclic pond creation and abandonment that contributes to the spatial complexity of the landscape. Beavers deserve greater inclusion in peatland conceptual models and further research is needed in the peatlands beavers are known to inhabit.

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– Dan

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LIST OF ABBREVIATIONS

A	Area
A_1	Pond surface area measurement corresponding to h_1
A_2	Pond surface area measurement corresponding to h_2
A_{ERR}	Magnitude of area error
$A_{\max}$	Surface area maximum at $h_{\max}$
B_{I}	Bathymetric integral
B_{WC}	Bathymetric water capacity
C:N	Carbon to nitrogen ratio
c	Pond morphometry coefficient
D_{ACT}	Point on the actual bathymetric curve
D_{EST}	Point on the estimated bathymetric curve
D_{len}	Length of the beaver dam
DEM	Digital elevation model
E_{k}	Exceedance probability
E_{RMS}	Root mean square error
EPC	Exceedance probability curve
h	Pond stage/hydraulic head
h_0	Unit height of water surface (1 m for SI units)
h_1	Pond stage measurement corresponding to A_1
h_2	Pond stage measurement corresponding to A_2
$h_{\max}$	Maximum dam height/pond stage
K	Hydraulic conductivity
LOI	Loss on ignition
LORCA	Long term apparent rate of carbon accumulation
LORNA	Long term apparent rate of nitrogen accumulation
MAD	Median absolute deviation
MSS	Mineral suspended sediments
NPP	Net primary production
n	Sample size
OM	Organic matter
OSS	Organic suspended sediments
p	Probability value
P	Perimeter
r	Pearson’s correlation coefficient
R^2	Coefficient of determination
R_{A}	Relative area
R_{D}	Relative depth
RDA	Redundancy analysis

rtkGPS	Real time kinetic global positioning system
s	Scaling coefficient
S_I	Shape index
SPI	Standardized precipitation index
SRW	Sibbald Research Wetland
TOC	Total organic carbon
TSS	Total suspended sediments
UOM	Unidentified organic matter
V_{ERR}	Magnitude of volume error
V_{land}	Volume of land mass within reference solid
V_{max}	Maximum volume of the pond at h_{max}
V-A-h	Volume-area-depth
VIF	Variance inflation factors
WT	Water table position

1. Introduction

1.1 Objectives

Peatlands store nearly a third of global soil carbon (Gorham, 1991; Loisel et al., 2017) and over half of the soil carbon in Canada alone (Tarnocai, 2009). An urgent concern with regards to these ecosystems is whether they will remain carbon sinks as the climate warms. In addition to carbon sequestration, peatlands reduce downstream flood risks, provide clean water, contribute to climate regulation (Whitfield et al., 2011), and play host to a diverse range of plant and animal species. One species in particular, the beaver (*Castor canadensis* in North America and *C. fiber* in Eurasia), has been residing in northern peatlands for many thousands of years (Gorham et al., 2007; Kaye, 1962). Identified as a keystone species and ecosystem engineer, beaver are well known for their ability to create and maintain various forms of wetland habitat (Hood and Bayley, 2008; Naiman et al., 1986). Their instinctual ability to fell trees, build dams, dredge canals, and impound large volumes of water, can alter the physical, hydrological, and biogeochemical function of landscapes on a scale comparable to that of humans (Hood and Larson, 2015; Johnston, 2012). Such alterations have been studied in riverine systems with mineral soils; however, this type of knowledge is lacking in peatlands, despite there being widespread habitation of beaver in these environments (Johnston, 2001; Morrison et al., 2015). Peatlands have organic soils and their function, in terms of carbon storage, is inextricably linked to hydrological conditions defined by an intricate web of feedbacks from numerous autogenic (internal) and allogenic (external) drivers (Waddington et al., 2015). The extent to which beaver is a driver is still undetermined, and without this knowledge, our understanding of peatlands is incomplete.

The primary goal of this dissertation is to enhance our understanding of how beaver activity alters peatland function and transforms these landscapes over time. The following four objectives have been created to meet this goal: 1) Characterize beaver pond morphometry and surface water storage in a variety of different physiographic settings in the western hemisphere; 2) Determine if beaver-mediated sediment aggradation occurs in peatlands at a regional scale and assess the potential impact of such on beaver-meadow soils; 3) Determine the impact of beaver activity on water table dynamics at the peatland scale; and, 4) Disentangle the drivers of peat accumulation in a beaver meadow over time to further elucidate the legacy impacts of beaver activity in these environments.

1.2 Organization of the Dissertation

This dissertation was written in manuscript style and is comprised of seven (7) chapters including the introduction. Chapter 2 is a literature review and Chapters 3 to 6 include the body of research conducted to meet the objectives. The geographic extent of the research is large in Chapter 3 and then it becomes smaller and smaller throughout subsequent chapters until, eventually, the research is constrained to three locations within a montane fen. The flow of research through the chapters is portrayed in Fig 1.1.

In Chapter 3, the research begins with a study of beaver pond morphometry and surface water storage (overtop both mineral and organic soils) in montane and lowland regions of the western hemisphere. Chapter 4 then focuses in on a particular region (i.e. montane peatlands in the Canadian Rocky Mountains) and investigates beaver-pond soils and soil forming processes. Chapter 5 examines beaver-mediated groundwater impacts across a Rocky Mountain fen, and Chapter 6 investigates the importance of soil forming factors, including beaver, within different areas of the same peatland. Finally, the dissertation concludes in Chapter 7, with a synthesis of the research and a discussion of how peatland form and function is altered by beaver.

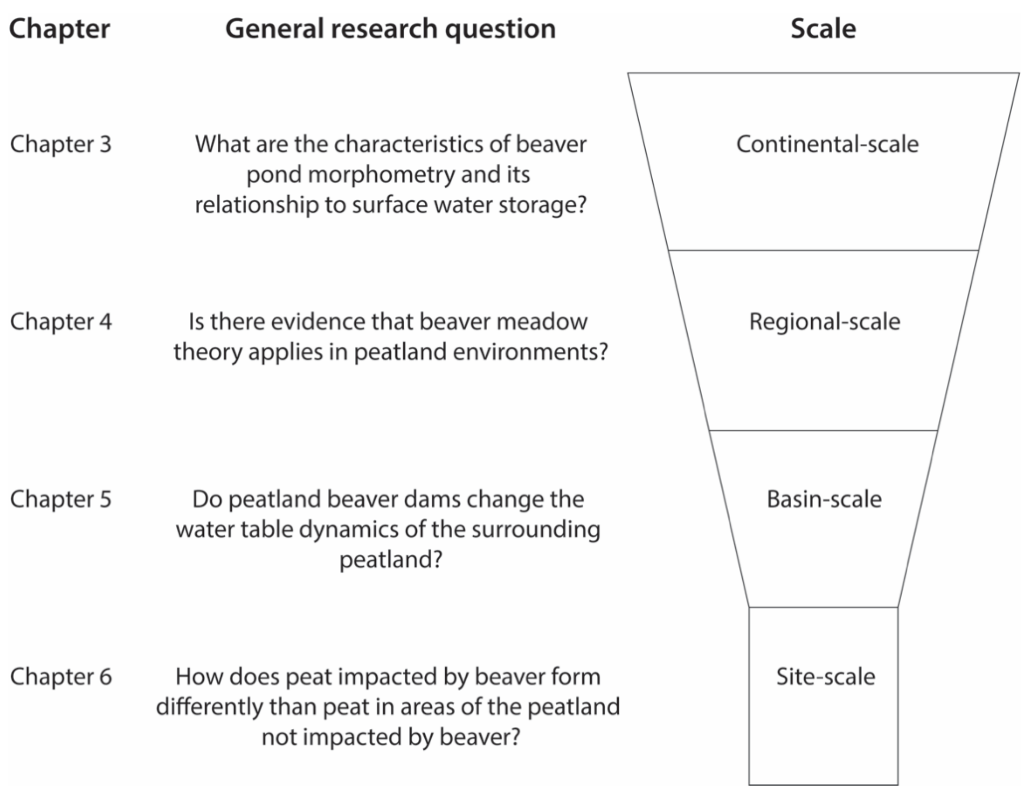

Fig 1.1 Organization of research chapters within dissertation

2. LITERATURE REVIEW

2.1 Peatland Formation and Development

Peatlands form in landscapes where drainage is impeded or where sustained flows from surface and subsurface sources exceed losses from evapotranspiration. Such conditions create water tables at or near the land surface, which promotes the growth of hydrophytic vegetation (Waddington et al., 2009). Once the plants carry out their life cycles, residues only partially decay before they become continuously waterlogged and most aerobic decay processes are inhibited. As a consequence, the production of vegetation is greater than the decay, and the organic matter eventually accumulates to form peat. Peatlands can form via one of two processes - by the gradual infilling of organic matter into shallow water bodies, termed terrestrialization, or by the accumulation of organic matter overtop saturated mineral soils, termed paludification (Lavoie et al., 2005a).

Considering the significant role of hydrology in peat formation, peatland type is classified according to the dominant inputs of water and the plant species that colonize as a result. Peatlands that are ombrotrophic (i.e. solely dependent on water from atmospheric inputs such as precipitation, fog and snow) are classified as bogs. Their peat is composed mainly of *Sphagnum spp*., ericaceous shrubs and cottongrass (*Eriophorum spp*.). Peatlands that are minerotrophic (i.e. receive water and nutrients from a combination of surface, ground and atmospheric sources) are classified as either fens, swamps, or marshes depending on whether the peat is composed of sedges and brown moss (*Drepanocladus spp.*), highly decomposed woody material, or aquatic macrophytes, respectively (NWWG, 1997).

Given the importance of the plant community and the hydrological inputs to peatland classification, it is understandable that prolonged changes to these variables will result in changes to peatland type. This process, known as hydroseral succession, is a commonly encountered form of autogenic control in these environments (Charman, 2002). The evidence of this succession is found in the peat stratigraphy and it often transitions from ‘open water’ to ‘fen’ to ‘bog.’ Open water areas gradually fill with organic and mineral material until the water table is at or near the surface. Nutrient rich groundwater promotes the growth of sedges and grasses typical of fen environments. Eventually, enough peat accumulates that the surface vegetation of fens becomes disconnected from the groundwater and thus reliant on precipitation for future growth. In this nutrient poor environment, *Sphagnum spp.* dominates, further acidifying the system and completing the transition to bog. Although, this is most common form of hydroseral succession, there are many different allogenic factors that can influence the reverse scenario (Charman et al., 1995). For example, in a Minnesota peatland, climate was responsible for multiple reversals during the Holocene (Glaser et al., 1996). Wet periods would create peat mounds such that the system would recharge groundwater and a bog would form. During dry periods, however, gradients reversed and discharge prevailed, thus creating groundwater mounds and establishing fen environments.

The details of peatland biogeomorphology are complex and still largely unknown. In the past four decades, research has focused on creating conceptual models that describe how these systems function through characterization of the ecological, hydrological, and geochemical qualities of the peatland surface and its stratigraphy. The following section is, therefore, a summary of that literature.

2.1.1 The diplotelmic model and beyond

Traditionally, peatlands have been described using Clymo's (1984) steady-state ecohydrological model that exploits the concept of a two-layered peat profile, defined by Ingram (1978). The upper layer (acrotelm) is the staging ground for the vegetative life cycle and is a relatively thin layer with high hydraulic conductivity (K). The lower layer (catotelm) is a thick, dense, water saturated layer with low K (Clymo, 1984). The two layers are separated by the water table, which is always at a constant depth beneath the surface. Aerobic microbes decompose organic residue produced in the acrotelm and, as this proceeds, residues become richer in their slower decaying components. Eventually, plant structure collapses at the base of the acrotelm, subsequently lowering the K and causing the water table to rise. Once submerged by the water table, the remaining residue becomes part of the catotelm, where the slow diffusion of oxygen through water inhibits aerobic decomposition. Anaerobic decomposition continues in the catotelm; however, at a much slower pace than the rate at which residues are produced in the acrotelm. As a result, the peat profile thickens until mass loss in the catotelm is equal to mass gain in the acrotelm, at which point the peat growth has reached an asymptotic limit (Clymo, 1984).

Although there has been considerable research into peatland ecohydrological function, our overall understanding is still quite limited. This gap is largely due to the non-linear nature of many concurrent processes, ecological and biogeochemical feedbacks, and the spatial and temporal heterogeneities inherent to these systems. As a result, many studies have deemed the model proposed by Clymo (1984) inadequate, and favour discarding it for a new conceptual approach that addresses these complexities, but is still general enough to describe peatlands over a variety of different landscapes (Baird et al., 2012; Belyea and Baird, 2006; Cunliffe et al., 2013; Holden et al., 2006; Holden and Burt, 2003; Morris et al., 2011). One such approach leaves behind the concept of a single, rigid boundary between the acrotelm and catotelm, and replaces it with multiple, asynchronous boundaries (Morris et al., 2011). Each boundary defines a dichotomy of variation between the processes under consideration (e.g. oxygen content, water flux, redox state, etc.), and recognizes that different zones can overlap with one another. This approach describes peatlands in a way that allows for the identification of mechanistic links and hot spots. Hot spots, defined as three-dimensional areas within a landscape, where ecological, hydrological and/or biogeochemical process rates are elevated (McClain et al., 2003), are of particular interest to a variety of resource management issues because they often determine the magnitude and direction of important feedbacks (Morris et al., 2011). For example, in the context of peatland hydrology, water table depth has been recognized as an important metric by which other feedbacks can be measured (Waddington et al., 2015). Therefore, water table hot spots, (i.e. areas of the peatland where water tables fluctuate at elevated rates relative to the rest of the peatland) may be useful in interpreting spatial heterogeneity in peatland form and function.

2.1.2 Peatland biogeomorphology

The biogeochemical and hydrological processes that occur throughout the peat profile are vital components to understanding how peatland ecosystems form, function, and endure over many millennia. Together, they dictate how carbon cycles to and from the atmosphere are based on rates of primary production and decomposition. Net primary production (NPP) exceeds decomposition in peatlands; therefore, they are a net-sink of carbon in the long-term, storing upwards of 550 Gt of carbon globally (Yu et al., 2010). NPP is controlled by photosynthetic radiation, temperature, water table depth, water chemistry, and the availability of nitrogen and phosphorous (Blodau, 2002). Accordingly, the NPP varies considerably between different peatland types (e.g. bogs, fens) because the controlling factors determine the plant community structure that eventually becomes peat. This structure is a crucial component to how carbon accumulates over time because, along with water table depth, decomposition is controlled by the unique microbial consortiums associated with each plant community (Lin et al., 2012), the different functioning of vascular vs. non-vascular plants (Joabsson et al., 1999; Shannon et al., 1996), and the higher fractions of recalcitrant organic matter in the different types of vegetation (Bauer, 2004; L.S. Chasar et al., 2000; Frolking et al., 2001). Hence, the balance between NPP and decomposition is very sensitive to environmental conditions from the local hydrology to the regional climate. This sensitivity is expressed in the peatland stratigraphy and studies that analyze peat cores have shown that the rate of carbon accumulation can fluctuate over millennial, centennial, inter-annual, and seasonal timescales (Loisel and Yu, 2013).

In most peatland environments, carbon accumulation via the ratio of NPP to decomposition is the primary mechanism that contributes to the vertical peat column. However, peatlands are also exposed to other factors of environmental change, which manifests in the stratigraphy as unique peat and mineral horizons. Peat is susceptible to erosion, and peat sediments can be transported by wind and water to different locations (Tallis, 1998). The rate of peat erosion is significantly increased by the disturbance of the surface vegetation, but peat erosion still occurs at lower rates by being exposed to natural agents such as frost, drought, rain and wind. Peat sediment is distinguished from non-disturbed peat by being more rounded, less fibrous, and having a lower bulk-density (Clement, 2005). Deposits of peat sediment have been found in many low-energy fluvial systems (Evans and Warburton, 2005), but also in the stratigraphy of peatland floodplains (Wójcicki, 2012).

Many peatlands also have unique mineral horizons that arise from either atmospheric deposition or the peatland's geologic and topographic setting. Atmospheric deposits include tephra and dust. Tephra is ash that is deposited over landscapes by volcanic explosions, whereas dust primarily originates from deserts but can also be the result of human activity (Chambers et al., 2012). For example, a recent study has linked dust deposits in peatlands of North America with the early settlement and land clearance of the continent by Europeans (Ireland et al., 2014). Mineral deposits that arise from the peatland's geologic and topographic setting are marl, gyttja and sand. Marl is composed of calcium carbonate that precipitates out of shallow, groundwater-fed ponds. It is often found as a layer underlying the entire peatland, but can also be found interbedded between layers of peat (Zoltai and Johnson, 1985), therefore suggesting major changes to historic hydrological regimes. The same is true for gyttja and sand, which are typical mineral deposits that form in lakes (Grundling et al., 2013).

The fact that peatlands accumulate carbon over time and are sensitive to environmental change makes them a rich historical archive from which previous climate/ hydrological regimes can be inferred. The analysis of peatland stratigraphy is a field of research that began nearly a century ago with the use of fossil pollen to reconstruct historic climates (Cain, 1939). Since then, new techniques have been developed that greatly enhance our understanding of which factors control the inception, development, and heterogeneity of these ecosystems. Peatland chronology is constrained with ^{210}Pb, ^{14}C, 'Bomb carbon,' or tephra (Chambers et al., 2012). Chronologies are then combined with bulk density, organic-matter content, and carbon-to-nitrogen ratio tests to model short- and long-term accumulation rates (Loisel and Yu, 2013). Finally, ecohydrological changes, such as depth to water table, can be reconstructed with proxy indicators such as testate amoebae, stable isotopes, and plant macrofossils (Loisel and Garneau, 2010).

The vast majority of literature that analyzes peatland stratigraphy is done in ombrotrophic bogs. This tendency is advantageous for the sake of palaeoclimate reconstructions because these systems document the history of atmospheric processes (Chambers et al., 2012). However, research limited to these environments brings little insight into the formation of more complex peatland landscapes. Fen landscapes of the Rocky Mountains, in particular, express deep complexity in their stratigraphy (Morrison et al., 2015), the source of which is relatively unexplored.

2.1.3 Peatland carbon cycling

About a third of the carbon uptake by photosynthesis (i.e. NPP) is returned to atmosphere as CO_2 by autotrophic (i.e. plants) and heterotrophic (i.e. microbes and soil fauna) respiration in the aerobic active layer (acrotelm) of the peat (Bubier et al., 1998; Heikkinen et al., 2002). These processes break down the structure of the plant litter such that it becomes submerged by the water table and increases the concentration of dissolved organic matter (DOM) (Moore and Dalva, 1993). Once submerged, CO_2 is still produced from DOM, but in conjunction with anaerobic processes that also produce CH_4 (Corbett et al., 2012). The DOM that is not consumed in the zone of inundation is transported downwards into the peat profile through advection with the peat-pore water (Levy et al., 2013). This occurence is supported by evidence from stable carbon isotope studies that show the CO_2 and CH_4 being produced at depth in the pore waters of the peatland is much younger (i.e. more ^{13}C enriched) than the adjacent peat (Chanton et al., 1995, 2008; Chasar et al., 2000b).

Methanogenesis is dominated by two processes in peat — acetate fermentation and CO_2 reduction (Chasar et al., 2000a). In groundwater fed systems, calcite dissolution is a source of dissolved inorganic carbon, but it is usually minor in comparison. In most of the systems studied, the majority of CH_4 is produced via acetate fermentation in the zone of inundation that extends approximately 20 cm below the water table (Sundh et al., 1994). However, the presence of acetoclastic methanogens and the quantity of substrate available for acetate fermentation are highly correlated to the type of vegetation (Hines et al., 2008; Rooney-Varga et al., 2007). Vascular plants tend to facilitate these microbes whereas sphagnum moss has antimicrobial properties that impede them (Lin et al., 2012). Moreover, sedge (i.e. *Carex*) fens have been observed to produce much more CO_2 and CH_4 than woody-*Sphagnum* bogs (Bridgham et al., 1995). This increase in CO_2 emissions is because of the large pool of labile carbon substrates provided by vascular plant roots along with their ability to use aerenchyma to transport O_2 into, and CO_2 and CH_4 out of, submerged soils, thus facilitating continued aerobic respiration (Chanton et al., 2008; Corbett et al., 2012) and the release of built up gas that can decrease effective porosity (Glaser et al. 2004), respectively. Only after the pool of labile carbon becomes completely exhausted will methanogens switch to reducing bicarbonate with hydrogen (Whiticar, 1999). Increasing temperatures can stimulate more activity via CO_2 reducing pathways, but in general, acetate fermentation tends to dominate in shallow subsurface peat, and CO_2 reduction prevails in older less reactive peat (Hornibrook et al., 1997). This trend is especially apparent in *Sphagnum* bogs where acetate fermentation is often insignificant in CO_2 and CH_4 production (Hines et al., 2008; Rooney-Varga et al., 2007). The underlying reasons for this trend are not well understood; however, two mechanisms have been proposed. One is that the enzyme phenol oxidase, responsible for the degradation of recalcitrant phenol compounds, is inhibited by the lack of oxygen in peat bog environments (Freeman et al., 2001). The other is that decay end products from peat decomposition build up in deep peat pore waters, thereby reducing the Gibbs free energy and denying terminal electron acceptors to decomposers (Beer and Blodau, 2007).

Not all of the CH_4 produced in the subsurface is released to the atmosphere; instead, it is oxidized by methanotrophs that release CO_2 as a byproduct. First, the CH_4 is transported to the surface either by ebullition, diffusion, or by plants (Joabsson et al., 1999) and then it is consumed by microbes that have mutualistic relationships with mosses at the surface (Liebner et al., 2011; Nichols et al., 2009). Methanotrophs are usually found within the rhizosphere of the peat, so the type of vegetation and depth of the water table will dictate how much CH_4 is ultimately released to the atmosphere (Roulet et al., 1997).

2.1.4 Surface complexity

Surface complexity refers to the array of distinct microforms such as hummocks, lawns, hollows and pools that create unique spatial patterns across peatland landscapes. The position and alignment of these features are important as they have significant control over stores and flows of water, nutrients, and carbon (Waddington et al., 2010). Hummocks, lawns and hollows form in response to feedbacks from the thickness of the active layer (acrotelm) and the fluctuation of the water table at a given location (Belyea and Clymo, 2001). The surface of a hollow is often below the water table, thereby forming a shallow open water area for a period of the year. This is in contrast to peat pools, which are much deeper and more perennially saturated. Peat pools often form intricate networks ranging in size from localized systems to vast complexes covering the regional landscape (Holden, 2006). The formation of these structures still remains a subject of controversy; however, a common theme in most theories is that peat pools developed as secondary structures after the accumulation of significant peat (Comas et al., 2005). Foster and Wright (1990) investigated 15 pools in Sweden and concluded that peat pools were very old and began forming shortly after the peat was initiated. Recent studies suggest that the underlying stratigraphy of the peatland plays a major role in pool formation. Lowry et al. (2009) used ground-penetrating radar to find that many peat pools were situated above areas where the peat/sand-gravel interface was thinning, which led him to suggest that groundwater flowing through these areas was being forced upwards by the low hydraulic conductivity of the surrounding peat. Comas et al. (2011) furthered this argument by showing evidence and giving a detailed account of how pool formation was influenced by underlying post-glacial landforms in a large peatland in Maine. Peat pools are usually oriented perpendicular to the prevailing slope (Belyea and Lancaster, 2002) and, once established, they can expand laterally either by coalescing with adjacent pools after the breakdown of intervening peat ridges, or by introducing oxygen to the previously anaerobic peat columns and causing accelerated decay at the margins (Comas, 2011). Peat pipes have been observed connecting adjacent pools and their role in the morphology of these systems has yet to be studied (Belyea and Lancaster, 2002).

2.2 Peatland Hydrology

In peatlands, water table depth is a powerful predictor of the ecohydrological and biogeochemical processes that regulate fluxes of carbon, thereby influencing how peatlands form (Waddington et al., 2015). A relatively small change in the position of the water table initiates a number of different feedback mechanisms and will govern whether the peatland is collecting, storing or transmitting water (Spence et al., 2011). It is for this reason that the fluctuation of the water table at different spatial and temporal scales is of particular interest to researchers. The typical water table regime in a peatland varies. In an undisturbed bog, the water table is expected to be stable and near the surface for most of the year (Holden et al., 2011). Fen water tables, however, are much more dynamic at the site level, and range from fluctuations of tens of centimeters to over a meter (Duval and Waddington, 2011). There are a number of hydrological factors that contribute to water table behavior in peatlands; therefore, the following section reviews the processes that are known to have the most impact on water table regimes.

2.2.1 Storage

In theory, storage in peat is a product of the water table height and specific yield (Price, 1992). However, estimating the peat-matrix storage in this manner can introduce significant error (Proulx-McInnis et al., 2013) because specific yield changes with depth (Price, 1996). There is no single value for specific yield in a peat soil and reported values have ranged from 0.48 (Price and Schlotzhauer, 1999) to 0.19 (Spence et al., 2011) in fens alone. Saturated peats tend to be 90-98% water by volume, but they do not necessarily act as reservoirs because much of the water is tightly held (Holden, 2006). The peat's ability to retain water is a function of its internal pore structure (Clymo, 1984) and its compressibility (Hobbs, 1986), both of which are controlled by the plant community it is comprised from (Ingram, 1982; Weiss et al., 1998; Whittington et al., 2007). The peatland surface and volume exhibits elasticity in that it expands and compresses in a cyclical fashion — driven by inter-annual freeze/thaw cycles and changes in water table depths (Roulet, 1991). Whittington et al. (2007) showed that the extent of this fluctuation is influenced by the plant community structure of the peat, and Price (2003) showed that the process is seasonal and accompanied by changes in K. Compression, in particular, has been shown to reduce pore size, thus water storage, but also increase water retention through matric forces (Heiskanen, 1995; Rezanezhad et al., 2016a); a phenomenon that has been noted as a potential mechanism by which peatlands cope with environmental stress (Price, 2003).

2.2.2 Surface runoff

Different types of peatlands behave differently to surface water inputs and outputs. As one would expect, bogs store most of the water they receive, peat plateaus are important generators of surface runoff and channel fens convey most of their water to the basin outlet (Hayashi et al., 2004). Since the water table is already at or near the land surface, undisturbed peatlands often respond rapidly to rainfall events with sharp rises in the water table and the generation of saturation-excess overland flow (Holden, 2006). Studies have shown that between 35-78% of this runoff is conveyed in the near surface by macropores (Baird, 1997; Holden et al., 2001). Once drying begins, and the water table drops a few centimeters below the surface, free drainage ceases and any further drops in the water table are dominated by evapotranspiration (Evans et al., 1999; Holden, 2006).

2.2.3 Evapotranspiration

Evapotranspiration (ET) is an important control on water table position. In a perched basin (composed of fens, bogs, swamps and marshes) in Northern Alberta, annual ET was measured at rates twice that of precipitation, thus causing constant water table drawdown (Peters et al., 2006). Open water areas, adjacent to or contained within peatlands, evaporate even faster and can enhance this effect (Petrone et al., 2007). Plant community composition also plays a role in governing ET rates. For example, vascular plants were shown to account for 60-80% of the latent heat flux in a bog in Eastern Ontario (Admiral and Lafleur, 2007). These findings are especially important, in our current context of environmental change, because net ecosystem productivity in peatlands is largely dependent on non-vascular plants, which only survive if water tables remain within 5-10 cm of the peat surface (Dimitrov et al., 2011).

2.2.4 Subsurface flow

Many of the challenges faced in calculating peatland water storage also complicate our ability to understand groundwater flow. Groundwater patterns are largely governed by hydraulic gradients and unsaturated and saturated hydraulic conductivity (K_{uns} and K_{sat}, respectively) within the peat matrix (Fraser et al., 2001). Despite the fact that it is fairly easy to measure these variables, they can exhibit significant variability within small increments of space and time (Holden, 2006). Hydraulic gradients, for example, have been shown to change with the transition between wet and dry periods. Fraser et al. (2001) observed vertical gradient reversals as a result water table drawdown due to evapotranspiration, and Ferone and Devito (2004) observed the same reversal of flows, but from a pond-peatland complex. K_{sat} values change regularly over time, as discussed previously, but they also change within tiny areas of space. The traditional model proposed by Clymo (1984) describes K_{sat} values that decrease with depth in the peat profile; however, this is not always the case. Holden and Burt (2003) found that K_{sat} values can vary more at different points along a upland blanket peat than vertically at the plot scale, and Janzen and Westbrook (2011) found the same in a mountain peatland.

Some studies have argued that different peat layers have characteristic K_{sat} values not because of depth but, instead, because of their vegetative components (Beckwith et al., 2003; Whittington et al., 2007). Watters and Stanley (2007) furthered this argument by suggesting that the plant community structure of the peat corresponds to K_{sat} values, and thus the geomorphology of stream channels in peatlands is more influenced by the biological community makeup than by alluvial processes. Ingram (1983) determined the order of peat K_{sat} for different plant species as *Phragmites spp.* > *Carex spp.* > *Sphagnum spp.*, but, there are few, if any studies that have quantified a relationship between K_{sat}, plant species, and depth.

Another factor that affects subsurface flow is biogenic gas. The accumulation of this gas in pore spaces has been shown to decrease K_{uns} vertically by up to 5-8 times (Beckwith and Baird, 2001) and horizontally by a factor of two (Baird and Waldron, 2003). Methane ebullition occurs from both the deep and shallow parts of the peat profile (Glaser et al., 2004), which suggests that K_{uns} values will increase as the gas is released. The highly variable range of K_{uns} in the profile likely does more than just direct peat matrix flow as a number of studies have identified the role that variable K_{uns} and K_{uns} values play in the creation of preferential flow paths. For example, this variability may be partly responsible for the creation of macropores, peat pipes, and peat pools.

Darcy's Law does not govern all subsurface flow through peatlands; some is conveyed through macropores and peat pipes. Macropores are generally defined as pores larger than 1mm in diameter and peat pipes are defined as much larger continuous forms of macropores that can transport large volumes of water (Holden, 2006). The formation of macropores and peat pipes is still poorly understood; however, some common postulations include: peat morphology as a result of topographic controls (Holden, 2006); peat cracking from desiccation (Holden and Burt, 2002); faunal tunneling (Holden and Gell, 2009); and the opening of pores by root penetration (Smart et al., 2013). In a recent study, macropores were observed along the acrotelm/catotelm boundary, where there is an obvious K_{sat} discontinuity (Cunliffe et al., 2013). Cunliffe et al. (2013) also found that the horizontal K_{sat} values parallel to a peat pipe's orientation were higher than those perpendicular, thereby suggesting that K_{sat} values were likely instrumental in the pipe's formation. Regardless, macropores and peat pipes have been identified in numerous peatlands and are considered important conduits for water sediments and solutes (Holden, 2006). They often form intricate networks that are well connected to the peat surface, thereby transporting large amounts of near surface runoff in addition to peat matrix throughflow (Cunliffe et al., 2013). Lowry et al. (2007) also suggested that peat pipes might deliver focused discharge from groundwater aquifers and cause temperature anomalies in the streambed. Nevertheless, only two studies thus far have tried to quantify the volume of water carried by these systems; Holden and Burt (2002) and Smart et al. (2013) who reported that peat pipes delivered 10% and 13.6% of total streamflow, respectively.

2.3 Beaver

2.3.1 Population

Beaver are mammals of the order Rodentia and are found naturally throughout the northern hemisphere. The species *C. canadensis* (the North American beaver) resides in North America and the species *C. fiber* (the European beaver) in Eurasia. Once abundant in numbers, the beaver population today is slowly recovering from the fur trade. In North America, beaver trapping played a significant role in the early exploration and history of the continent. Prior to European colonization, beaver populations were estimated at 60-400 million individuals, spanning a range of approximately 15 million km (Naiman et al., 1988). Not long after the Europeans arrived on the east coast of North America, beaver pelts were being harvested to satisfy the demand for felt hats that could not be met by the trapping of the European beaver in Eurasia. The early trapping was so intensive that beaver populations rapidly declined and trappers were forced to move west, which led to the establishment of trading posts and settlements across the continent (Innis, 1956). Eventually, populations in the west were also overexploited (Johnson and Chance, 1974) and the beaver was nearly extirpated from the entire continent by the year 1900 (Naiman et al., 1988). At the same time, beaver populations in Europe had also dwindled to only 1,200 animals, leaving the beaver at risk of global extinction (Halley et al., 2012).

Fortunately, the demand for beaver pelts was replaced with silk shortly after the turn of the twentieth century. Coupled with reintroduction and conservation programs, beaver populations slowly recovered (Marston, 1994). The most recent estimate of the global beaver population (year 2000) is ~30 million individuals (Whitfield et al., 2014), the large majority of which is thought to be *C. canadensis* in North America since the current estimate of the *C. fiber* population is only ~1 million individuals (Halley et al., 2012). The past century has also seen changes to the historic range of beaver after they were completely removed from some areas in Europe (Halley et al., 2012) and North America (Lanman et al., 2012), but also introduced to others such as South America (Baldini et al., 2008). Despite all these changes, many factors suggest that the beaver population will continue to grow. Jarema et al. (2009) used a species-climate envelope model to predict that changes under expected climate change scenarios will promote increased beaver density, and Flynn (2006) found that increasingly dense road networks might actually create more suitable beaver habitat. Furthermore, beaver populations are likely to benefit from a current lack of natural predators and increased regulations on trapping.

2.3.2 Activities

Before providing a summary of beaver activities, it important to note that, with the exception of a limited number of studies, most of everything known about them is from observations in riverine environments. In appreciation of their ability to create extensive lentic habitat and enhance biodiversity, beaver have been recognized as "ecosystem engineers" (Jones et al., 1994) and identified as "keystone species" (Naiman et al., 1986). The water/land interface is paramount to their survival because they live in water yet feed primarily on terrestrial trees and shrubs. Ideal habitat for beaver is often low grade, moderately flowing water bodies surrounded by deciduous vegetation (Suzuki and McComb, 1998), but beaver can also flourish in habitats where there is no stream, like peatlands (Johnston, 2017, 2012). Given the right conditions, beaver will harvest woody biomass, build dams and impound large amounts water, thereby increasing their habitat and food supply, and protecting themselves from predators (Naiman et al., 1988). Meanwhile, the newly created lentic habitat has impacts on the localized geomorphology, biogeochemical cycling, species richness, and hydrology (Gurnell, 1998).

Harvesting alone has a significant impact on forest succession (Nummi and Kuuluvainen, 2013; Wolf et al., 2007) as beavers can harvest as much as 1.4 metric tons of woody biomass per ha per year (C. A. Johnston and Naiman, 1990). By replacing deciduous stands and shrubs with herbaceous plants, beavers actually reverse succession (Walbridge, 1994). Much of the harvested biomass is used for food and the rest is used for building dams, dens, and food caches. Beavers also change aquatic connectivity of the landscape by digging canals that extend away from the main body of their pond (Hood and Larson, 2015; Rebertus, 1986). These canals serve to extend the beaver's foraging area and, in some cases, are a means to link different water bodies together (Cowell, 1984). Between canal excavations and dam building, beavers have been reported to mitigate the effects of drought by increasing the amount of open water nine-fold, shortly after being reintroduced into an area (Hood and Bayley, 2008). Furthermore, the impact of beavers on the landscape can continue long after they leave. Sediments inundated by beaver dams can be rich in nutrients that become available for vegetative growth when ponds drain, leading to the formation of species rich "beaver meadows" (Butler and Malanson, 1995; Ives, 1942; Naiman, R.J., Pinay, G., Johnston, C.A., Pastor, 1994; Polvi and Wohl, 2012; Ruedemann and Schoonmaker, 1938). The degree and time-scale to which a beaver meadow establishes, however, is controlled by the quality of the sediments and the availability of the nutrients. For example, Westbrook et al. (2011) found that sediments accumulated in beaver ponds had lower available nutrients than the underlying soils, likely due to the higher fraction of recalcitrant organic matter found in the sediments.

2.3.3 Hydrogeomorphic impacts

The spatiotemporal dynamics of a landscape is the net-result of hydrological processes interacting with localized controls over time (McDonnell et al., 2007; Zehe et al., 2014). Beavers can have a significant impact on the hydrological processes within a basin. Probably the most obvious impact of beaver activity is the large pools created behind their dams. Dams act like low weirs in that they create water storage, elevate water tables, and impact both high and low flows (Gurnell, 1998). The amount of water stored by these dams is a function of the dam dimensions and the local valley geomorphology (Johnston and Naiman, 1987). Beavers typically construct dams by creating a tight arrangement of small branches secured by mud and stone (Jung and Staniforth, 2010). The dam's capacity to hold back water is usually relative to the maintenance it receives by resident beavers and the accumulation of sediment in its pore spaces over time (Woo and Waddington, 1990). Large volumes of sediment become trapped in beaver ponds as the dams slow down streamflow velocity, sometimes to a complete halt (Butler and Malanson, 2005; Naiman et al., 1986). As such, the removal or failure of beaver dams releases huge volumes of water and sediment downstream, which, in some cases, can be catastrophic (Butler and Malanson, 2005; Green and Westbrook, 2009; Hillman, 1998).

Although, the beaver pond is the most visible signature of beaver activity, and a focus of most literature, dams in unconfined valleys have been shown to induce overbank flooding in vast downstream areas as well as areas adjacent to the pond (Westbrook et al., 2006). This type of flooding scours the landscape with nutrient rich sediment and eventually leads to the formation of spatially heterogeneous beaver meadows (Westbrook et al., 2011) and increased channel complexity (Polvi and Wohl, 2012). Furthermore, the open water expanse by overbank flooding and the subsequent changes to the vegetative community increase the rate of evapotranspiration (Burns and McDonnell, 1998; Hill and Duval, 2009; Newton et al., 1996; Olson and Hubert, 1994; Woo and Waddington, 1990) and the rate of decomposition, making beaver ponds hotspots for CO_2 and CH_4 release (Bubier et al., 1993; Roulet et al., 1997; Webster et al., 2013; Wik et al., 2016).

The impacts of beaver dams are not limited to the land surface. Indeed, K_{sat} values and streamflow gradients matter; in areas where dams raise local water tables, the consequent increase in hydraulic head can divert streamflow into the subsurface, altering hyporheic flow regimes and increasing transient storage (Jin et al., 2009; Lautz et al., 2006; Lowry, 1993). Subsurface flow is commonly observed to follow a 'looping pattern', where it is diverted in directions away from the stream, which circumvents the dam and then returning in downstream locations (Janzen and Westbrook, 2011; Lowry, 1993; Shaw, 2009; Westbrook et al., 2006). This same pattern has been observed vertically in the hyporheic zone, where flow is pushed underneath the dam only to resurface once it has cleared the dam's location (Briggs et al., 2012; Janzen and Westbrook, 2011; Lautz et al., 2006). Although these flow patterns have been observed, they are not necessarily transporting large volumes of water. For example, Janzen and Westbrook (2011) observed that a stream in a montane peatland was losing water around beaver dams, but only a small fraction of the lost water was actually travelling via the observed hyporheic flow paths.

2.4 Knowledge Gap - Beaver and Peatlands[1]

An often overlooked but potentially significant impact on peatland development and C flux is the presence of beavers in North America (*C. canadensis*), Eurasia (*C. fiber*) and, more recently, in parts of southern Patagonia (introduced *C. canadensis*). Historically, beaver were abundant and widespread throughout the northern hemisphere (Naiman et al., 1988), and gnawed wood found deep in numerous peat profiles is evidence that they colonized many of these environments shortly after the Last Glacial Maximum (Gorham et al., 2007; Kaye, 1962). The discovery of these fossils together with the fact that beavers alter the ontogeny of riparian ecosystems (Westbrook et al., 2011) suggest that peatland function may also be impacted by beaver habitation.

Beaver habitation in peatlands is well documented. A recent study of Rocky Mountain wetlands found that 73% of the peatlands surveyed had evidence of beavers (Morrison et al., 2015). Studies in Minnesota found that 88% of all beaver ponds in Voyageurs National Park were built on organic soils (Johnston, 2001, 2017) and that in Cass, Crow Wing, and Hubbard counties, peatland beaver dams outnumber their stream counterparts by more than three times (Ray et al., 2001). A recent estimate puts the total area covered by beaver ponds north of the 50°N at 17,558 km^2 (Wik et al., 2016). Moreover, many peatland environments in southern Patagonia have been colonized by beavers since their introduction in 1946 (Henn et al., 2016; Westbrook et al., 2017). Despite their prevalence in these environments, research into beaver-related impacts on peatlands is relatively unexplored.

Beavers are central place foragers that will only inhabit an area if they have a reliable supply of deciduous tree and shrub vegetation (Milbrath, 2013). Thus, they are limited to peatlands where such browse is available like wooded bogs and fens. Open water is not always a prerequisite for beaver colonization in these environments; beavers can create their own ponds by releasing floating mat vegetation in bog depressions, and by excavating peat and using the material to dam

[1] Adapted from section 5.1 of Loisel et al. (2017). Daniel Karran is the lead author and major contributor of the section, with minor contributions from Julie Loisel. Cherie Westbrook provided useful comments on the content of this review.

groundwater seepage and diffuse flow at the surface (Rebertus, 1986; Westbrook et al., 2017). Beavers also excavate canals that allow for safe transport to sources of browse that are distant from the pond (Johnston, 2001; Rebertus, 1986). A study done in isolated morainal wetlands of Alberta found that canal excavation increased the volume to surface area ratio of beaver ponds by nearly 50% (Hood and Larson, 2015). There are currently no studies that document such changes by beavers in peatlands; however, this re-plumbing and alteration of basin morphometry would likely have lasting effects on carbon storage in the localized area of the pond.

Once the food supply around a pond is exhausted, the beaver colony will abandon it and migrate to other locations. This cyclic behavior of pond creation and abandonment makes beaver ponds transient features on the landscape. Ponds that are abandoned along streams will generally fall into disrepair and eventually washout within decadal times scales (Woo and Waddington, 1990). Ponds that are excavated and built to dam flowing water with low energy (e.g. groundwater seepage, diffuse surface flow) may persist for much longer time spans, but this has yet to be shown in the literature. There have also been few studies that quantify the size and number of beaver ponds in peatlands. The size of the beaver pond depends on the local topography (e.g. width of the stream channel, adjacent riparian area, and dam height) (Rosell et al., 2005), and in the relatively flat, low relief terrain, which characterizes most peatlands, ponds can potentially be quite large. Furthermore, the number of beaver ponds in these environments can also be quite high. Milbrath (2013) showed that the recovery of beaver populations from the fur trade in the Pine Butte Fen of Montana led to the creation of 42 new beaver ponds over a 72-year period (i.e. 1937–2009), and totaled 75 beaver ponds in just a ~5 km2 area.

Beaver ponds contribute 0.8–1.0 Tg yr^{-1} of atmospheric CH_4 globally (Whitfield et al., 2014; Wik et al., 2016), and were found to be the largest CH_4 emitters among all the wetland types in boreal environments (Bubier et al., 1993; Roulet et al., 1992). A recent study indicates that ice-free season CH_4 emissions from beaver ponds in the northern high latitudes are up to seven times higher than those from other types of water bodies, mostly because beaver ponds are often shallow and characterized by a C-rich substratum (Wik et al., 2016). In addition, an in-depth study of a peatland beaver pond in Ontario showed that the combined amount of CO_2 and CH_4 released from the pond was the equivalent of over 200 g C m^{-2} yr^{-1} (Roulet et al., 1997). In the same region, Webster et al. (2013) modeled the flooding of a fen by beavers and found that the presence of only a few beaver ponds could potentially offset the C sequestered by peat accumulation at the ecosystem scale. This notion is contrary to other studies that have suggested that beaver ponds accelerate peat accumulation by the inhibition of aerobic processes, decreased C mineralization (Updegraff et al., 1995) and the NPP of aquatic plants (Johnston, 2001, 2014, 2017). In any case, the sources and underlying mechanisms of C sequestration in peatland beaver ponds requires further elucidation.

One of the more apparent links between beaver activity and C sequestration is the localized impact that beaver dams have on water tables (Gurnell, 1998; Westbrook et al., 2006). As discussed in Section 3, water table position and stability have significant influence on NPP and C decomposition in the near surface peat. Beavers have been reported to raise water tables in a fen through dam construction (Lowry, 2008); however, they have also been reported to drain fens by lowering water tables via channel excavation (Westbrook et al., 2017). Small dams can inundate large areas if the peatland is relatively flat, and rises in the water table above the surface of the peat can steepen the hydraulic gradients such that subsurface flow regimes change (Janzen and Westbrook, 2011). Such changes may have implications for C cycling in deeper peat because pore-water residence times would be expected to decrease (Morris and Waddington, 2011), and the transportation of labile C substrates into deeper parts of the peat profile would be expected to increase (Levy et al., 2013).

Inundation of the peatland surface by beaver ponds also has a profound impact on the vegetative community. Not only do beaver ponds foster the growth of aquatic plants (Johnston, 2001), they can also alter dynamics in succession. The flooding of a bog by beavers in Northwest Connecticut caused the decimation of the forested wetland community, which was then replaced by minerotrophic fen vegetation (Mitchell and Niering, 1993). Moreover, the flooding of fens in southern Patagonia has drowned the native sedges and mosses and facilitated the invasion of exotic European plant species (Westbrook et al., 2017). This change in vegetation is further amplified by the fact that beavers can harvest, annually, up to 1400 kg ha^{-1} of woody biomass for food and building supplies (C. A. Johnston and Naiman, 1990). As a result, nutrient-poor areas dominated by shrubs become replaced by wetter and more eutrophic herbaceous plant assemblages (Walbridge, 1994). These changes likely have a long-lasting impact on peatland development since they alter fundamental processes that control its function as a C sink.

Beaver ponds connected to peatland streams may foster sedimentation processes, which, in mineral systems, is a well-established paradigm (Naiman et al., 1986; Ruedemann and

Schoonmaker, 1938). In mineral systems, sediment layers up to 1-m thick have been measured in active beaver ponds (Butler and Malanson, 1995; Kramer et al., 2012) and layers up 2-m thick have been found in the underlying stratigraphy where relic ponds were located (Persico and Meyer, 2009). Sediment layers have also been found in beaver inhabited peatlands (Morrison et al., 2015); however, a connection between the sediment layer and beaver activity has yet to be confirmed. Even a small increase in the inorganic material influx has the potential to greatly inflate soil density and accretion rates (Loisel et al., 2014), which could lead to an overestimation of carbon accumulation in studies where carbon density is assumed to remain constant throughout peatland development.

The impact of beaver activity on peat is likely to leave a lasting signature in the peat core stratigraphy. Paleoecologists/hydrologists should be aware of this impact because a prolonged rise in the water table associated with beaver may falsely signal a shift to a wetter climate and the opposite may be true when the dam breaks. Based on macrofossil analysis of a montane fen core in Alberta, Kubiw et al. (1989) speculated that beavers were responsible for an unexpected water table rise at approximately 7000 cal. BP, and McIntyre et al. (1991) used pollen and diatom analysis to suggest that a beaver dam flooded a peat-marl complex around 5100 cal. BP. Multi-proxy designs should be prepared for potential signatures of beaver activity, which may include: (1) abrupt shifts in vegetative communities, possibly from terrestrial to aquatic; (2) sediment layers associated with high water tables and lacustrine environments, and (3) increased methanogenesis. Furthermore, studies intent on connecting peatland development with beaver-mediated ecohydrological processes are needed to inform future multi-proxy designs and elucidate our conceptual understanding of these systems.

A beaver's ability to engineer its surroundings has a profound impact on landscapes. However, previous studies in peatlands have been limited to the local impacts of beaver ponds, despite evidence from mineral soil environments that show the cumulative impacts of numerous beaver ponds is notable at regional scales. For example, Hood and Bayley (2008) studied the impact of beavers on wetland area in Elk Island National Park, Canada. They determined that the number of active beaver lodges explained the variability in open water area better than climatic variables, and that beavers play a dramatic role in maintaining wetland habitat in periods of extreme drought. Considering the close link between C sequestration and basin hydrology in peatlands, similar studies are needed in these environments, especially in regions like the Rocky

Mountains, the boreal forest, and Hudson Bay Lowlands, where beaver activity in peatlands has been detected (Morrison et al., 2015; Sjörs, 1959; Turetsky and St. Louis, 2006).

3. Rapid Surface Water Volume Estimates in Beaver Ponds[2]

3.1 Preface

Beaver ponds are common surface-water features found in watersheds throughout the northern hemisphere and in southern South America. The shape and size of each pond are extremely variable, depending on the physiography in which it forms. Many beaver ponds are also transient through space and time as they proceed through a lifecycle of creation, abandonment, and washout. Such characteristics challenge our ability to include beaver ponds in hydrological balances and models because quantifying how much surface water they store requires significant time and energy when using standard approaches. Simpler methods are needed, such as statistical and analytical approaches that exploit the relationship between surface-water storage and beaver pond morphometry. The goal of this chapter is to characterize beaver pond morphometry in a variety of different environments and explore tools useful for estimating surface water storage in them.

[2] Karran, D.J., Westbrook, C.J., Wheaton, J.M., Johnston, C.A., Bedard-Haughn, A., 2017. Rapid surface-water volume estimations in beaver ponds. Hydrology and Earth System Sciences 21, 1039–1050. doi:10.5194/hess-21-1039-2017. Daniel Karran is the major contributor and lead author of the manuscript. Joe Wheaton, Carol Johnston provided data and useful feedback on the manuscript content and structure. Angela Bedard-Haughn provided useful feedback on the manuscript content and structure. Cherie Westbrook was the primary supervisor for this piece and provided the idea, as well as assisting with the analysis, writing, and structure.

3.2 Abstract

Beaver ponds are surface-water features that are transient through space and time. Such qualities complicate the inclusion of beaver ponds in local and regional water balances, and in hydrological models, as reliable estimates of surface water storage are difficult to acquire without time and labour intensive topographic surveys. A simpler approach to overcome this challenge is needed, given the abundance of the beaver ponds in North America, Eurasia and southern South America. We investigated whether simple morphometric characteristics derived from readily available aerial imagery or quickly measured field attributes of beaver ponds can be used to approximate surface water storage among the range of environmental settings in which beaver ponds are found. Studied were a total of 40 beaver ponds from four different sites in North and South America. The Simplified V-A-h approach, originally developed for prairie potholes, was tested. With only two measurements of pond depth and corresponding surface area, this method estimated surface water storage in beaver ponds within 5% on average. Beaver pond morphometry was characterized by a median basin coefficient of 0.91, and dam length and pond surface area were strongly correlated with beaver pond storage capacity, regardless of geographic setting. These attributes provide a means for coarsely estimating surface water storage capacity in beaver ponds. Overall, this research demonstrates that reliable estimates of surface water storage in beaver ponds only require simple measurements derived from aerial imagery and/or brief visits to the field. Future research efforts should be directed at incorporating these simple methods into both broader beaver-related tools and catchment-scale hydrological models.

3.3 Introduction

The volume of water stored at the surface of wetlands, ponds and lakes (as a function of stage) is of great concern to those responsible for assessing risks and balancing water supplies for societal demands. Arriving at reliable estimates of such storage is difficult without some knowledge of the feature’s morphometry; i.e., information that is often time-consuming and impractical to acquire, especially when the features are numerous and transient through space and time (Milly et al., 2008). This is particularly true for beaver ponds owing to their cyclic creation and abandonment.

Beaver dams and their associated ponds are ubiquitous in streams and wetlands in the northern hemisphere and southern South America (Whitfield et al., 2014). Beaver dam densities have been reported to exceed 40 dams per kilometer (Macfarlane et al., 2017), which makes them one of the most frequent obstructions to flowing water (Naiman et al., 1986; Pollock et al., 2003). Beaver dams increase open water area within watersheds (Hood and Bayley, 2008) and ponds bring numerous ecosystem benefits (Johnston, 2012). But, beaver ponds can also be viewed as burdensome or even dangerous from an anthropomorphic perspective (Butler and Malanson, 2005; Green and Westbrook, 2009). Such concerns, whether positive or negative, generally centre around the pond's capacity to store water and sediment, highlighting the need for quick and accurate surface-water storage estimation methods.

Numerous hydrological investigations have sought to estimate surface water storage in other types of wetlands (Trigg et al., 2014; Xu and Singh, 2004). For hydrological modellers, an ideal approach is one that overcomes the need for often time-intensive topographic surveys and that is more practical for use in models at varying scales and locations. Previous studies have addressed this problem by defining statistical relationships between surface area and volume for wetlands of specific physiographic regions (Gleason et al., 2007; Hubbard, 1982; Lane and D'Amico, 2010; Wiens, 2001). Such approaches have been useful for modelling entire watersheds (Gleason et al., 2007), but limited for estimating storage in individual wetlands because depth and basin morphometry (i.e. surface area, volume, depth) are not considered (Huang et al., 2011; Lane and D'Amico, 2010; Wiens, 2001). Brooks and Hayashi (2002) presented an equation that includes depth and basin morphometry, but to use it, basin morphometry must be predefined and no such information yet exists for beaver ponds.

Another approach, the Simplified Volume-Area-Depth (V-A-h) method (Hayashi and van der Kamp, 2000), accounts for depth and calculates basin morphometry for each individual wetland. Requiring only two measurements of depth and surface area, it has been shown to provide reliable estimates of surface water storage in the pothole wetlands of the North American prairies for which it was designed (Minke et al., 2010). Prairie potholes are depressional wetlands that have fairly regular shapes, i.e. concave profiles with smooth slopes. Beaver ponds, by contrast, typically encompass a bathymetry that is far more complex because their size and shape is controlled by the dimensions of the dam and the land surface that becomes flooded upon dam establishment (Johnston and Naiman, 1987). Whether statistical or analytical approaches can reliably estimate water storage in beaver ponds has yet to be determined. Our goal was thus to explore tools useful for estimating surface water storage in beaver ponds. We studied beaver ponds across much of their habitat range and: i) evaluated the utility of the Simplified V-A-h method in estimating surface water storage; ii) evaluated correlations between surface water storage and beaver pond morphometry; and, iii) described beaver pond morphometry in relation to surface water storage capacity.

3.4 Methods

3.4.1 The Simplified V-A-h method

The Simplified V-A-h method is based on a simple power equation (Hayashi and van der Kamp, 2000), where the area of a pond (A), at a given height above the pond bottom (h), is described as:

$$A = s\left(\frac{h}{h_0}\right)^{2/c}, \tag{3.1}$$

where h_0 is the unit height of the water surface (e.g. 1 m for SI units), s is a scaling coefficient that represents the area of a circle (m^2) with a radius that corresponds to h_0, and c is a dimensionless morphometry coefficient that represents the shape of the bathymetric curve (i.e. the area-depth relationship of the pond). The volume of the pond is then determined by integrating all the area profiles below h to give:

$$V(h) = \int_0^h s\left(\frac{h^*}{h_0}\right)^{2/c} dh^* = \left(\frac{s}{1+2/c}\right)\left(\frac{h^{1+2/c}}{h_0^{2/c}}\right). \tag{3.2}$$

Using Eq. (3.1) and Eq. (3.2) requires parameterizing the s and p coefficients. The Simplified V-A-h method arrives at these values by rearranging Eq. (3.1) to give (Minke et al., 2010):

$$s = A_1\left(\frac{h_1}{h_2}\right)^{-2/c}, \tag{3.3}$$

And

$$c = 2\left(\frac{Log\left({h_1}/{h_2}\right)}{Log\left({A_1}/{A_2}\right)}\right), \tag{3.4}$$

where A_1 and A_2 are surface areas of the pond at corresponding depths of h_1 and h_2, respectively, and $h_1<h_2$. With only two measurements of area and depth in time, Eq. (3.3) and Eq. (3.4) can be used to calculate s and c coefficients that are then reinserted into Eq. (3.1) and Eq. (3.2) to define the entire area-depth and volume-depth relationship of the pond.

3.4.2 Beaver pond morphometry

3.4.2.1 Metrics for surface water volume estimations

A beaver pond's capacity to store surface water is defined simply by its bathymetry, and can be directly calculated if an accurate topographic survey is available. The problem here relates to how well we can approximate that volume given some simple measures of the dam and pond dimensions. To discover if metrics exist, a series of morphometric variables were generated in addition to the c coefficient described in Eq. (3.1). They include: the maximum dam height (h_{max}) defined as the difference in elevation (m) between the dam crest and the lowest point in the pond; the maximum surface area (m^2) of the pond (A_{max}) at h_{max}; and, the length (m) of the dam (D_{len}) measured along its crest. Regression analysis was then used to determine if any of the variables are correlated to the maximum volume of the pond (V_{max}).

3.4.2.2 Morphometric analysis

Understanding the underlying mechanics of the Simplified V-A-h method and how morphometry relates to a pond's capacity to store water requires a deeper analysis of the bathymetric curve. The bathymetric curve is equivalent to the hypsometric curve defined by Strahler (1952) as the ground surface area of a landmass with respect to elevation. To compare curves for ponds of different size and relief, it is necessary to express the variables as relative depth (R_D) and relative area (R_A) as:

$$R_D = \frac{h}{h_{max}}, \tag{3.5}$$

and

$$R_A = \frac{a}{A_{max}}, \tag{3.6}$$

where, h is the stage (m) elevation of the pond and a is the corresponding surface area (m^2) at any given h. For ease of visual interpretation, we express the bathymetric curve as R_D vs. 1-R_A (Fig. 3.1). Power functions described by Eq. (3.1) can then be fit to a bathymetric curve with the following equation:

$$R_D = (1 - R_A)^{c/2}, \tag{3.7}$$

where the c coefficient here is equal to the c coefficient in Eq. (3.1). This allows for a visual aid in the analysis of error by superimposing estimated curves produced via either Eq. (3.1) or Eq. (3.4) to the pond's actual bathymetric curve. It also eliminates issues of scale between different ponds so that bathymetric curves can be visually compared to one another.

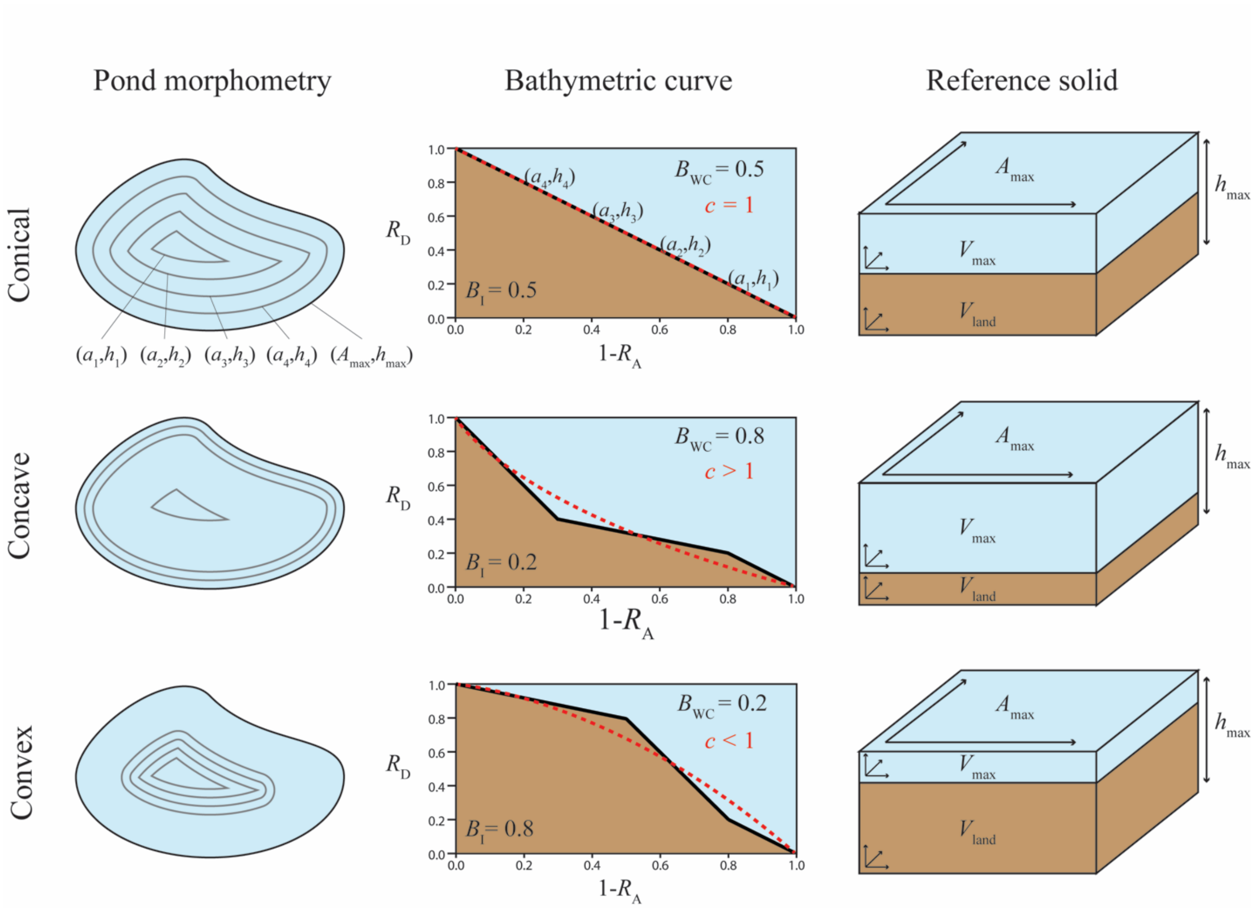

Fig. 3.1 Perceptual diagram of the relationship between morphometric variables. The area (a) at a given stage of the pond (h) is a point on the bathymetric curve (thick black line), where RA is the relative area and RD is the relative depth. The bathymetric integral (BI) is the integration of everything below the bathymetric curve and the pond's capacity to store water (BWC) is the integration of everything above the bathymetric curve. The morphometry (c) coefficient represents the shape of the bathymetric curve in the power function equation (red-dashed line; Eq. (3.7)). The reference solid is the box created by multiplying the maximum height of the dam (hmax) by the maximum surface area created by the pond (Amax), and is entirely comprised of land (Vland) and/or water (Vmax) proportional to BI and BWC.

From the relative bathymetric curve, it is possible to compute the Bathymetric Integral (B_I), a modified form of the hypsometric integral defined as the measure of landmass volume with respect the entire reference solid created by the maximum dimensions of the pond (Fig.3.1; Strahler, 1952):

$$B_{\mathrm{I}} = \frac{V_{\mathrm{land}}}{h_{\mathrm{max}} A_{\mathrm{max}}} = \int_0^1 R_{\mathrm{A}} \, dR_{\mathrm{D}} \, . \tag{3.8}$$

Equation 3.8 produces values between 0 and 1, with 1 representing a reference solid entirely composed of landmass. Using the B_I, we introduce a new metric that represents the pond's bathymetric capacity to store water (B_{WC}). Since the total volume of the reference solid is comprised of either land or water, the B_{WC}, relative to the reference solid, is expressed as:

$$B_{\mathrm{WC}} = 1 - B_{\mathrm{I}} = \frac{V_{\mathrm{max}}}{h_{\mathrm{max}} A_{\mathrm{max}}} \, . \tag{3.9}$$

The B_I and B_{WC} are quantitative measurements of the pond's morphometry and capacity to store water, respectively. The value in using these metrics is that they facilitate the comparison of surface water storage capacity among beaver ponds and other wetland types.

Finally, we described the shape of the beaver pond surface using a dimensionless Shape Index (S_I), which is essentially the ratio of the pond perimeter to the circumference of a circle with the same area (Hutchinson, 1957):

$$S_{\mathrm{I}} = \frac{P}{2\sqrt{\pi A_{\mathrm{max}}}} , \tag{3.10}$$

where P is the perimeter of the pond (m). Ponds with $S_I = 1$ have shapes that are perfectly circular, whereas ponds with $S_I > 1$ are increasingly complex. Pond shape is an important metric as much of the interaction between surface water and groundwater happens at the shoreline (Shaw and Prepas, 1990). We chose S_I as it is easy to interpret and enables a relative comparison between the shapes of beaver ponds and other types of wetlands (Minke et al., 2010).

3.4.3 V-A-h models for surface water storage estimation in beaver ponds

Three versions of the power function model described by Eq. (3.1) were tested in this study. They are referred to as the full, simplified, and optimized models. The simplified model is the actual test of the Simplified V-A-h method and the other two models were included to aid in the analysis of this approach.

The full model is a power function fitted to the complete dataset of each pond's bathymetry (i.e. empirical fit). We arrive at values for s and c by fitting a simple power function, $y = ax^b$, to the pond's bathymetric curve, and assume $a = s$ and $b = 2/c$ in accordance with Eq. (3.1). Non-linear least squares regression was used to determine the best-fit; the ability of this model to make accurate area and volume estimates depends on its 'goodness-of-fit' to the dataset. Analysis of the Full model was included to: i) identify the c coefficient that best describes each beaver pond's morphometry; and, ii) assess the overall suitability of power functions to describe beaver pond bathymetry.

The simplified model is a power function using s and c coefficients created from the same two relative measurements of depth (i.e. h_1 and h_2 as a percentage of $h_{\max}$) in each pond. Minke et al. (2010) evaluated the Simplified V-A-h method by applying it to two scenarios: a dry one where h_1 and h_2 are taken at 0.1 m and 25% of $h_{\max}$, and a wet one where h_1 and h_2 are taken at 50% and 75% of $h_{\max}$. They found that estimation errors were lowest using the wet scenario; therefore, we chose this scenario to simulate the application of the simplified V-A-h method as it may be practically used in the field.

The optimized model differs from the Simplified model through parameterizing coefficients via the optimum combination of h_1 and h_2 for each pond. This required calculating s and c coefficients at every possible combination of h_1 and h_2 along the bathymetric curve (Note: h_1 and h_2 are expressed as a percentage of $h_{\max}$ from 1–100; therefore, the total number of combinations where $h_1 < h_2$ is 5000 for each pond). Each set of s and c coefficients was then reinserted into Eq. (3.1) and Eq. (3.2) to estimate area and volume, respectively, and the set that produced the least combined area and volume error was selected as the optimum. The optimum model was included in this study to discover how best to use the Simplified V-A-h method with regards to differences in pond morphometry.

Error for all three models was evaluated using root mean square error (E_{RMS}), defined as:

$$E_{\mathrm{RMS}} = \sqrt{\frac{1}{m}\sum_{i=1}^{m}(D_{\mathrm{ACT}} - D_{\mathrm{EST}})^2}\,, \qquad (3.11)$$

where m is the number of data points, D_{ACT} is the point on the actual bathymetric curve calculated from the pond itself, and D_{EST} is the point on the estimated bathymetric curve derived from the s and c coefficients at a given combination of h_1 and h_2. Finally, to allow for coherent comparisons of error among the different beaver ponds, the magnitude of error, referred to as A_{ERR} (%) for area and V_{ERR} (%) for volume, was calculated by dividing the E_{RMS} by the actual area and volume of the pond at 80% of h_{max}. This particular depth was chosen to avoid inconsistencies in error magnitudes that arise when the evaluation depth is set too close to the minimum and maximum (Minke et al., 2010).

3.4.4 Test sites

Forty beaver ponds were selected for this study and simulated in digital elevation models (DEMs). Our sample design captured the range of structures built by beavers along streams with mineral and organic substrates in both mountainous and lowland terrain. Beaver ponds were thus analyzed from multiple locations where bathymetric data existed, which included: Kananaskis Provincial Park, Alberta, Canada; Escondido, Tierra del Fuego, Argentina; the Logan River watershed, Utah, USA; and, Voyageurs National Park, Minnesota, USA. Details of the location, terrain, number of ponds, survey methods, and survey resolution for each site are provided in (Table 3.1).

3.4.5 DEM creation and manipulation for variable calculations

Sites selected for this study were former beaver ponds that had drained sufficiently to either reveal pond bottom bathymetry or allow it to be surveyed. Beaver ponds extracted from LiDAR, when available, were fully drained with visible relic dams, whereas some ponds surveyed by total station and rtkGPS often were still full with water up to their crest elevations, but not enough to impede point collection by wading. DEMs that relied on total station and rtkGPS surveys were created with Surfer® v10 (Golden Software, Colorado) using ordinary kriging. The beaver ponds were then isolated from the unneeded areas of the DEM by extracting all the points in the raster below and upstream of the dam crest (i.e. h_{max}), which was done in ArcGIS v10.2 (ESRI, 2015) as was the calculation of the morphometric variables. The *V-h* relationship and bathymetric curve of each pond were calculated at 5-cm increments using a script written in Python™ that utilizes the 'volume' feature of ArcGIS Toolbox. The *V-h* relationship and bathymetric curve of each pond were the primary inputs for the three models, which were built and run in R Studio (RStudio Team, 2015). Finally, the bathymetric curve for each pond was established using linear interpolation to create 100 points, i.e. 1–100% of h_{max}.

Table 3.1 Site locations, characteristics and details of topographic pond surveys. "n" is the number of ponds studied at each site.

Site	Latitude and Longitude (°,’)	n	Soil Substrate Type	Terrain	Survey method	DEM resolution (m)
Kananaskis Provincial Park, AB, Canada	51° 3.553’ N, 114° 52.009’ W	10	Organic	Mountainous	rtkGPS	1
Escondido, Tierra del Fuego, Argentina	54° 36.908’ S, 67° 44.540’ W	3	Organic	Mountainous	rtkGPS	1
Logan River Watershed, UT, USA	41° 50.327’ N, 111° 33.668’ W	14	Mineral	Mountainous	Total Station	0.1
	41° 49.568’ N, 111° 34.516’ W	2	Mineral	Mountainous	Total Station	0.1
	41° 48.868’ N, 111°35.553’ W	5	Mineral	Mountainous	Total Station	0.1
Voyageurs National Park, MN, USA	48˚ 32.773’ N 93˚ 4.328’ W	1	Organic	Lowland	LIDAR	1
	48˚ 27.975’ N 92˚ 53.864’ W	3	Mineral	Lowland	LIDAR	1
	48˚ 30.405’ N 92˚ 40.331’ W	1	Mineral	Lowland	LIDAR	1
	48˚ 31.262’ N 92˚ 52.794’ W	1	Mineral	Lowland	LIDAR	1

3.5 Results

3.5.1 Beaver pond morphometry

Pond morphometric characteristics are provided in Table 3.2 and examples of the DEMs from each location are provided in Fig. 3.2. The 40 ponds well represented the various types of beaver ponds that are created in riverine and wetland habitats (Baker and Hill, 2003), with max dam heights (h_{max}) ranging from 0.25–2 m and dam lengths (D_{len}) spanning 3–308 m, with medians of 0.83 m and 40 m, respectively. Pond volumes (V_{max}) ranged between 1–9,001 m^3 and showed strong power correlations to D_{len}, h_{max} and A_{max} (Fig. 3.3). Among the ponds, there was considerable variability in shape as S_{I} values ranged from 1.5–5.3 (mean = 2.6). No strong correlations (i.e. -0.10 > R^2 < 0.10) were found between S_{I} and the other morphometric variables used in this study (i.e. c, B_{I}, B_{WC}, D_{len}, h_{max}).

Table 3.2 Pond morphometric characteristics, including the full model morphometry (c) and scaling (s) coefficients, shape index (SI), bathymetric integral (BI), bathymetric water capacity (BWC), length of the dam (Dlen), and maximum depth (hmax), area (Amax), and volume (Vmax) of the ponds.

Location	Pond #	S_I	B_I	B_{WC}	p	s (m^2)	D_{len} (m)	h_{max} (m)	A_{max} (m^2)	V_{max} (m^3)
Kananaskis	1	2.05	0.75	0.25	0.69	889	164	1.50	2974	1135
	2	2.37	0.77	0.23	0.61	356	152	1.75	2006	867
	3	2.57	0.69	0.31	0.97	959	127	0.85	686	186
	4	1.79	0.77	0.23	0.61	123	27	1.50	446	163
	5	3.71	0.77	0.23	0.62	705	226	1.95	5496	2503
	6	3.47	0.74	0.26	0.67	1845	199	2.00	16357	9001
	7	1.76	0.76	0.24	0.56	1334	308	1.85	12912	5734
	8	2.55	0.75	0.25	0.63	701	159	1.80	3787	1757
	9	1.71	0.68	0.32	0.92	290	39	1.25	448	184
	10	1.51	0.66	0.34	1.05	247	30	1.10	297	113
Escondido	11	2.32	0.59	0.41	1.16	5352	162	0.55	1528	325
	12	1.72	0.45	0.55	2.58	2181	59	0.30	748	130
	13	1.99	0.54	0.46	1.61	3223	124	0.55	1342	344
Logan	14	2.19	0.66	0.34	1.06	438	7	0.30	54	6
	15	2.03	0.72	0.29	0.83	464	3	0.25	15	1
	16	1.89	0.56	0.44	1.51	87	4	0.60	41	11
	17	2.63	0.75	0.25	0.67	112	17	0.75	52	10
	18	2.14	0.70	0.30	0.91	91	19	0.80	63	15
	19	2.17	0.67	0.33	0.97	138	10	0.65	53	11
	20	1.95	0.67	0.33	0.94	352	16	0.45	50	8
	21	2.47	0.64	0.36	1.11	179	11	0.50	45	8
	22	2.70	0.67	0.33	0.98	96	7	0.45	17	2
	23	1.90	0.64	0.36	1.20	56	10	0.55	23	5
	24	1.97	0.69	0.31	0.80	430	27	0.60	82	15
	25	2.37	0.59	0.41	1.36	154	6	0.30	22	3
	26	2.83	0.75	0.25	0.68	124	21	0.90	90	19
	27	2.79	0.73	0.27	0.75	114	5	0.60	36	6
	28	1.73	0.67	0.33	0.96	278	13	1.00	265	87
	29	4.32	0.81	0.19	0.45	975	87	1.00	980	189
	30	3.43	0.71	0.29	0.79	620	21	0.85	374	94
	31	5.31	0.69	0.31	0.90	551	43	0.85	432	115
	32	2.61	0.69	0.31	0.83	1647	46	0.50	210	32
	33	2.59	0.66	0.34	0.99	409	51	1.65	1123	621
	34	2.40	0.58	0.42	1.41	470	12	0.45	130	26
Voyageurs	35	4.65	0.71	0.29	0.83	3683	144	1.10	4725	1517
	36	3.82	0.70	0.31	0.94	4539	161	1.10	5928	1999
	37	3.54	0.72	0.28	0.78	36105	57	0.40	2297	264
	38	2.52	0.66	0.34	0.88	11836	58	1.10	12985	4740
	39	2.72	0.61	0.39	1.11	18033	97	0.90	12482	4350
	40	2.78	0.63	0.37	1.18	4867	41	0.55	1504	316

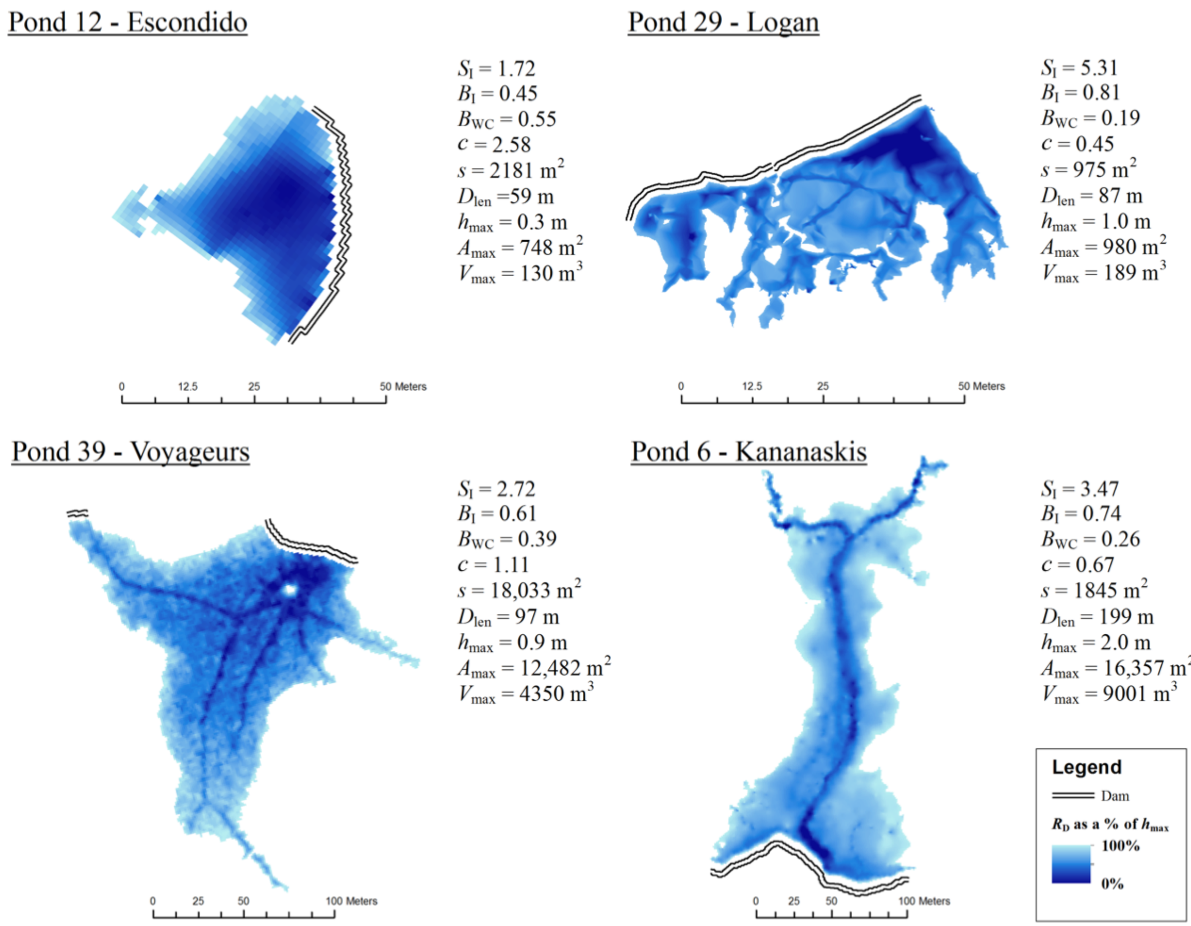

Fig. 3.2 Four examples of detrended beaver pond DEMs used for this study, one from each study area. (SI = shape index, BI = bathymetric integral, BWC = bathymetric water capacity, c = morphometry coefficient (full model), s = scaling coefficient, Dlen = dam length, hmax = maximum height of the dam, Amax = maximum surface area of the pond, and Vmax = maximum volume of the pond).

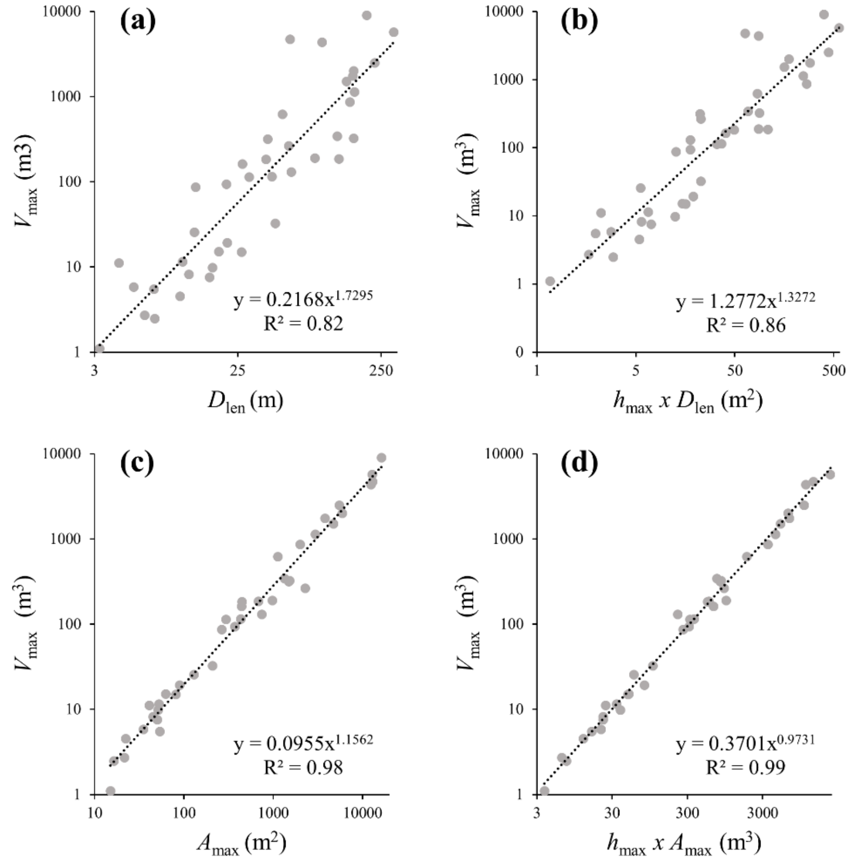

Fig. 3.3 Power regression relationships between the maximum volume of the beaver ponds (Vmax) and: (a) the length of the beaver dams (Dlen); (b) the product of the maximum depth of the ponds (hmax) and the length of the beaver dams; (c) the maximum surface area (Amax) of the ponds; and, (d) the product of the maximum surface area and maximum depth of the pond.

The *c* coefficients for the beaver ponds followed a log-normal distribution, and ranged from 0.45–2.58 (median of 0.91) (Fig. 3.4). Of the 40 beaver ponds analyzed, 70% (28) had *c* coefficients that were <1, indicating that beaver ponds tend to have convex bathymetries. Most beaver ponds tended to be more convex than they are concave, given the shape of the bathymetric curves (Fig. 3.5) and the range of B_I (0.45–0.85; median of 0.69). In all but one case, V_{land} was greater than 50% of the total volume of space, indicating that most beaver ponds are shallow, which limits the volume of surface water they can store. This phenomenon is well described by the strong exponential relationship between the *c* coefficient ($R^2 = 0.96$) and B_I and B_{WC} (Fig. 3.6). Soil substrate type (Table 3.1; organic vs. mineral) did not affect the value of the *c* coefficient, as evidenced by a *t*-test ($p = 0.97$).

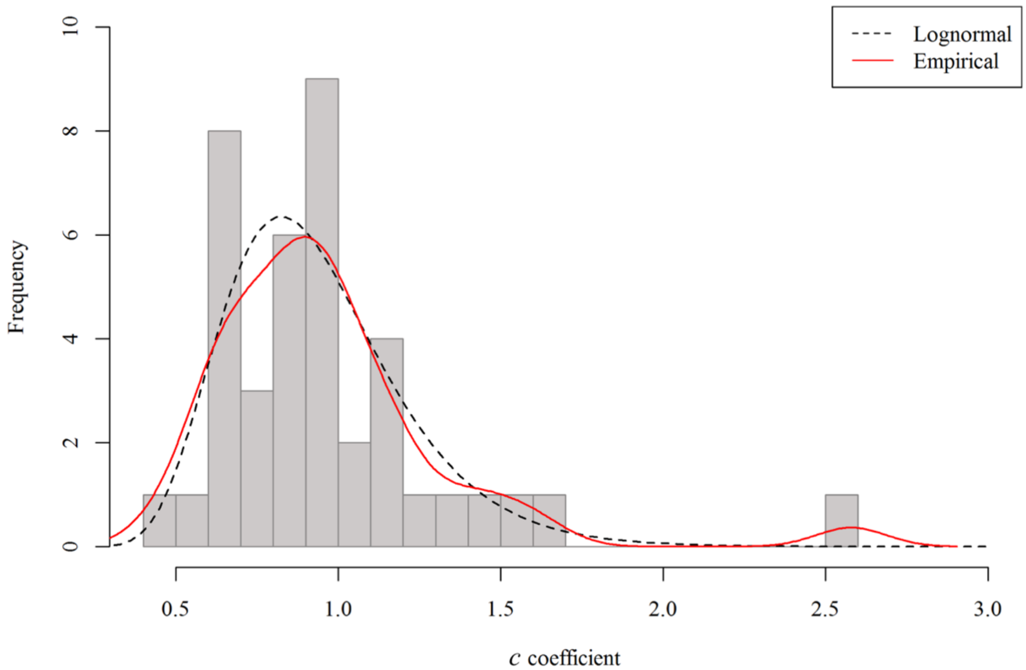

Fig. 3.4 Distribution of morphometry (c) coefficients (full model) for all beaver ponds sampled (n=40).

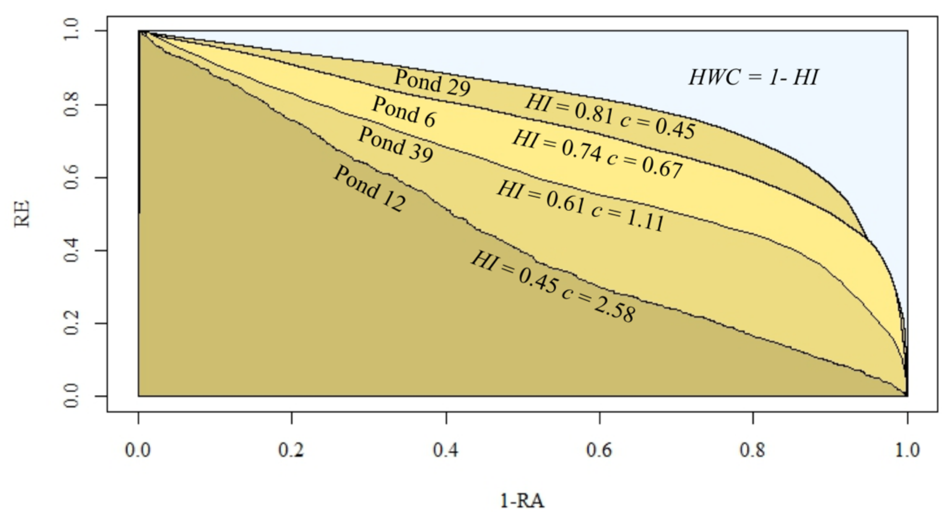

Fig. 3.5 Bathymetric curves for ponds shown in Figure 1. RD is relative depth, RA is relative area, BI is the bathymetric integral, BWC is the bathymetric water capacity, and c is the optimum morphometry coefficient.

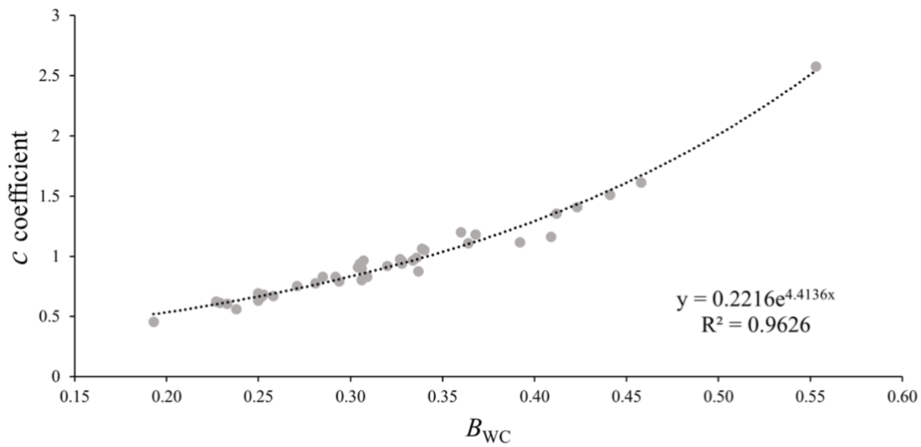

Fig. 3.6 Relationship between the morphometry (c) coefficient (full model) and the bathymetric water capacity (BWC).

3.5.2 Surface water storage estimations

The full model had the lowest A_{ERR}, and the optimized model had the lowest V_{ERR} (Fig. 3.7; Table 3.3). The highest A_{ERR} and V_{ERR} was associated with simplified model estimates, which also produced the greatest variability of error among the different ponds. With regards to study locations, full V_{ERR} ranked as Escondido<Voyageurs<Logan<Kananaskis, whereas full A_{ERR} ranked Logan<Escondido<Kananaskis<Voyageurs. Overall, the beaver ponds in Kananaskis proved most difficult to model (i.e. highest V_{ERR} and A_{ERR} overall); however, mean error for the full model remained below 5% for both area and volume estimates.

Table 3.3 V-A-h model performance comparisons based on the mean (± standard deviation) volume (VERR) and area (AERR) error magnitude. "n" is the number of ponds studied at each site.

Site	n	Full		Simplified		Optimized	
		V_{ERR}(%)	A_{ERR} (%)	V_{ERR}(%)	A_{ERR} (%)	V_{ERR}(%)	A_{ERR} (%)
Kananaskis	10	4.3 ± 3.1	3.8 ± 2.1	7.2 ± 6.0	14.6 ± 12.3	2.3 ± 1.6	4.2 ± 2.5
Escondido	3	3.1 ± 1.4	3.8 ± 0.7	4.3 ± 2.5	6.7 ± 3.8	1.6 ± 0.7	4.0 ± 0.9
Logan	21	4.0 ± 2.6	3.6 ± 1.7	4.6 ± 3.5	9.9 ± 8.5	2.0 ± 1.2	3.9 ± 1.9
Voyageurs	6	3.8 ± 1.8	4.1 ± 1.6	3.8 ± 1.8	4.1 ± 1.6	1.9 ± 0.9	4.4 ± 1.7
All Ponds	**40**	**4.0 ± 2.5**	**3.8 ± 1.7**	**5.2 ± 4.1**	**11.0 ± 9.4**	**2.1 ± 1.2**	**4.0 ± 1.9**

Compared to the full model (Fig. 3.7), the simplified model had higher V_{ERR} in 65% of cases (26 ponds) and higher A_{ERR} in 98% of cases (39 ponds), whereas the optimized model had lower V_{ERR} in 100% of cases but slightly (<1%) higher A_{ERR} in 100% of cases. The optimum *c* coefficients for volume tended to be slightly different than the optimum *c* coefficients for area, which are the coefficients derived from the empirical fit of the full model. The optimum model proved useful for revealing the two points on the bathymetric curve that can be used to obtain the optimum c coefficient for volume estimates. Pond 7 had the largest A_{ERR} and V_{ERR} (Fig. 3.7), and so was selected for more detailed study (Fig. 3.8). The optimum points were found at the approximate location of where the empirical fit intersects with the bathymetric curve. Thus, using the optimum points in Eq. (3.4) computes a c coefficient that is closest to the same coefficient generated by the curve fitted by non-linear least squares regression. The points used by the simplified model for Pond 7 fall on segments of the bathymetric curve that are farther away in distance from the empirical fit; hence, the c coefficient generated by these points creates a curve that is farther away from the bathymetric curve, which ultimately leads to a less accurate estimate of volume.

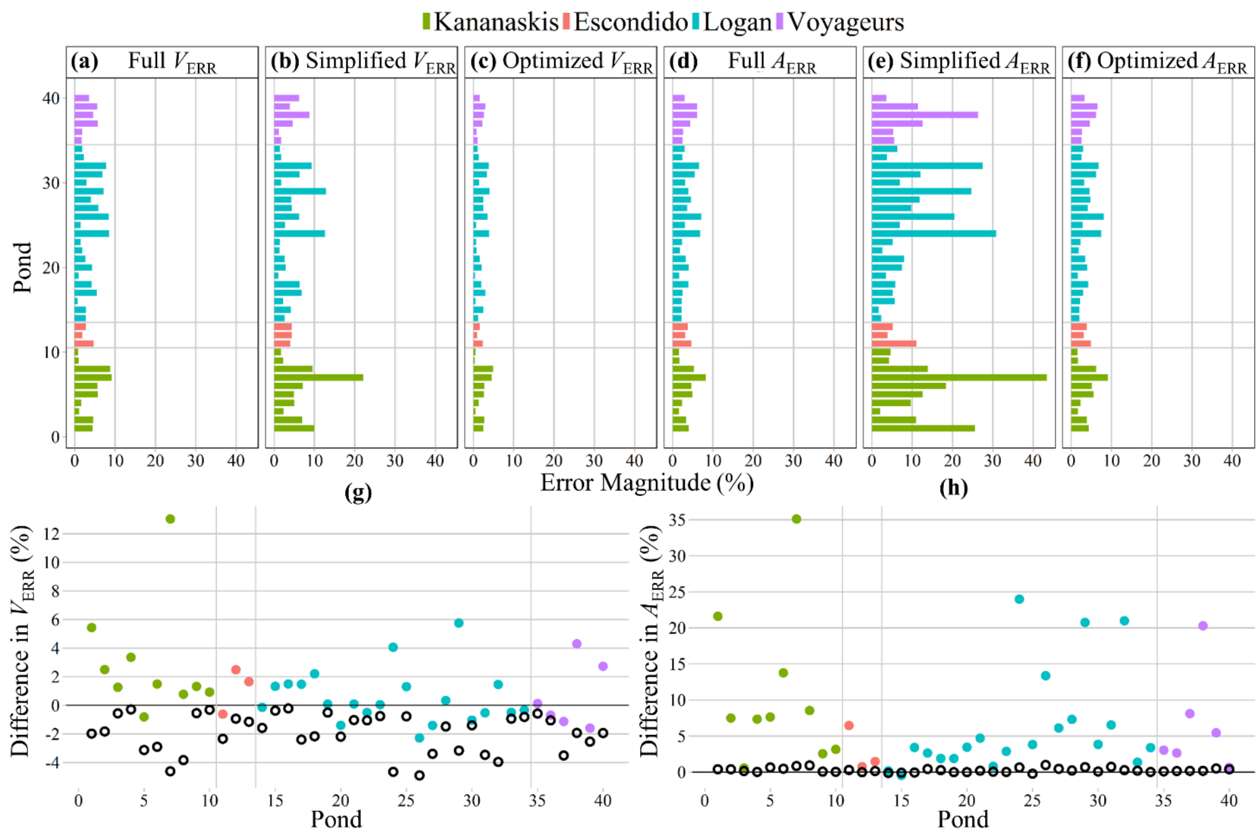

Fig. 3.7 Volume (VERR) and area error (AERR) from each beaver pond using the three different approaches (a-f). Plots on the bottom show the difference in volume (g) and area (h) error of the Simplified (solid circles) and Optimized (open circles) models relative to the Full model (the Full model is represented by the solid black line at zero on the y-axis). Bars and solid circles are colour coded by location as per the legend at the top of the figure.

In a number of ponds, the empirical fit nearly overlapped the entire bathymetric curve, and in such cases, there were many combinations of h_1 and h_2 that produced reasonable estimates of volume. For example, Pond 10 had the lowest Full A_{ERR} and V_{ERR} of all the beaver ponds. In this case, there were 1899 combinations of h_1 and h_2 that produced estimates with total error below 5%, and the distance between the points ranged from 1% to 84% of $h_{\max}$. Overall, the error was not sensitive to distance between h_1 and h_2 if the points were on or near the Full fitted curve. That said, the average minimum and maximum for h_1 (for all the optimum combinations for each pond) was 18–74%, respectively, and for h_2, it was 42–98%, respectively.

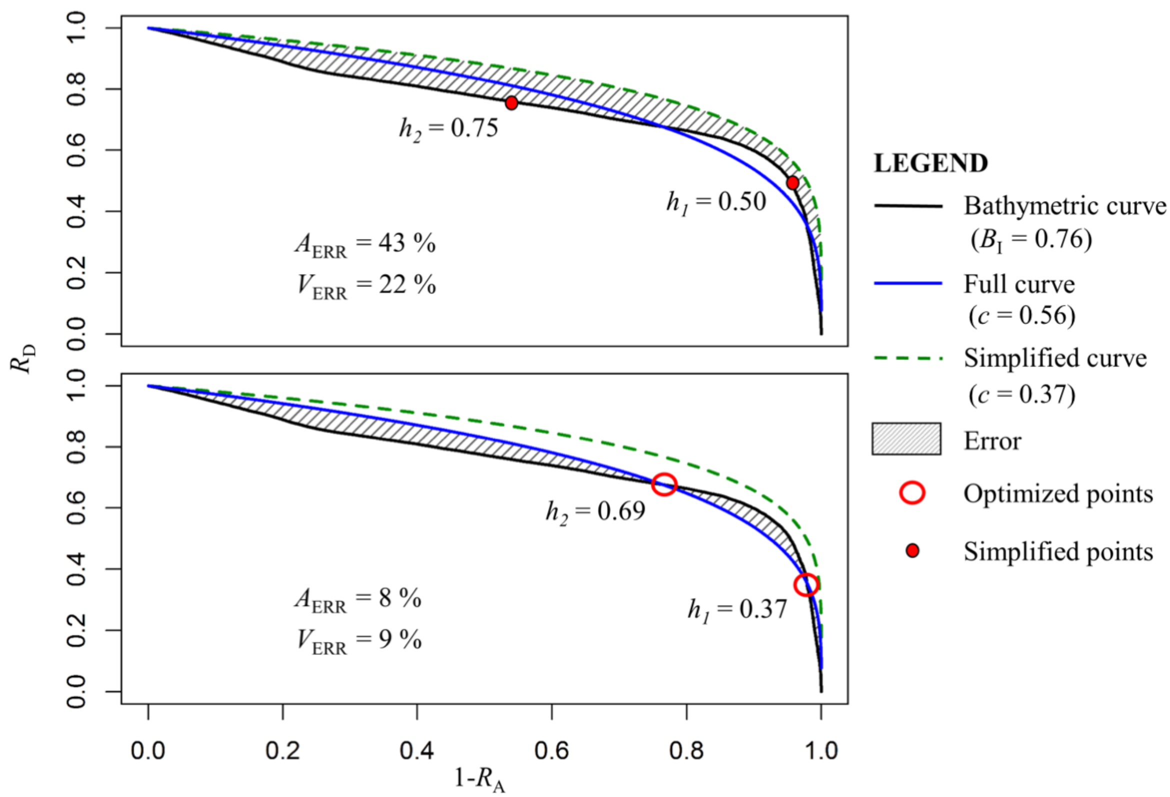

Fig. 3.8 Comparison of the bathymetric curve for Pond 7 with the Full and Simplified curve. The top shows the area (AERR) and volume (VERR) error associated with the Simplified curve that was calculated using Simplified depths h1 and h2 and the bottom shows the error associated with the Full curve and the optimum location for depths h1 and h2. RD is relative depth, RA is relative area, BI is the bathymetric integral, and c is the morphometry coefficient.

3.6 Discussion

The Simplified V-A-h method estimated surface water storage in the beaver ponds with high accuracy. Also, strong statistical relationships were found between surface water storage capacity in beaver ponds and the dimensions of the dam and pond. The beaver ponds studied have a convex shape that permits less water storage than do other open water wetland types. Surface water storage estimates can be made in beaver ponds without the need for topographic surveys if pond morphology is used instead.

3.6.1 V-A-h model performance in beaver ponds

The low full A_{ERR} and V_{ERR} overall indicates that beaver pond morphometry is adequately described by power functions. This is because the bathymetric curve proved resilient to fluctuations in 'elevation' inherent to the impounded land surface. Also, the dams, intricate canals and holes that beaver create in the areas they inhabit (Hood and Larson, 2015) do not warp the shape of the bathymetric curve enough that a power function becomes inappropriate to sufficiently describe it. However, it appears that volume estimations are more resilient to aberrations in the bathymetric curve than are area estimates. The power functions in the full model are fitted to pond bathymetry. When the power curve moves up and down, A_{ERR} will increase, but sometimes the V_{ERR} can decrease because volume is the integration of everything above the bathymetric curve. When the curve moves slightly up or down from the empirical fit, irregularities on the bathymetric curve are captured, which improves volume estimations at the sacrifice of area estimations. This explains why the optimum c coefficients for volume are different than they are for area. It also explains why, in many cases, the simplified model had V_{ERR} that was less than 10%, while A_{ERR} was greater than 25%. Without a complete set of pond bathymetry, it is unlikely that users of the Simplified V-A-h method would be able to discern the optimum points for h_1 and h_2; however, as long the chosen values for h_1 and h_2 are selected within the range identified here (i.e. 18–74% of h_{max} for h_1 and 42–98% of h_{max} for h_2), fairly accurate estimates of surface water storage should be expected. Overall, the simplified model performed reasonably, exceeding 10% V_{ERR} in only three cases. Given that the Simplified V-A-h method appears to work well across the broad range of beaver pond bathymetry reported here, and across a wide range of prairie potholes (e.g. Minke et al., 2010), it should be a robust enough approach to be used other open water wetlands.

3.6.2 Beaver pond morphometry and surface water storage capacity

Our results show that c coefficients in beaver ponds are lower overall than those reported in prairie wetlands (Hayashi and van der Kamp, 2000) and those reported in forest pools in New England (Brooks and Hayashi, 2002). Because of the strong exponential relationship between c coefficients and B_{WC}, we can conclude that beaver ponds typically store less water than depressional wetlands. For example, the prairie potholes studied by Hayashi and van der Kamp

(2000) had a median c coefficient of 3.22. Using Fig. 3.6, this c coefficient is equivalent to a B_{WC} of 0.61, which is almost double the median beaver pond B_{WC} equivalent of 0.32. The most likely explanation for this is the ontogeny of beaver ponds compared to other open water wetland types. Beaver ponds occur via inundation of an existing channel and adjacent riparian area surface, whereas prairie potholes are bowl-shaped geomorphic depressions created by the deposition of glacial till (Richardson et al., 1994). These different origins are reflected in the shape of the bathymetric curves, and they also explain the strong statistical relationships between surface water storage capacity and the dimensions of the dam and pond. The stream channel in Fig. 3.5, for example, is represented on the far-right side of the bathymetric curve. Beaver ponds built on deeper and narrower stream channels tend to have lower c coefficients than ponds built on wider, less constrained channels. This happens because there is a rapid expansion of surface area inundated as the dam exceeds the height and width of the stream channel; a phenomenon that is well described by the 'power' relationships between D_{len}, h_{max}, A_{max} and V_{max}. Pond 12 is a good example of this phenomenon; the c coefficient was highest (2.58) and a distant outlier compared to the other ponds. The uniqueness of this site is that the beavers built a small dam (0.3 m) with excavated peat and impounded groundwater seepage rather than damming channel flows. Even though the dam is relatively small, it has a large B_{WC} (0.55) relative to the other ponds because the dam is entirely dedicated to impounding a mostly flat land surface. In contrast, Pond 6, which was also built in a peatland, has a much lower B_{WC} (0.26) because most of the dam height (2 m) is dedicated to impounding water in an incised stream channel. An advantage of using the B_{WC} metric over pond volumes is that it allows for a comparison of surface water storage capability in a way that is independent of pond size and shape.

3.6.3 Why surface water storage in beaver ponds varies through time

There are a wide variety of reasons that water storage in beaver ponds vary through time. Some are the result of hydrologic and geomorphic processes, whereas others are the direct result of the ecosystem engineering activity of beaver and/or lack thereof. Among the most common factors include: 1) partial dam breaches by floods (Woo and Waddington, 1990); 2) aggradation of sediments from upstream sources (Butler and Malanson, 1995); 3) inactive/passive lowering of water surface by dam degradation (Woo and Waddington, 1990); 4) active manipulation of dam height and extent by beaver; and, 5) the excavation of extensive channel networks by beaver (Hood and Larson, 2015). Channel excavation, for example, increases the cumulative area at lower depths of the bathymetric curve, and so increases both the *c* coefficient and B_{WC}. This equates to an increase in surface water storage and we would expect mature ponds (Woo and Waddington, 1990), where beavers have been active for many years, to have higher *c* coefficients overall than ponds that were recently built in the same environment. However, the extent by which excavation impacts surface water storage may be partially offset by sediment aggradation, which averages 0.26–2.54 cm/yr in riverine environments (Butler and Malanson 1995). Ponds can thus accumulate large volumes of sediment relative to their surface area (Naiman et al., 1986), which would, over time, increase B_I and decrease the amount of surface water storage in the pond. Studies that explore the influence of beaver pond age on surface water storage are needed.

An interesting consideration is the significance of this variation through time. For any single beaver dam, the results could be dramatically different, but if the population of beaver ponds sampled reflects ponds at various stages of development (Woo & Waddington 1990), the temporal variation is presumably captured in the spatial variation by sampling over a larger area. For individual beaver ponds, it would be worth testing whether or not the simple methods presented herein still work reasonably well if dam lengths and dam heights are measured or specified to reflect actual stage instead of just the crest stage. It may be that the variation in water surface storage could be reasonably estimated by considering different crest elevations. Such an analysis may allow exploration of the role of active beaver maintenance on water storage and we postulate that active maintenance increases such storage. We have observed, in many systems, that a very high quantity of beaver dams are actually 'maintained' by very few beavers that move around quite regularly. Such mobile beavers should spend less time maintaining water surface elevations than those that stay locally and just maintain one complex and lodge. The water storage benefit of beaver ponds in areas that are very under-seeded with beavers and below population capacity (even if at dam capacity), is that the benefit is minimized where beaver populations are not close to carrying capacity.

3.6.4 Tools for surface water storage estimation in beaver ponds

There are a variety of ways our results can be used to estimate surface-water storage in beaver ponds under different data availability scenarios. In situations where only aerial or remotely sensed imagery is available (i.e. world-wide), dam length and pond area can be approximated and used in the generalized power regression relationships presented in Fig. 3.3. This is a quick and easy way to incorporate surface-water storage capacity of beaver ponds into land-use planning decisions and watershed-scale hydrological models. However, this approach is not suitable for detailed study in individual beaver ponds as it does not account for pond morphometry (Huang et al., 2011; Wiens, 2001). Including dam height should improve estimates. Measuring dam height in the field is quick and straight forward, but it can also be reasonably approximated with remotely sensed imagery alone using spectral-depth correlation methods (e.g. Passalacqua et al., 2015). If dam heights are available, we recommend using our median *c* coefficient (0.91) for beaver ponds in the equation presented by Brooks and Hayashi (2002):

$$V_{\max} = \frac{A_{\max} \times h_{\max}}{1 + {}^{2}/_{c}}. \tag{3.12}$$

This equation is a modified form of Eq. (3.2) used to estimate surface water storage capacity. It is easily incorporated into spatially distributed hydrological models. Fang et al. (2010) had success in using this approach, albeit for prairie potholes, in their Cold Regions Hydrological Model.

With a moderate amount of data, the Simplified V-A-h method offers an alternative that produces surface-water storage estimates with minimal error. The advantage of this method over the others is that it is robust, it is customized to each pond's basin morphometry, and it calculates a coefficient of scale (i.e. *s* coefficient) for use in estimating surface water storage across the range of pond stages, unlike the generalized power regression models and Eq. (3.12), which are limited to estimates of $V_{\max}$. Combined with a few field visits and something as simple as automated water level observations, the Simplified V-A-h method can be a powerful tool. But, it also has practical application in relatively data rich environments. For example, many LiDAR datasets are collected when beaver ponds are not fully drained. If the beaver pond is not entirely full, the measurements for A_2 and h_2 can be measured within the vertical distance between the crest of the dam and the surface of the water, thus allowing an appropriate *c* coefficient to be derived. Furthermore, the Simplified V-A-h method is increasingly practical with the advent of new technologies. For example, Structure from Motion software facilitates the creation of high resolution DEMs from ordinary photographs (Javernick et al., 2014). Theoretically, with both tools, one field visit to collect a few pictures and depths measurements should be all that is needed to make reliable estimates of wetland surface water storage.

3.6.5 *Implications of study results*

The results of our study provide some simple tools that enable surface water storage in beaver ponds to be estimated without the need for topographic surveys. This allows environmental managers to better assess the risks and benefits associated with beaver ponds that appear on landscapes, and allows the easy inclusion of the surface water storage component of beaver ponds into hydrological models at various scales. This study also demonstrates that beaver pond morphometry is different than other types of wetlands, which requires consideration. For example, based on this analysis we might expect beaver ponds to reach their capacity faster during rainfall events, while impounding larger surface areas than depressional wetlands. Although we show that some beaver ponds store less surface water than other wetland types, their relevance to local and regional water balances should not be underestimated. Beaver population recovery, post fur trade, has led to the creation of between 9,494–42,236 km^2 of new beaver ponds globally (Whitfield et al. 2014). Using Whitfield et al.'s (2014) estimates and our median c coefficient (0.91) and median dam height (0.83 m) in Eq. (3.12), we crudely estimate that between 2.5 and 11 km^3 of water are stored in beaver ponds.

3.7 Conclusions

The primary goal of this study was to test the utility of readily applicable tools for estimating surface-water storage in beaver ponds. We examined whether the Simplified V-A-h method was appropriate for this purpose and described beaver pond morphology to explore its relationship to surface water storage capacity. A number of valuable insights were revealed. The Simplified V-A-h method proved to be a simple and effective tool as it was able to estimate beaver pond surface water storage with an average volume error of 5%. The median basin coefficient for beaver ponds was 0.91, suggesting that they tend to have a convex basin morphometry, and that they typically store less water than other wetlands studied in the same way. Pond capacity was strongly correlated to the dimensions of the dam and surface area of the pond, further cementing the idea that beaver ponds exhibit characteristic traits in pond morphometry that make reliable estimates of surface water storage possible without the need for topographic surveys. Future research efforts should be directed at applying these simple methods more remotely, and incorporating them into both broader beaver-related planning tools and catchment-scale hydrological models.

4. Mineral-Sediment Trapping in Beaver Ponds Lowers the Organic Fraction of Peat[3]

4.1 Preface

Beaver dams alter hydrological processes at the surface, which has profound impacts on surrounding soils. In mineral/riverine soil environments, beaver dams introduce nutrients and sediments to the soil matrix and change the production and decomposition rates of organic matter. Over a beaver dam's lifecycle, this process results in a net-accumulation of carbon. However, this research has never been applied to environments with organic soils. The goal of this chapter is to conduct a preliminary exploration of peatland beaver ponds at a regional scale to see whether processes reported in mineral systems also occur in peatlands. To achieve this goal, we ask the following questions: (i) are peatland soils underneath beaver ponds depleted in organic matter relative to the peatland areas not impacted by the pond, and (ii) are peatland beaver ponds sinks for mineral and organic sediments?

[3] This work is included as a supplementary material for the manuscript submitted in Chapter 6 of this dissertation. Daniel Karran is the major contributor and lead author of this chapter. Carlie Elliott provided data, analysis and useful comments on the writing and structure of the chapter. Cherie Westbrook and Angela Bedard-Haughn were co-supervisors for this research, helping with the experimental design, providing data as well as useful comments and suggestions on the structure and writing of this chapter.

4.2 Abstract

Beaver ponds accumulate carbon in the mineral environments in which they are built, but whether they do the same in organic soil environments, such as peatlands, has yet to be shown. To investigate this, we sampled many beaver-inhabited peatlands in the western Canadian Rocky Mountains. We looked at differences in the organic matter content between peat soils inside and outside the area inundated by beaver dams. We also used a simple mass-balance approach to test whether peatland beaver ponds can function as sinks for suspended sediments (both mineral and organic). Our results show that peat soils underlying beaver ponds or in beaver meadows are significantly depleted in organic matter relative to the peat that is undisturbed. Furthermore, significantly more suspended sediments entered the beaver ponds than exited, indicating that beaver-mediated sediment aggradation in peatlands is an important process to be considered. Overall, our results suggest that the processes elicited by beaver ponds lowers the organic fraction of peat bulk volumes and does not produce a net gain in carbon storage. Such findings have implications for carbon dynamics in peatlands where beaver are found.

4.3 Introduction

Beaver ponds have significant impacts on the carbon dynamics of the landscapes in which they are found. Even though they emit the most methane (CH_4) of all northern open water/wetland types (Wik et al 2016), beaver ponds are still associated with a net gain in soil carbon storage (Johnston, 2017). However, studies that show a net gain in soil carbon have been limited to mineral soil environments, and the impacts of beaver ponds in organic soil environments, such as peatlands, is lacking investigation.

In mineral soil environments, beaver ponds accumulate carbon as they transition through their lifecycle of being actively maintained ponds to highly productive beaver meadows. For example, in Voyageurs National Park, beaver-impounded soils had nearly twice the carbon than soils that were never impounded (Johnston, 2014). Carbon enters the pond as organic matter via the production of both aquatic/semi-aquatic (when ponded) and terrestrial (when meadow) plants (Johnston, 2001), and by transport from beaver activity and fluvial processes (Wohl et al., 2012). Carbon is released by the pond either as gaseous emissions to the atmosphere or dissolved organic carbon to the stream after anaerobic decomposition (Bridgham et al., 1998; Roulet et al., 1997;

Updegraff et al., 1995). Overall, losses to the atmosphere and stream do not offset what aggrades in ponds of mountain headwater streams (Wohl et al., 2012) and is produced in meadows of low-gradient inland basins (Johnston, 2014).

Beaver ponds are also common features in peatlands (Loisel et al., 2017), where they are reported as hotspots for carbon dioxide (CO_2) and CH_4 release (Bubier et al., 1993). Combined emissions of CO_2 and CH_4 from a peatland beaver pond in Ontario amounted to over 200 g C m^{-2} yr^{-1} (Roulet et al., 1997). These studies and others (e.g. Weyhenmeyer 1999) assume that the source of these emissions is the carbon rich peat underlying the ponds; however, the source has yet to be shown and, if true, peatland beaver ponds may be carbon-losing systems unless they function like their mineral soil counterparts. A key difference between peatlands and mineral soil environments is that peatlands already store significant volumes of soil carbon prior to their impoundment by beaver (Loisel et al., 2017).

There is evidence to support the notion that peat soils underneath beaver ponds are depleted in carbon relative to the rest of the peatland not impacted by ponds. For example, Johnston (2017) found that an organic soil extracted from a Minnesota beaver pond had less than half the carbon per unit volume at the surface than it did at depth. This finding is consistent with that of Updegraff et al (1995) and Bridgham et al (1998) who also report organic beaver meadow soils depleted in carbon. These studies attribute their findings to enhanced aerobic and anaerobic decomposition of more labile substrates, but this may oversimplify the full story. It is also possible that the addition of foreign sediments diluted the carbon concentration on a per-volume basis, (Loisel et al., 2014) and further enhanced decay and turnover processes (Broder et al., 2012; Wang et al., 2016a). In mineral soil environments, sediment aggradation is a well-established component of the beaver meadow formation theory (Correll et al., 2000; Maret et al., 1987; Naiman et al., 1986; Ruedemann and Schoonmaker, 1938), but whether this occurs in low energy peatland streams has not been tested. Hence, the purpose of our study is to identify if and how beaver ponds may be impacting peatland soils at a regional scale. To do this, we ask the following questions: (i) are peatland soils underneath beaver ponds depleted in organic matter (OM) relative to the peatland areas not impacted by the pond, and (ii) are peatland beaver ponds sinks for mineral and organic sediments?

4.4 Methods

4.4.1 Sampling strategy

To meet our objectives, we sampled numerous beaver-impacted peatlands in the Montane Cordillera ecozone of western Alberta, Canada (Fig. 4.1). Sampling locations were selected from previous work that detailed beaver-impacted peatlands in the area (Morrison et al., 2015), and one of the sites, the Sibbald Research Wetland (SRW), was selected for intensive sampling. A site was chosen if the soil could be classified as Organic (i.e. at least 40 cm of peat comprised of >30% organic matter by weight) as outlined by *The Canadian System of Soil Classification* (ACECSS, 1998), and if there was evidence of recent or current beaver activity such as dams/ponds. In total, 19 beaver-impacted peatlands were selected, inclusive of the SRW. Soil and water samples were collected from each site and analyzed for OM content and suspended sediments, respectively.

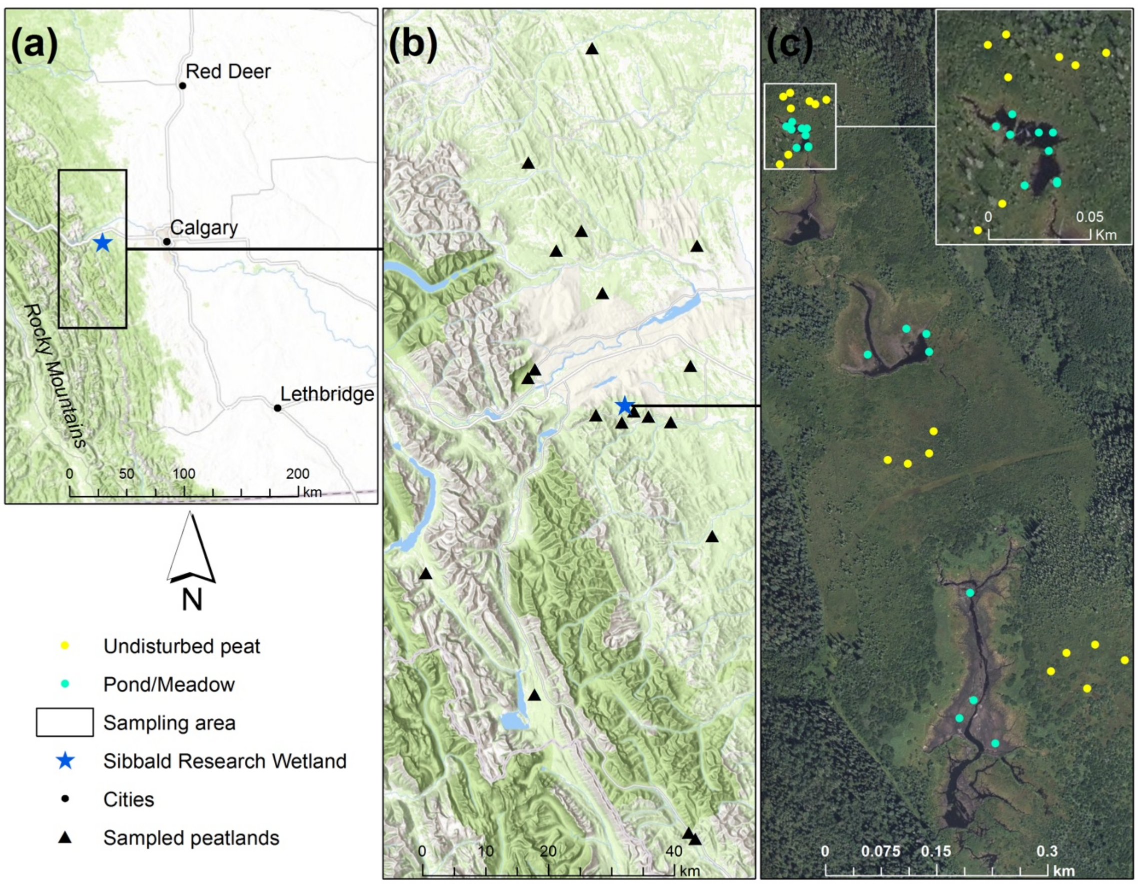

Fig. 4.1 Map of the study region (a), the location of the sampled peatlands (b), and the location of intensive sampling at the Sibbald Research Wetland (c).

4.4.2 Sampling locations

Regional sampling of peatlands was spread out across the entirety of Kananaskis Provincial Park and three different Municipal Districts, where the topography ranges from glaciated mountain valleys in the west to rolling foothills in the east (Fig. 4.1). Intensive soil sampling was conducted at the SRW, a rich through-flow fen in the Kananaskis region (Front Range) of the Canadian Rocky Mountains, approximately 70 km west of the city of Calgary (Westbrook and Bedard-Haughn, 2016). The stratigraphy of the SRW peatland is variable, with peat depths ranging from 0.5 to 7 m, and is underlain by an unquantified amount of clay and alluvium. Multiple intermittent inlet channels feed Bateman Creek, which is a low grade (~1.2%), second-order tributary that drains the peatland. Beavers (*C. canadensis*) have constructed dams at numerous locations along Bateman Creek and there are currently several beaver ponds visible on the landscape.

4.4.3 Organic matter content

At each of the of sampling locations, two shallow peat cores (both 50-cm long) were extracted with a Russian-type peat corer to test the difference in OM between the pond/meadow and the peatland area undisturbed by beaver dams. The first core was taken from the pond and the other core was taken from the adjacent peatland. If the site had active beaver ponds, the pond core was taken from within the ponded area. If no ponds existed, the core was taken from the beaver meadow. The second core was taken from the peatland interior, at least 15 m beyond the high-water mark created by the dam. Before each core was extracted, the surface vegetation was removed so that it did not confuse the OM measurements of the bulk peat below, which is the target of this study.

Organic matter content was measured with Loss on Ignition tests (LOI). Each core was split in half to create two sections (one from 0 to 25 cm depth and another between 25 and 50 cm depth). One sub-sample that encompassed the length of each section (~25 cm^3) was then weighed and dried in a drying oven at 105°C for 24 hours to remove all moisture. Samples were then reweighed and then ground into fine particles by mortar and pestle. The subsequent mixture was subsampled and placed into a muffle furnace at 550°C for 5 hours. After ignition, pre-and post-ignition weights were used to calculate the percentage of OM. Differences in OM content between the pond/meadow and undisturbed peat were determined using a Wilcoxon signed rank test in R.

The intensive soil sampling at the SRW was done with a soil auger, and to ensure that samples reflected the bulk peat accumulating in the lower layer of the profile, samples, 10 cm in length, were collected from within a range of 15 – 25 cm of the peat surface (with the surface vegetation removed). A total of 18 samples were collected from 5 different beaver ponds/meadows (3 ponds, 2 new meadows), along with 18 samples from 5 different areas of undisturbed peat. The same procedure for LOI was used to process samples collected from the SRW. Differences in OM content between the pond/meadow and undisturbed peat were determined using a Mann-Whitney U test in R.

4.4.4 Total, organic, and mineral suspended sediments

Water samples were collected at the inlet and the outlet of each beaver pond and analyzed for total suspended sediments (TSS), organic suspended sediments (OSS), and mineral suspended sediments (MSS). Only 15 of the 19 sites selected had active beaver ponds. Water samples were collected in one litre polyethylene containers and refrigerated at 4°C before analysis in the lab. Samples were then passed through 1.5 μm fibreglass filters using a vacuum filtration device. After filtration was complete, the filters were removed and dried in a drying oven at 105°C for two hours. Filters were then reweighed to calculate for TSS and then placed in a muffle furnace at 550°C for 5 hours. Once ignition was complete, filters were reweighed to calculate for MSS, where OSS is the difference between TSS and MSS. Differences in TSS, OSS, and MSS between the inlet and outlet of the ponds was determined using a Wilcoxon signed rank test in R.

4.5 Results

4.5.1 Organic matter content of beaver-impacted peatlands

There was a highly significant difference in OM content between peat in the pond/meadows and the undisturbed peat (i.e. non-beaver impacted) at both depth ranges (Fig. 4.2). Of the 19 peatlands sampled, only 14 had beaver dams still retaining water; therefore, 14 of the pond cores were extracted from beneath the pond surface and 5 were taken from an exposed beaver meadow. The undisturbed peat had higher OM content than the pond/meadow peat in all cases (19/19) in the upper 0 to 20 cm depth, and in 95% of cases (18/19) in the lower 20 to 40 cm depth. The lowest median OM content was found in the upper 20 cm of the pond/meadow cores, which increased by

8% with depth. The undisturbed peat cores had a considerably higher median OM content of 73%, which did not change with depth. Mineral layers were visually evident in many of the cores extracted from the ponds/meadows, but none were evident in the undisturbed peat cores.

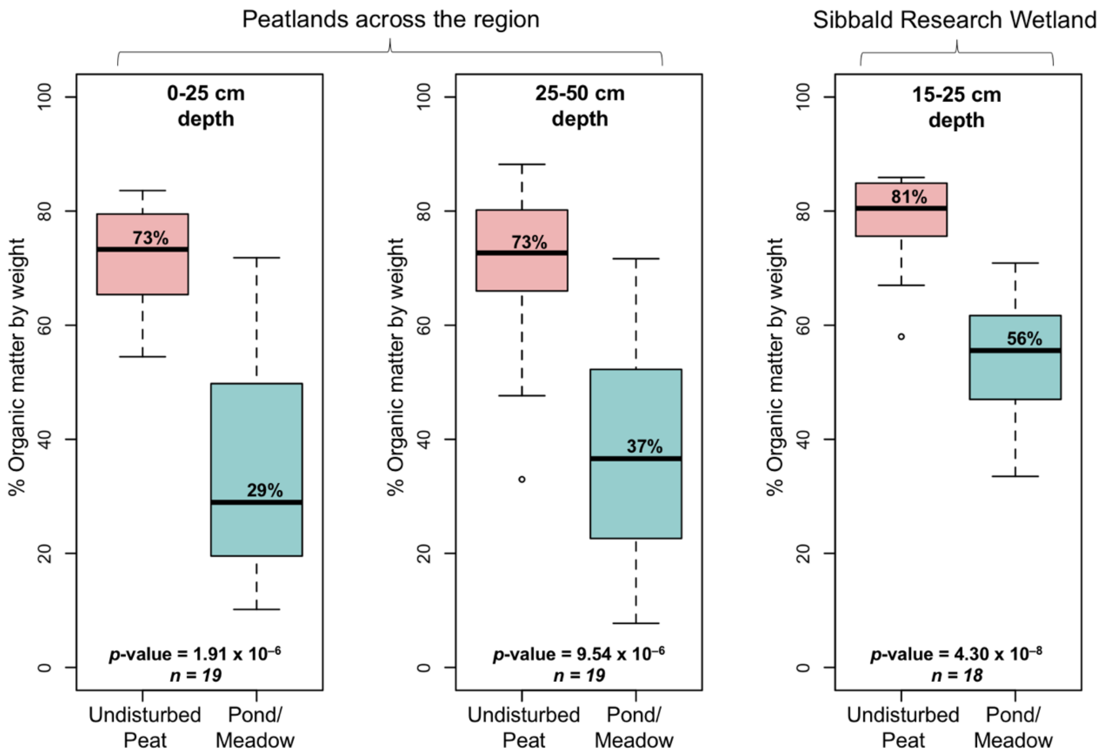

Fig. 4.2 Box and whisker plots of the organic matter content in both the pond/meadow peat and undisturbed peat of the regionally sampled peatlands and the samples collected at the Sibbald Research Wetland.

There was also a highly significant difference in OM content between the peat in the ponds/meadows and undisturbed areas of the SRW (Fig. 4.2). Median OM content in both areas of the SRW was higher than medians in the same areas regionally. Since the upper 15 cm of the peat is excluded from this sampling design, meaningful statistical comparisons to regional values are not possible. However, the upper half of the core (i.e. 0 to 25 cm) extracted from the undisturbed peat in the SRW had an OM content of 73%. This value is equal to the regional median of undisturbed peat from 0 to 25 cm (Fig. 4.2), which suggests that the SRW is a fair representation of peatlands in the region.

4.5.2 *The flow of TSS, OSS, and MSS through beaver ponds at a regional scale*

There was a highly significant difference between beaver pond inlet and outlet concentrations of TSS and a significant difference of OSS and MSS (Table 4.1). In 79% of cases (11/14), the TSS concentration was higher at the inlet than at the outlet of the beaver pond. Median TSS, OSS, and MSS at the outlet decreased by 72%, 57%, and 64% from the inlet, respectively. Organic and mineral fractions made up 51% and 49% of the inlet TSS, respectively, and 65% and 35% of the outlet TSS, respectively. A photograph of mineral sediment overtop peat in a beaver pond at the SRW is provided in Fig. 4.3.

Table 4.1 Differences in TSS, OSS, and MSS between the inlet and outlet of the beaver ponds sampled (n=14).

Variable	Location	Median concentration (g ml^{-1})	*p*-value (Wilcoxon signed rank test)	Average % of total TSS
TSS	Inlet	1.57×10^{-5}	1.3×10^{-2}	–
	Outlet	4.35×10^{-6}		–
OSS	Inlet	5.50×10^{-6}	6.4×10^{-3}	51
	Outlet	2.35×10^{-6}		65
MSS	Inlet	5.55×10^{-6}	1.6×10^{-2}	49
	Outlet	2.00×10^{-6}		35

Fig. 4.3 Photographic evidence of mineral sediment deposition on peat soil at Sibbald Research Wetland.

4.6 Discussion and Conclusions

Peat underlying the beaver ponds or in the beaver meadows had significantly lower OM content than the undisturbed peat in all the peatlands sampled regionally, and in the samples collected at the Sibbald Research Wetland. Furthermore, most of the beaver ponds sampled for TSS acted as sinks for both mineral and organic sediments. These findings suggest that although there are process similarities in how beaver meadows form in organic and mineral soil environments, the results, in terms of carbon storage, are different. Furthermore, reports of carbon depleted beaver meadows in the peatlands of Voyageurs National Park, Minnesota, weakens the notion that our findings are unique to the montane peatlands of western Canada. Like Johnston (2017), our stratified sampling design in the regional peatlands showed that the percentage of carbon is lower at the surface of the meadow than it is with depth. The addition of foreign sediments would partially explain this; however, it is more likely a combination of factors that alters the fraction of carbon in these areas.

Given our results, sediment aggradation in peatland beaver ponds has the potential to make considerable contributions to the peat matrix. If we assume the difference between the median TSS in the inlet and outlet of the beaver ponds (i.e. 1.13 x 10^{-5} g ml) is trapped, along with a typical peatland stream discharge of 0.5 to 1.8 m^3 s^{-1} (Candel et al., 2017; Holden, 2006), approximately 178 to 641 tonnes of sediment could aggrade in the ponds annually. Of this estimated mass, our results suggest that just under half would be mineral in origin (49%), which are more likely to become permanent additions to the underlying peat matrix as they are not susceptible to decomposition like the organic fraction. Assuming a particle density of 2.65 g cm^3, a typical peatland beaver pond could add ~33 to 118 m^3 yr^{-1} of mineral material to the affected area, similar to ranges reported in mineral soil environments (Butler and Malanson, 1995; Levine and Meyer, 2014; Pollock et al., 2007). This may explain mineral deposits found in peat cores near the periphery of beaver dams (Morrison et al., 2015; Wang et al., 2016a), but further work is needed to disentangle that which is beaver-mediated from that deposited by overbank floods in the absence of beaver dams (Candel et al., 2017). Moreover, sediment aggradation was not a significant process in all the ponds, demonstrated by the 21% of cases where TSS was not trapped. This agrees with Westbrook et al (2017), who found no visual evidence of mineral layers in the beaver-inhabited bogs and fens of Tierra del Fuego, Argentina. In such cases, the physiography of the peatland and source of the stream may not produce the energy required for sediment transport. Also, the age of the beaver dam may be a factor in how well the pond functions as a trap (Woo and Waddington, 1990).

In addition to lowering the organic fraction of peat bulk volumes, it is possible that the mineral sediments also enhance decomposition. Bridgham et al. (1998) found that carbon mineralization was strongly correlated with peat bulk density (r = 0.89) and advanced decomposition in peat soils has been observed near mineral layers deposited by atmospheric (Broder et al., 2012), fluvial (Wang et al., 2016a), and glacial processes (Comas et al., 2011). It is possible that the mineral sediments deposited during the pond phase speed up both aerobic and anaerobic decomposition by supplying extra electron acceptors. In terms of soil carbon storage, sediment deposition may be even more important after ponds wash out as lab incubations of beaver meadow peat show aerobic decomposition rates nearly double that of anaerobic ones (Updegraff et al., 1995). High CH_4 emissions from ponds are solid evidence that anaerobic decomposition occurs, but the amount coming from the underlying peat may be negligible. Considering that 51% of sediments trapped in the sampled ponds were organic, it is possible that much of the carbon emitted is transported from other areas of the peatland by moving water. Storm events flush waters into the stream that are enriched in both labile carbon substrates and dissolved organic carbon (Elder et al., 2000; Limpens et al., 2008). As this water becomes delayed by beaver ponds, some of the carbon is likely digested.

Overall, our results suggest that, unlike beaver ponds built in mineral soil environments, there is no apparent net-gain in carbon from peatland beaver ponds. Instead, beaver ponds promote sediment aggradation that may enhance decomposition. Such findings have implications for peatland carbon dynamics where beaver are found, and future work is needed to characterize the physical properties and processes that have contributed to peatland beaver meadow development over time.

5. BEAVER-MEDIATED WATER TABLE DYNAMICS IN A ROCKY MOUNTAIN FEN[4]

5.1 Preface

Beaver dams built along streams in mineral-soil landscapes do not only raise the stage of the stream, but also the adjacent water table. This has been reported by a few studies, but most reports are anecdotal or made with limited data. Studies that quantitatively show how beaver dams impact water tables over time do not exist. In peatlands, the water table is very near the surface and its height and stability are closely linked to the system's ability to function as a carbon sink. Thus, if beavers change peatland water table dynamics, they could ultimately change how the system functions as a whole. The goal of this Chapter is to address two questions: (i) do beaver dams raise water tables in peatland environments; and, (ii) do beaver dams stabilize water tables in peatland environments?

[4] Karran, D.J., Westbrook, C.J., Bedard-Haughn, A., 2018. Beaver-mediated water table dynamics in a rocky mountain fen. Ecohydrology. doi:10.1002/eco.1923. Daniel Karran is the major contributor and lead author of this manuscript. Cherie Westbrook provided data, helped with the idea formulation, and provided useful comments with regards to the content, structure and writing of the manuscript. Angela Bedard-Haughn also provided useful comments with regards to the content, structure and writing of the manuscript.

5.2 Abstract

Beaver dams are known to raise water tables in mineral soil environments, but very little is known about their impact in wetlands, such as peatlands. Peatlands tend to have shallow water tables, and the position and tendency of the water table to fluctuate (i.e. stability) is a factor controlling the system's ability to store carbon and water. Many peatland environments, especially fens, offer ideal habitat for beavers and the potential for beaver dams to influence this link by manipulating water table dynamics requires investigation. Our objective was to determine the influence of beaver dams on water table dynamics of a Rocky Mountain fen. We monitored water tables in the peatland for four years while beaver dams were intact and two years after they were breached by an extreme flood event. We found that, because of the unique way in which dams were built, they connected the peatland to the stream and raised and stabilized already high water tables within a 150-m radius. Beaver-mediated changes to peatland water table regimes have the potential to enhance carbon sequestration and the peatland's ability to respond to external pressures such as climate change. Furthermore, beaver dams increased surface and groundwater storage, which has implications for regional water balances, especially in times of drought.

5.3 Introduction

Peatlands store a substantial fraction of the global soil organic carbon pool (Loisel et al., 2017) because they develop in areas where hydrological inputs are greater than outputs and excess water inhibits the aerobic decomposition of organic matter (Clymo, 1984). This link between carbon and water storage is pivotal to understanding how these systems respond to external pressures and is the reason that much of the related scientific inquiry has been focused on water table controls (Menberu et al., 2016; Waddington et al., 2015). Some potential controls, however, lack thorough investigation. Such is the case with beaver dams, despite their presence in peatland habitats (Mitchell and Niering, 1993) and the profound hydrological impact that beavers are known to have in mineral soil environments (Westbrook et al., 2013).

Beavers need an abundant supply of deciduous shrubs and a reliable source of open water to survive (Gurnell, 1998); therefore, peatland habitat suitable for beaver colonization is generally limited to wooded bogs and fens (Loisel et al., 2017). Fens are often ideal for beavers as they frequently support the required vegetation and contain streams sustained by a steady supply of groundwater (Duval et al., 2012). These habitats are common in North America (Yu, 2006) and beaver are commonly found in them. For example, many Rocky Mountain peatlands are fens (Cooper et al., 2012) and 73% of those surveyed in Alberta showed evidence of beavers (Morrison et al., 2015). In South America, many of the montane fens of southern Patagonia have been colonized by invasive beavers since they were introduced to the region in the late 1940s (Westbrook et al., 2017).

Studies in mineral soil environments have shown that, above the ground surface, beaver dams increase surface water area and storage (Karran et al., 2017), thereby enhancing groundwater-surface water interactions (Majerova et al., 2015; Puttock et al., 2017). This can induce changes below the surface by raising water tables such that groundwater flowpaths readjust and more recharge to underlying aquifers is possible (Lowry, 1993; Westbrook et al., 2006). Increased water storage, both above and below the ground surface, is the mechanism by which beaver dams augment high and low streamflows (Pollock et al., 2003; Puttock et al., 2017). Whether beaver dams have similar impacts in wetland ecosystems, such as peatlands, has yet to be shown.

In contrast to mineral soil environments, peatlands tend to have shallow water tables that are spatially/temporally variable and vulnerable to climatic variation (Duval and Waddington, 2011). Such variation has not only hydrological implications, but also ecological, as spatial patterns of vegetation are affected (Sulman et al., 2010). For example, moss and graminoid plant cover typically favours a high and stable water table, where the opposite is true for shrubs (Breeuwer et al., 2009; Waddington et al., 2015). Markedly different rates of litter production from these different plant assemblages plays a key role in peatland carbon sequestration (Belyea and Baird, 2006; Tuittila et al., 2012), as does the rate of litter decay, which is further influenced by water table position and stability (Chen et al., 2012; Whittington and Price, 2006).

Shifts in peatland plant assemblages have been reported after the construction of beaver dams, but connections to the water table have been purely anecdotal (Mitchell and Niering, 1993; Walbridge, 1994). Empirical studies that quantitatively show how beaver dams manipulate water tables in peatlands do not exist. The purpose of our study is then to determine if beaver dam construction in a peatland environment can be expected to have any influence on water table dynamics. Because peatland water tables are already so high, we hypothesize that the impact of beaver dams is minimal and limited to the spatial extent of the pond. Given a study design of ‘intact’ and ‘breached’ beaver dams, we address two questions: (i) do beaver dams raise water tables in peatland environments; and, (ii) do beaver dams stabilize water tables in peatland environments?

5.4 Methods

5.4.1 Study Site

Studied was the northern half of the Sibbald Research Wetland, a rich, flow-through fen in the southern Canadian Rocky Mountains, ~70 km west of Calgary, Alberta (Westbrook and Bedard-Haughn, 2016). The peatland developed in an unconstrained valley bottom underlain by alluvium and the sandstone of the Wapiabi formation. The peatland surface gradually slopes (1.2%) towards the southeast, covering an area of ~1.3 km^2 (Fig 5.1). The peatland forms the headwaters for Bateman Creek, a small second order stream that bisects the peatland and flows into the Bow River, which serves as a water supply for Calgary and surrounding area. The streamwater inputs are a combination of spring snowmelt, rain and groundwater. Climate normals (1981-2010), retrieved from Environment and Climate Change Canada’s Kananaskis weather station ~17 km west of the study site (station #3053600; ~1391 masl), report monthly temperatures ranging from -6.1 to 14.5 ˚C for January and July respectively, and annual precipitation of 639 mm, with 63% falling as rain mostly in June. Vegetation communities vary within the peatland and are primarily dominated by shrubs (e.g. *Salix* spp. and *Betula pumila*), sedges (*Carex* spp.), brown mosses (e.g. *Drepanocladus* spp. and *Scorpidium* spp.), and clusters of dwarf black spruce (*Picea mariana*). Peat depth is variable (Fig 5.1), and reaches depths upwards of 6.5 m. Saturated hydraulic conductivity (K) tested from numerous (n = 48) piezometer nests (i.e. one well and three piezometers) shows a K between 10^{-6} to 10^{-3} m/s in the wells, and a K that consistently ranged between 10^{-8} to 10^{-5} m/s at depths of 0.5 to 1.4 m in the piezometers (Janzen and Westbrook, 2011). Range differences in K between wells and piezometers is attributed to the more permeable peat near the surface, typical of most fens (Duval and Waddington, 2012).

5.4.2 History of beaver activity at the site

The trapping and subsistence hunting of beavers in and around the study site during the early 20th century are well documented (Binnema and Niemi, 2006), and is a probable reason that no beaver activity is apparent on the 1949 air photos. By 1958, however, beavers had returned to the peatland, as evidenced by several beaver ponds along Bateman Creek. Air photos from the subsequent decades (1966–2008) confirms that beavers remained very active in the peatland, maintaining a series of 15 to 20 dams. Some dams washed out or were abandoned during this period, but the largest ones persisted. However, in June 2013, a major flood event, caused by heavy rain on snow (Pomeroy et al., 2015), swept through the basin, breaching the active dams and displacing the resident beaver colony from the immediate area. By September 2015, there was no field evidence that beavers had returned to the site to repair any of the dams. Seven of the largest beaver ponds were surveyed in 2015 with a Leica GS15 real time kinetic GPS and combined with a LiDAR dataset collected in 2006 when the ponds were full (Fig 5.1). To document changes in beaver habitat pre- and post-flood, the cumulative surface area of beaver ponds within the study area was calculated from available aerial and satellite photos in ArcGIS (i.e. 2008, 2014, 2015).

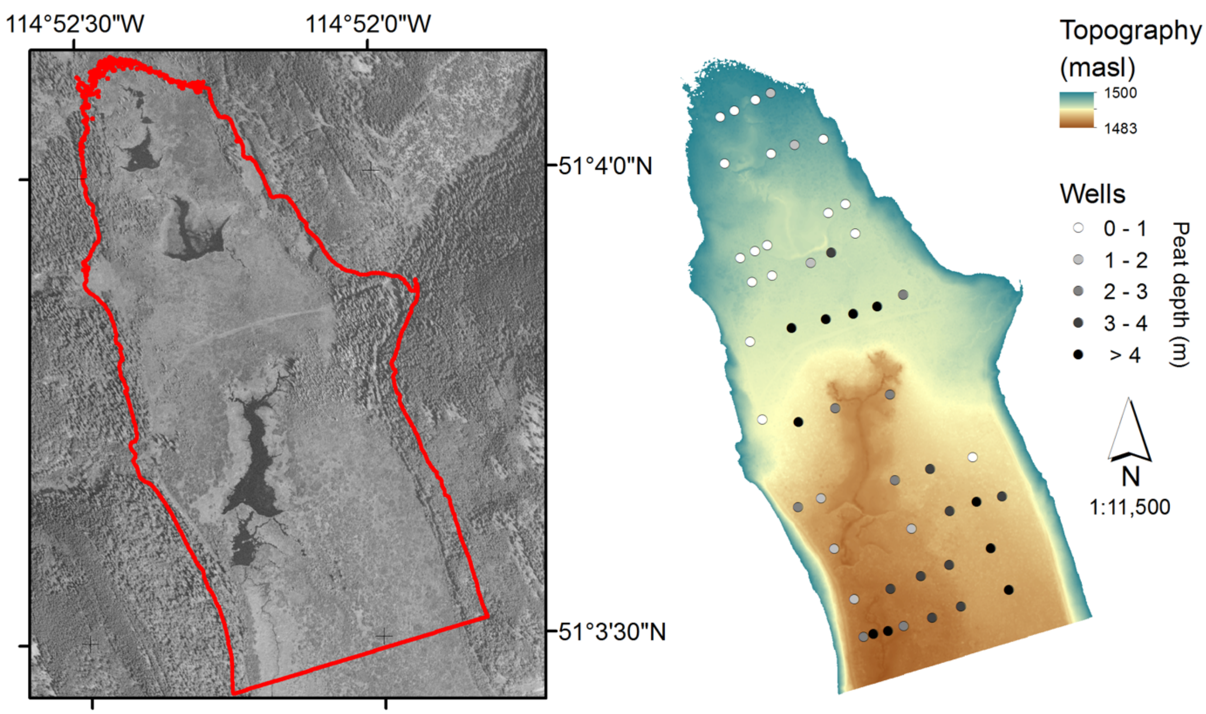

Fig 5.1 Satellite photo from 8 August 2008 of study site (left) and digital elevation model of peatland (right) with the location of wells in the well network. Wells are shaded relative to the depth of the peat measured at each location.

5.4.3 Well network

A network of 50 shallow wells was installed within the northern half (~0.57 km^2) of the study area in 2006 to monitor groundwater levels. The wells were installed in transects perpendicular to Bateman Creek across the width of the peatland. Four surface water wells were also installed in the largest beaver ponds to monitor pond stage. The wells were constructed with slotted 4-cm diameter PVC pipe wrapped in mesh tape, and installed with a hand auger to 0.6-1.5 m depths depending on the thickness of the peat and the range in the water table position. Peat depths were recorded at the time of installation by auguring down to the underlying alluvium. UTM coordinates and corresponding elevations of each well were taken with a Leica GS15 real time kinetic GPS. The water levels in the well network were monitored ~weekly June-September of 2006, 2007, 2008, 2009, 2014, and 2015. Groundwater levels were measured as per Westbrook et al. (2006). If a well was dry when measured, that measurement was not included in further analyses.

5.4.4 Climatic variability

Climate is often the primary allogenic (external) control on peatland water table dynamics (Waddington et al., 2015; Whittington et al., 2007). To represent climatic influence over the study period, a Standardized Precipitation Index (SPI) (Mckee et al., 1993) was created for each of the years using the SPEI package in R (Vicente-Serrano et al., 2010). To create the index, monthly precipitation for 1940-2015 was used from the Kananaskis meteorological station described in section 2.1. To fully capture wet/dry conditions during the summer season and account for hydrologic memory of the system (Shook and Pomeroy, 2011), SPI values were calculated for 4-, 6-, and 12-month periods ending 30 September of each year that well data were available. Cumulative precipitation for each field season (1 June – 30 September) was also calculated.

5.4.5 Groundwater flow characteristics

The ground elevation of each well was used to convert measurements of $WT_{i,j}$ to units of hydraulic head ($h_{i,j}$) in meters above sea level (masl). Seasonal head in each well was represented by the median h_i for all j through each year's summer season (i.e. 21 June – 21 September). The 'spline' algorithm in ArcGIS (ESRI, 2015) was used to create annual water table surfaces from all of the points in the well network, including those in beaver ponds. Changes to hydraulic head before and after the 2013 flood were analyzed by subtracting the seasonal water table in the driest year pre-flood from the seasonal water table in the driest year post-flood. Dry years were identified based on their SPI ranking. The LiDAR dataset was also subtracted from each seasonal water table surface to provide a visual effect of the proportion of water residing above the land surface during each period.

5.4.6 Water table dynamics

Water table dynamics were analyzed in the 50 groundwater wells. Of primary interest was the position of the water table, and its stability, a measure of the tendency of the water table to change position over time. Water table position ($WT_{i,j}$) is measured relative to the land surface in the i^{th} well on the j^{th} day, whereas stability is represented by the distribution of water table fluctuations. Water table fluctuations are calculated as:

$$\Delta WT_{i,j} = WT_{i,(j+1)} - WT_{i,j}. \quad (5.1)$$

Although the well network was monitored on a weekly basis, subsequent time steps (i.e. between j and j+1) were not always equal; some were longer/shorter given weather and/or other logistical constraints pertaining to work in the field. We assumed that the autogenic (within-peatland) feedbacks at each well-site change little over the study period, and that all the wells are subjected equally to the same external forcing (i.e. climate). These two assumptions negate the importance of having uniform time steps because each value of $\Delta WT_{i,j}$ is affected by the same set of external climate forcings over each interval.

5.4.6.1 Functional well groupings

Wells were divided into functional groups to reflect the primary goal of this study – determining beavers' influence on water table dynamics. The annual data sets were first partitioned into periods with intact (2006, 2007, 2008, 2009) and breached (2014, 2015) beaver dams. Then, datasets were further divided into groups based on their shared proximity to beaver dams and the stream (i.e. Bateman Creek). The reason for this subgrouping was to parse out the hydrologic influence of each as studies have shown that streams can influence water table position and stability in fens (Duval and Waddington, 2011). Beaver dam proximity was determined as the distance of a well from the location where each dam intersects the stream and impedes the main vector of streamflow. We chose this location because it is the point of the beaver-created hydraulic break in the stream channel. Proximity to the stream was calculated by measuring the shortest distance to Bateman Creek from each well. Wells located within 50, 75, 100, 125, and 150 m of beaver dams were grouped together, respectively, and wells within the same distance to the stream were similarly grouped. As no new information was provided by groups within 100 and 125 m proximity (of both beaver dams and the stream), these groups were dropped from subsequent analyses.

Exceedance Probability Curves (EPCs) were created from the distributions of well-head data for individual wells and for the various well groupings. Each EPC was calculated at quantiles of 0.5%, to give a set of exceedance probabilities (E_k), where k = 0.5,…..,100 and E_{50} is the sample median. Further, EPCs were created for each functional group, and the E_{50} was compared among EPCs to determine changes in water table position. Density plots were also created to provide visual evidence.

5.4.6.2 Water table stability

Water table stability was analyzed for each groundwater well. Quantitative definitions of water table stability depend on the goals and the geographic/geologic setting of an individual study. For our purposes, we define water table stability in a way that is ecologically meaningful for peatlands. Thus we use the median absolute deviation (MAD) of $\Delta WT_{i,j}$ values for each well because distributions are non-normal and MAD is more robust to outliers than the standard deviation. Numerous studies have shown that peatland form and function is impacted when annual water tables fluctuate >20 cm (e.g. Breeuwer et al., 2009; Duval and Waddington, 2011; Granath et al., 2010; Whittington and Price, 2006). For example, Menberu et al. (2016) showed that the optimum fluctuation for rich fens is ~8 cm. Conservatively, we categorized water table stability as high when MAD was 0–10 cm, medium when MAD was 10-15 cm, and low when MAD was >15 cm).

To scale values of $\Delta WT_{i,j}$ so that wells could be compared, each value of $\Delta WT_{i,j}$ was presented as a proportion by dividing it by the absolute maximum water table fluctuation observed in the corresponding well (i) over the entire six-year period:

$$Fp_{i,j} = \frac{\Delta WT_{i,j}}{\max\left|\Delta WT_{i,*}\right|}\,. \tag{5.2}$$

For each well, sets of $Fp_{i,j}$ were grouped into years with intact and breached beaver dams, as outlined in section 5.4.6.1. To test whether water table stability exhibits a regional dependency on beaver dams, semivariograms of well MAD values were created for each group using the distance to beaver dams as predictor variables. Spherical semivariogram models were fitted to data that were linearized by log-transforming MAD values and taking the square root of the dam distance. A 68-m lag interval was selected for semivariogram analysis as it was the lowest interval, greater than the average nearest neighbor well distance of 57 m, that created bins with at least 30 pairs (Olea, 2006). Semivariograms were constructed using the GSTAT package in R (Pebesma and Wesseling, 1998).

EPCs were also created for wells in each group and the Kolmogorov-Smirnov (KS) test was used to determine significant differences (i.e. $\alpha \leq 0.05$) between the curves. The KS test was chosen because it does not require any prior assumptions about the sample distribution and because it is robust to outliers (Kroll et al., 2015). The Bonferroni correction was first applied given the high number of tests ($n = 50$), meaning a significance of $\alpha/50 \leq 0.001$ was required for statistical significance (Cabin and Mitchell, 2000). Changes to water table stability were further analyzed spatially in relation to climatic conditions, as described by SPI values. MAD values from the wettest and driest years with intact and breached beaver dams were spatially interpolated to create maps of water table stability using the 'spline' algorithm in ArcGIS (ESRI, 2015).

5.5 Results

The beaver dams that were active prior to the flood were composed primarily of peat excavated from the pond bottom and piled above the peat surface, then reinforced on their faces by beaver-cut branches. In this way, the large dams were analogous to berm-like structures that extended far beyond the stream channel. Dams ranged in size from 15 to 308 m long and 0.5 to 2 m high. Breaching occurred at the location of the stream channel and the rest of the structure remained intact. Relic dams from beaver ponds that washed out prior to the study period were observed throughout the area. Prior to the flood in 2008, beaver ponds covered ~ 2.67×10^4 m^2 of the peatland. By the summer following the 2013 flood, this value was reduced by 41% to 1.57×10^4 m^2, and by the summer of 2015, the beaver ponds covered only 21% (i.e. 5.67×10^3 m^2) of their pre-flood area (Fig 5.2).

Summers of 2008 and 2009 were the wettest and driest years of the study period, respectively (Table 5.1). Aside from the particularly wet 6-month period ending September 2008, the climate during the study period was average, denoted by SPI values between -1 and 1. The wettest and driest years with breached beaver dams were 2014 and 2015, respectively.

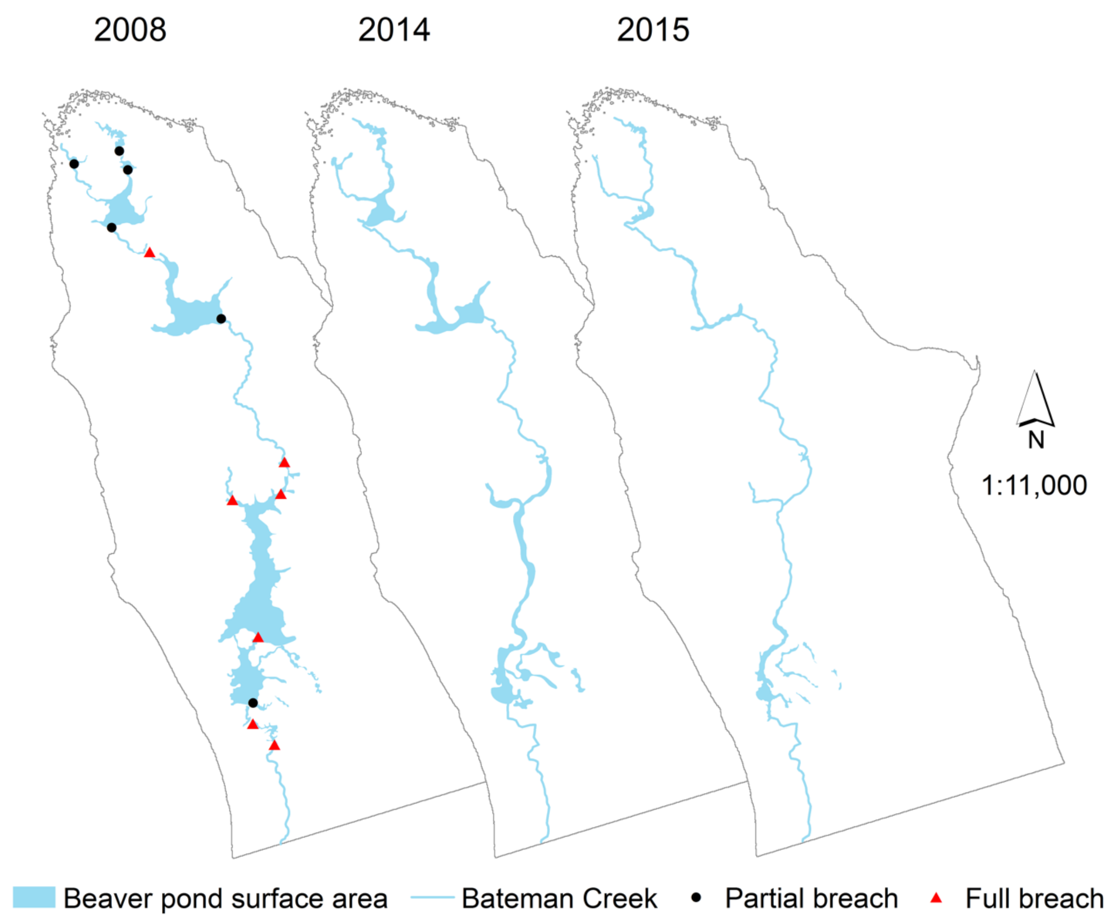

Fig 5.2 Location of dams that fully/partially breached during the 2013 flood and changes in pond surface area in the years following.

Table 5.1 Summer season precipitation and Standardized Precipitation Index (SPI) values for different scales ending 30 September of each year water tables were monitored.

Years	Precipitation (mm)	4-month SPI	6-month SPI	12-month SPI
2006	352	0.59	0.35	1.10
2007	397	0.99	0.95	1.17
2008	403	1.04	2.09	0.80
2009	246	-0.50	-0.60	-0.98
2014	329	0.38	0.65	1.05
2015	274	-0.19	-0.67	0.53

Changes to groundwater flow between the dry years of 2009 and 2015 (i.e. years with intact and breached dams, respectively) were localized around the beaver dams (Fig 5.3a). The general down-valley direction of groundwater flow was unchanged, but in the northern half of the study area, equipotential lines immediately downstream of dams changed from being mostly concave to convex, indicating that intact dams were redirecting more water away from the stream and into the peatland. Such changes are evident in the southern half of the basin, but the magnitude and lateral extent of the effect is dampened by the topographic relief. Hydraulic head was higher throughout the basin in 2009, except for the location of two alluvial fans in the northwest (Fig 5.3b). This change was greatest near the beaver dams and it gradually decreased with increasing distance away. Thus, the study area was much wetter when the dams were intact as a greater proportion of the water table resided above the land surface during that period (Fig 5.3c; 22.5% intact vs. 5.3% breached).

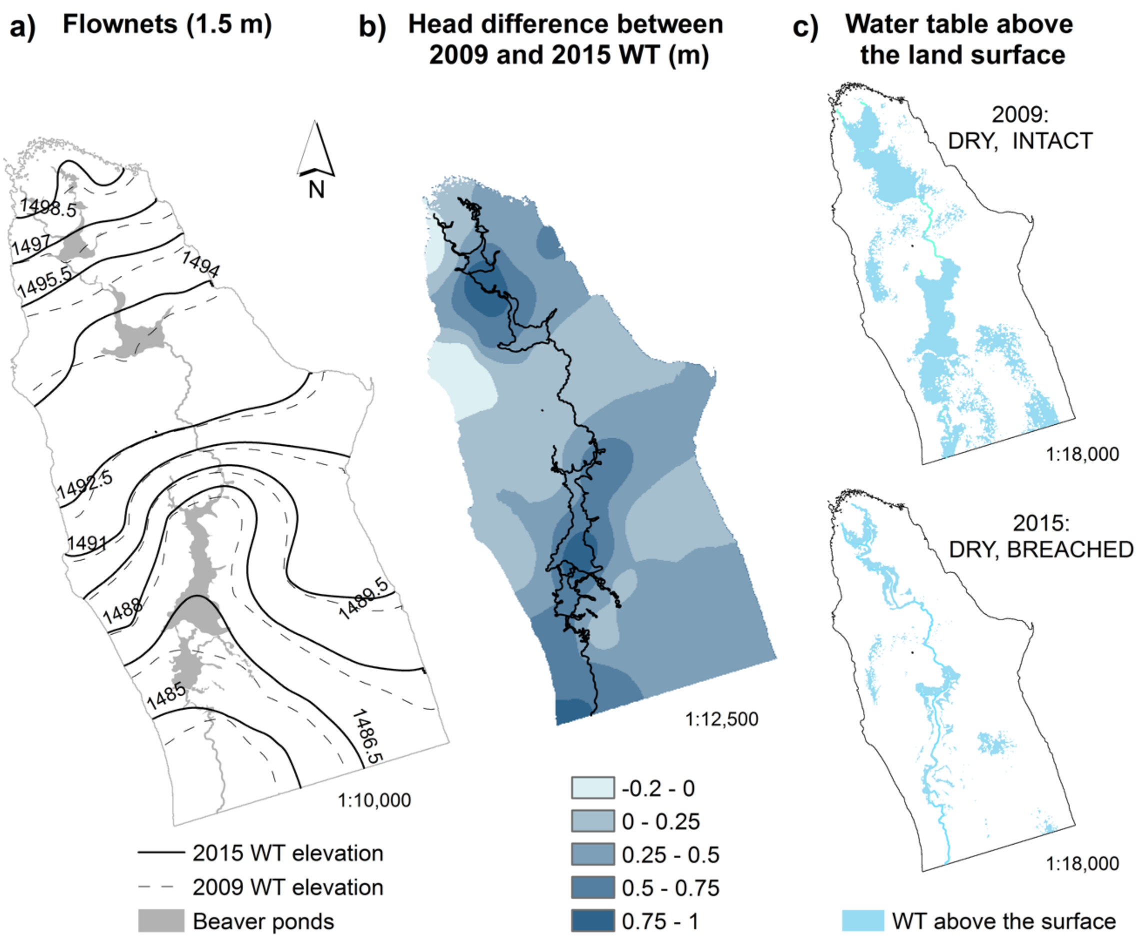

Fig 5.3 Groundwater flow nets (1.5 m) for the seasonal water table during the driest years with intact and breached beaver dams (a); the difference in head between seasonal water tables (b); and, the spatial distribution of the seasonal water table that resides above the surface of the peatland during the driest years with intact and breached beaver dams.

That the water table was higher when the dams were intact is supported by the summary statistics shown in Table 5.2. Although the range of data within each period is nearly the same, there is a considerable difference in how each dataset is dispersed. With intact dams, the water table tended to stay within ~ +5 and -20 cm of the surface of the peatland. Post-breach, however, the median water table position lowered 135% and the MAD nearly doubled.

Table 5.2 Summary statistics for water table positions in the groundwater well network grouped in the years with and without beaver.

Period	Min (cm)	Median (cm)	MAD (cm)	Max (cm)
Intact dams	-119.7	-7.3	12.2	18.0
Breached dams	-117.2	-17.2	23.2	17.3

Wells grouped by proximity to beaver dams had higher water tables than those grouped within the same proximity to the stream (Fig 5.4; Table 5.3). The higher water tables are most apparent in the years with intact dams at a 50-m proximity, where the difference between the dam and stream EPC is the greatest. In the first three quartiles, the stream EPC is < 5 cm below the dam EPC; however, in the upper quartile, the stream EPC diverges further below the dam EPC, reaching a maximum of 34.7 cm at the 88th percentile (i.e. E_{88}). The difference between the dam and stream EPC becomes smaller as the distance away increases but is still evident at 150 m.

Table 5.3 Median water table position (cm) ± MAD for the different groups of wells in the years with beaver dams and the years without beaver dams.

Grouping	Period	Proximity (m) 50	75	150
Beaver dams	Intact dams	-1.9 ± 6.1	-3.9 ± 7.6	-6.3 ± 10.8
	Breached dams	-15.3 ± 21.4	-17.6 ± 21.9	-17.6 ± 22.1
Stream	Intact dams	-3.6 ± 7.7	-4.7 ± 9.2	-6.3 ± 11.3
	Breached dams	-17.6 ± 24.6	-18.2 ± 23.3	-17.2 ± 23.2

After the dams breached, there was less difference between beaver dam and stream groups; the E_{50} of the dam and stream EPC was lower at all dam/stream proximities (Fig 5.4; Table 5.3). At 50-m proximity, the E_{50} of the dam EPC is lowered by 13.4 cm and E_{50} of the stream EPC is lowered by 14 cm. The difference between these two EPCs is still less than 5 cm in the first two quartiles; however, it increases to 15.7 cm at top of the third quartile (i.e. E_{75}), reaching a maximum of 23.2 cm at the 85.5 percentile ($E_{85.5}$). This indicates that, although still higher overall, wells within 50 m of the then breached beaver dams better resemble wells within 50 m of the stream, a phenomenon that becomes more striking as the distance away increases. Maximum difference of EPCs within 75 m is reduced from 12.1 cm to 6.8 cm and the maximum difference of EPCs within 150 m is reduced from 6.3 cm to 0.03 cm after the flood, indicating that the dams no longer have a substantive impact on water tables at this proximity. The E_{50} of the stream EPCs were all lowered to within 1 cm of each other and only slight changes can be detected between each distribution. Overall, intact beaver dams raised water tables and average of 12.8 cm higher within a 150-m radius.

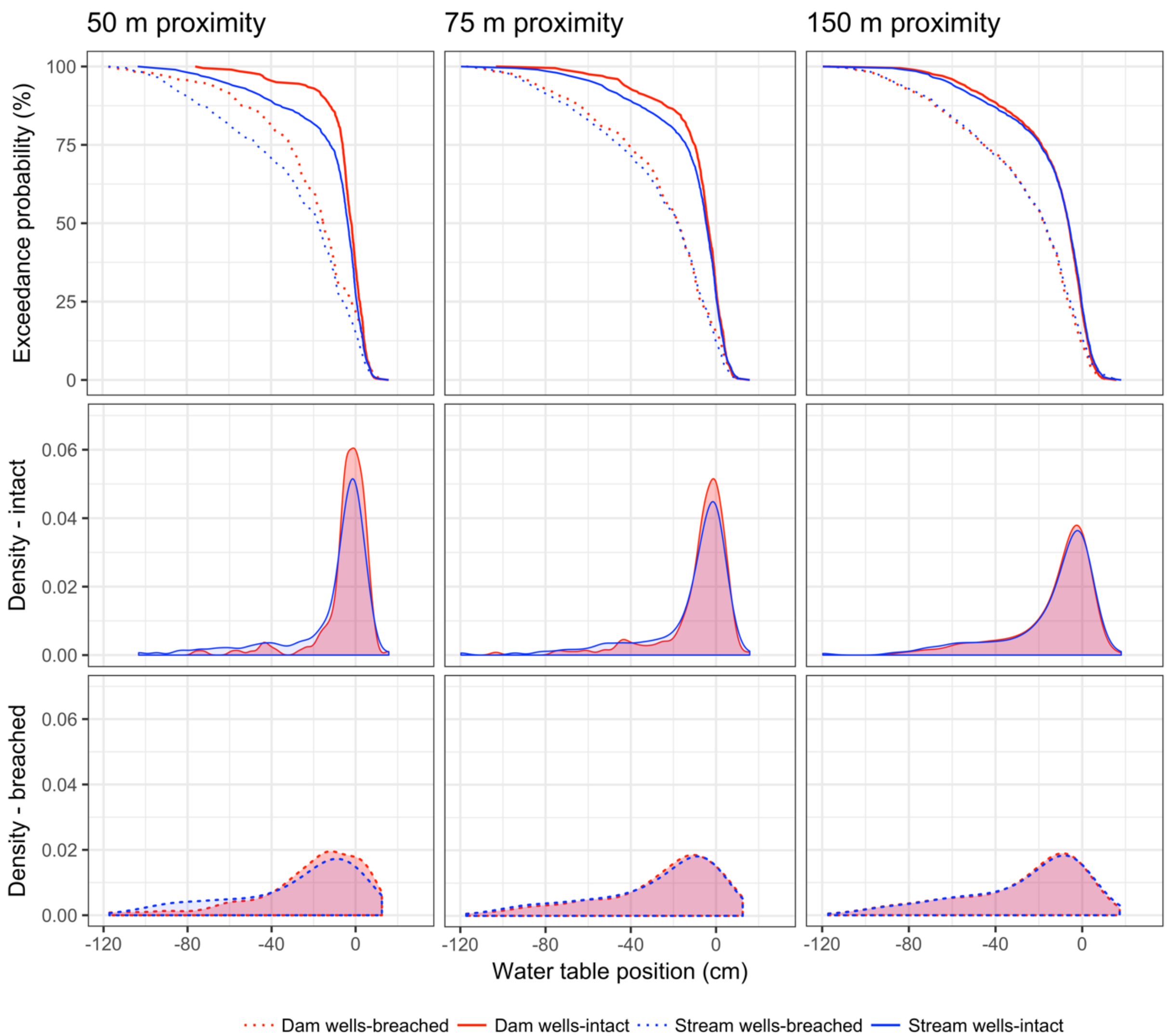

Fig. 5.4 Distributions of water table positions (cm) for the different groups of wells in the years with intact and breached beaver dams. Distributions expressed as exceedance probability curves (top) and density plots (middle and bottom).

Water tables are also more stable during the period with intact dams as evidenced by amplitude of the distributions (Fig 5.4) and the MAD values (Table 5.3). In the period with intact dams, water table stability decreases with increasing proximity to dams. The same is true for the stream wells; however, stability is higher in the dam wells, evidenced by lower MAD values. The density plots (Fig 5.4) show a slightly narrower distribution of water tables in dam wells vs. stream wells. In the years with breached dams, MAD values increased 3-fold for wells within 50-m proximity and increased over 2-fold for wells within 75-m and 150-m proximity. There is less difference between the dam and stream distributions at all proximities in years with breached dams, indicating that prior controls on water table stability are relaxed post-2013 flood.

A clear regional dependency exists between water table stability and the intact beaver dams, demonstrated by the semivariogram model (Fig 5.5a). With intact dams, the fitted semivariogram model has a sill of 0.58, nugget of 0.04, and range of 152 m. Post-Breach, the regional dependency still exists but the zone of influence is ~25% smaller, with a sill of 0.38, nugget of 0.06, and range of 115 m (Fig 5.5b).

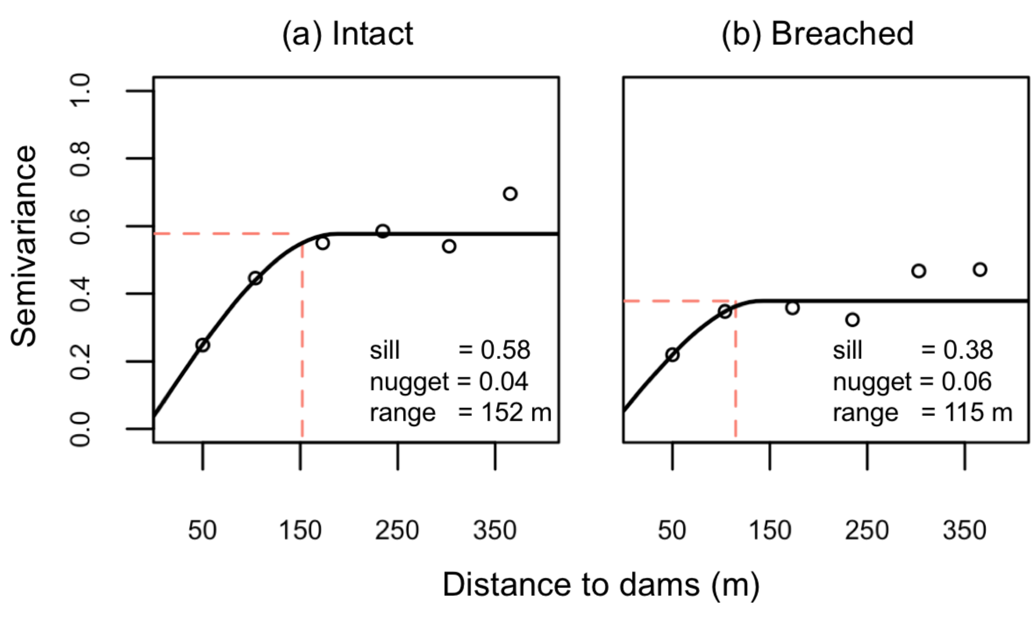

Fig. 5.5 Spherical semivariogram models for water table stability using the distance to beaver dams as predictor variables, when the dams were intact (a) and breached (b). The zone of influence boundary is denoted by the dashed red lines.

Water table stability between the years with intact and breached dams was significantly different in 23 of the 51 wells (Fig 5.6; P <0.001). All were within 150 m of beaver dams and comprised 90% of wells in the 50-m dam group, 93% of wells in the 75-m dam group, and 63% of wells in the 150-m dam group. Water table stability maps (Fig 5.7) showed that in 2008, the wet year with intact dams, 100% of the wells exhibit high WT stability (Table 5.4). In the dry year of 2009, 78% of the wells exhibited high stability and the number of wells with medium and low stability increased by 8% and 14%, respectively. Areas near the ponds tend to have stable groundwater tables, especially immediately downstream of the dams. The only exception was around the largest pond in the center of the peatland, where the adjacent land surface steeply slopes, rising nearly 2 m over a distance of ~20 m. In 2014, the wet year after the flood, the number of wells exhibiting high stability decreased by 16%, and the number of wells exhibiting medium stability increased by 12% despite it being a relatively wet year. Stability remained high to medium around beaver ponds that retained most of their water, but was medium to low around ponds where the dams breached and most of the pond water drained. By 2015, when beaver ponds only covered 21% of their pre-2013 flood surface area, only 38% of wells had high stability. No correlation between water table stability and peat depth occurred pre- ($R^2 = 0.009$) or post-flood ($R^2 = 0.003$).

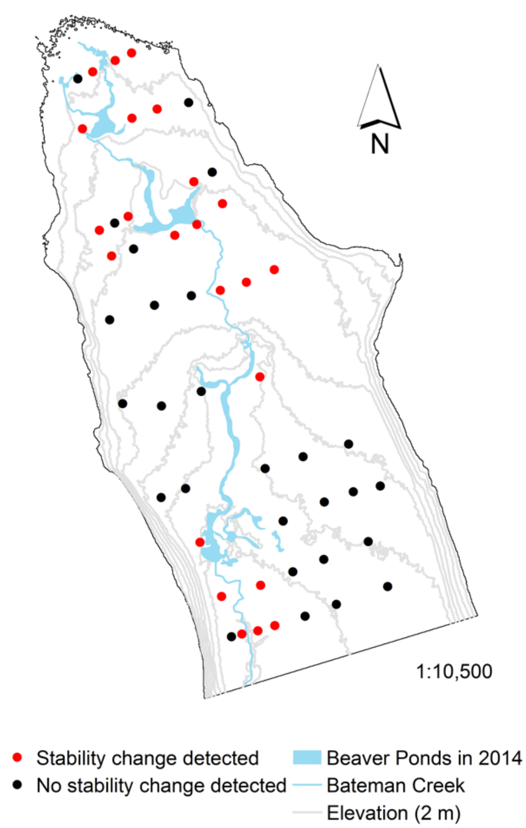

Fig. 5.6 Location of wells where changes in water table stability were detected post-breach after the flood. Pond surface area reflects area measurements from a satellite photo taken 20 September 2014.

Table 5.4 Number of the 50 wells experiencing low, medium, and high water table stability during wet and dry years with beaver and without.

Condition	Climate	Year	No. wells with stable groundwater hydrographs High (MAD: 0-10 cm)	Medium (MAD: 10-15 cm)	Low (MAD: >15 cm)
Intact dams	Wet	2008	50	0	0
	Dry	2009	39	4	7
Breached dams	Wet	2014	31	13	6
	Dry	2015	19	18	13

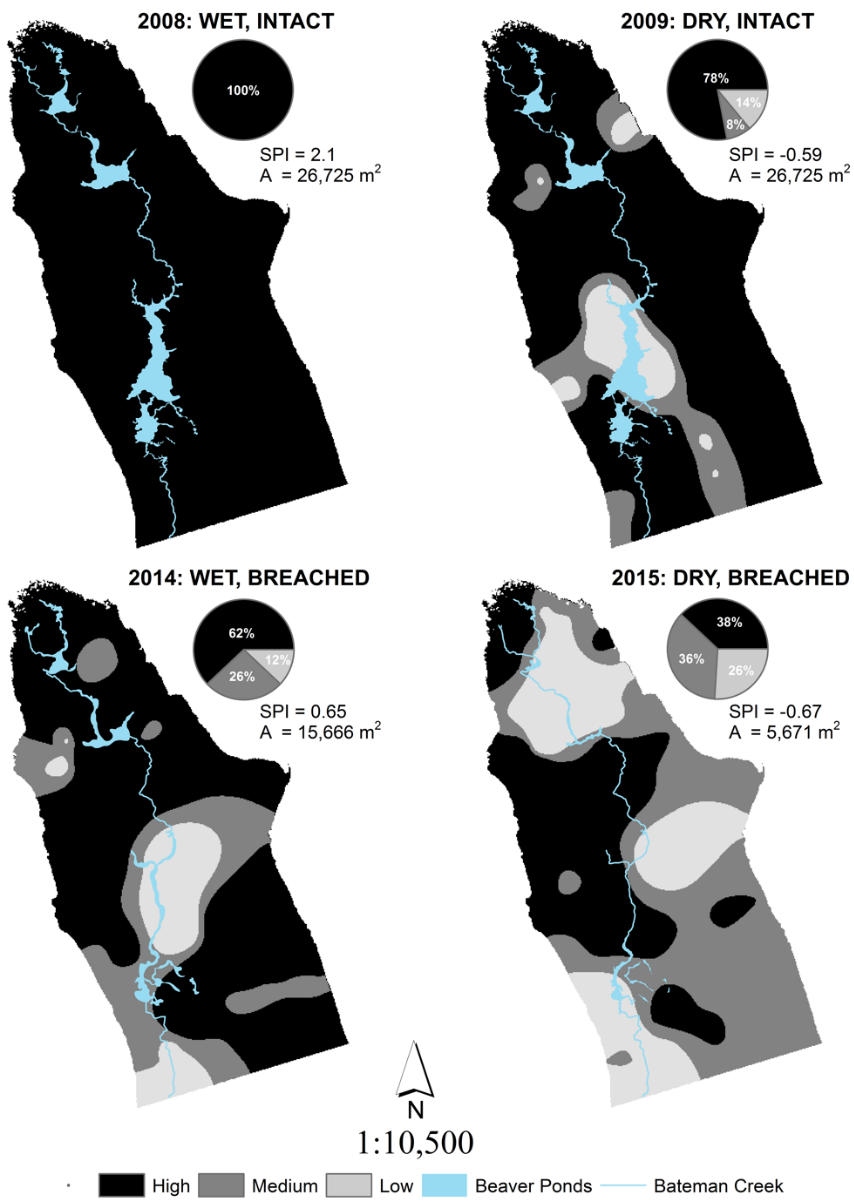

Fig. 5.7 Water table stability maps for wet and dry years with intact and breached beaver dams. Standardized precipitation index (SPI) values are for a 6-month scale (April 1 – September 30) and pond surface areas (PSA) were measured from satellite photos dated 8 August 2008, 20 September 2014, and 18 August 2015. No photo for 2009 was available and PSA for that year is substituted with 2008 observations.

5.6 Discussion

Contrary to our hypothesis, our results show that beaver dams can elevate and stabilize the groundwater table in wetlands, such as peatlands, even though water tables are typically near the ground surface. We observed that, within a 150-m radius of dams, the median water table was on average 12.8 cm higher and more than twice as stable during the period dams were intact. That beaver dams, or the lack thereof, were the cause of higher water tables is evident in EPCs and distributions of the various well groupings, and by the semivariogram models and locations of significant changes to stability. In the distributions with intact dams, there exists a clear signal (i.e. amplitude) that dampens as proximity from the dam/stream increases. After the dams were breached, this signal almost completely disappears – water table distributions for the dam groups are still slightly higher than the stream groups but the distributions for the stream groups are nearly identical at all proximities. This suggests that, in contrast to Duval and Waddington (2011), the stream appears to have little influence on water table position at this peatland and that pre-flood control was almost entirely being asserted by beaver dams. The same can be said for water table stability. Semivariograms show that when dams were intact, there was a clear regional dependency with water table stability at a range of 152 m. Post-breach, the partially breached dams still had some influence, but over a considerably smaller area, which is consistent with the significant changes to well distributions that were only detected within the 150-m beaver dam footprint.

The unique way beaver build dams in peatland environments is likely the mechanism by which they can raise water tables that already typically reside near the surface. Unlike dams built in mineral systems (Naiman et al., 1988), beavers not only dammed the stream channel, they also extended the dams by excavating peat and piling it above the land surface, as has been observed in Argentine fens where beavers are exotic species (Westbrook et al., 2017). Soil excavation by beavers in their native range has been reported, but primarily for developing burrows in stream banks (Meentemeyer et al., 1998) and for creating canal networks to provide safe access to food and lodging (Hood and Larson, 2015). By building dams in this manner, beavers created durable, berm-like structures. Given the reasonably flat topography of the peatland, the dams could inundate much larger surface areas than dams constrained by the stream channel alone (e.g. Janzen and Westbrook, 2011). Because of near surface water tables and the gradual slope of the peatland, dams typically decreased hydraulic gradients in upstream areas and increased hydraulic gradients in downstream areas. At the peatland scale, the modified gradients did not change the principal direction of groundwater flow, but it did change flow paths in and around the ponds. Due to their length and tendency to curve in many directions, some dams made lateral hydrologic connections within the studied area of the peatland, similar to that observed in mineral soil environments (Wegener et al., 2017). The new connections caused groundwater flow to be redirected away from the stream and into longer down-valley flow paths, consistent with the prediction of Janzen and Westbrook (2011). Contrary to reports in mineral soil environments (Lowry, 1993; Westbrook et al., 2006), we found no evidence of flow paths 'looping' back to the stream further down-valley. Thus, the beaver dams acted as focal points for groundwater recharge by hydrologically connecting the peatland to the stream and increasing hydraulic head throughout.

Water table stability was higher during the period with intact dams for a few reasons. First, when beavers actively maintain dams, they ensure that water levels remain at the dam crest (Woo and Waddington, 1990), sustaining hydraulic gradients and a reliable supply of water to the peat aquifer. Second, the water table was raised to a position in the peat profile that made it more resistant to fluctuation. The surface layer of peat is typically characterized by high specific yield, which steadily declines deeper into the profile (Kettridge et al., 2015). As such, water tables residing in or above the upper layer experience lower magnitude fluctuations as more water is required per unit area to induce a given change in water table depth (Holden et al., 2011). Our results show that, within ~150-m proximity of dams, water tables went from fluctuating in the upper 17-cm layer of the peat with intact dams to fluctuating in the upper 40-cm layer of peat with breached dams. Based on position alone, water tables residing within the intact dam range are inherently more stable. This change, although small, is hydrologically significant as transmissivity increases as the water table rises into peat layers with a higher K. The change is also ecologically significant as it can affect key ecosystem processes as described in the following section.

5.6.1 Implications of study results

Previous groundwater-surface water literature has explored the role of beaver in influencing the hydrology of mineral systems (e.g. Lowry, 1993; Westbrook et al., 2006). We extend that body of literature to peatlands. Our results have ecological and hydrological implications for mountain fens and other beaver-inhabited peatlands that share a similar physiography.

Beavers can have a rather impressive impact on water table dynamics in peatlands - supporting previous work that argued dams were responsible for raising the water table thereby causing shifts in vegetation (Mitchell and Niering, 1993; Walbridge, 1994). We further show that beavers stabilize the water table, which buffers the impact of climate induced variation and is a crucial factor controlling the growth of different plant assemblages. For example, peat-forming bryophytes and shrubs both tolerate only specific ranges of water table fluctuation (Breeuwer et al., 2009; Menberu et al., 2016), and combined with the macrophytes that grow in the area of the pond (Ray et al., 2001), beaver dams likely promote the development of peatland plant assemblages that are entirely unique. Thus, the legacy impacts of beaver habitation in peatlands may span across much longer time scales than that of periodic pond creation and abandonment. Higher and more stable water tables have been shown to increase carbon sequestration in mountain fens (Chimner et al., 2002), and enhance peatland resiliency to climate change. With regards to the latter, a recent concern is that moderate drops in water table position, expected with future climates, will cause vegetative shifts that increase the frequency of wildfire and thereby deplete sequestered carbon stocks (Kettridge et al., 2015). Scenarios like this might be mitigated by beavers, that not only raise and stabilize the water table, but also harvest the shrub vegetation more prone to ignite. Some of the net carbon storage may be offset by methane released from the ponds (Loisel et al., 2017), but this is likely negligible compared to an outcome where lowered water tables allow for increased oxidation of peatland carbon sinks (Ballantyne et al., 2014; Strack et al., 2008).

Beaver dams in peatland systems also increased both surface and groundwater storage in the basin. The beaver ponds themselves store sizeable volumes of water and even after dams breach, the structures left behind likely have enduring impacts on water storage and stormflow attenuation. The large ponds we surveyed persisted for over 60 years before partially or fully breaching during the flood of 2013. The location of the breach was limited to the stream channel and the rest of the dam was left intact. Based on the pond surface area measured (Karran et al., 2017), partially breached dams were retaining appreciable volumes of water post-flood in 2014. By 2015, dams fell into further disrepair (Hay, 2010; Woo and Waddington, 1990), but some water was still retained in the depressions left by excavation. In all cases, the berm-like structures remained on the landscape along with others that belonged to beaver ponds that washed out prior to the beginning of our study in 2006. This phenomenon of beaver dams remaining long after beavers have departed has been reported by other studies in the region (Toop and de la Cruz, 2002), and the persistence of these features suggests that they could trigger overbank floods during future peak streamflow events (Westbrook et al., 2011), thereby attenuating stormflow release downstream.

We estimate groundwater storage was enhanced by the beaver dams by 2.57 to 7.7 x 10^4 m^3 across the entire peatland (1.3 km^2), based on typical specific yields for peat of 0.2 – 0.6 (Hogan et al., 2006; Kettridge et al., 2015; Whittington and Price, 2006) and the basin-wide water table rise of ~9.9 cm. More water in storage means more water available for release as baseflow. Pollock et al. (2003) argued that, because of the high volume of water needed to augment streamflow during summer lows, it was more likely that a greater proportion of water was coming from aquifers recharged by beaver than by the surface water impounded behind the dam. Increased recharge would be of particular importance during times of drought (Hood and Bayley, 2008); especially since many low-order streams in the Canadian Rocky Mountains originate in peatlands inhabited by beavers (Morrison et al., 2015).

5.7 Conclusions

Our purpose was to determine the impact that beaver dams have on water table dynamics at the peatland scale. Dams made valley-wide connections between the stream and the peat aquifer, raising and stabilizing water tables to within 150-m radius. Beavers do this by using excavated peat to build durable, berm-like structures that, in some cases, spanned hundreds of meters across the basin. Like mineral systems, beaver dams have a significant impact on surface and groundwater resources in wet landscapes with shallow water tables. Beaver-mediated changes to peatland water table regimes have the potential to change plant assemblages such that carbon sequestration and the peatland’s ability to respond to external pressures like climate change is enhanced. Furthermore, beaver dams increased surface and groundwater storage, which has implications for regional water balances, especially in times of drought. Future research efforts should be focused on the transferability of these beaver-related impacts to other types of peatland environments where beavers are found (e.g. boreal forest). Considering the potential for beaver dams to alter peatland carbon sequestration, investigations via palaeohydrological reconstructions and ecohydrological models are needed to bring insight to the legacy impacts of beavers in peatland environments.

6. DISENTANGLING THE SOIL-FORMING FACTORS THAT DRIVE SPATIAL COMPLEXITY IN A BEAVER-INHABITED MONTANE FEN[5]

6.1 Preface

In riverine/mineral soil environments, beavers are agents of soil formation as their ponds accumulate nutrient-rich sediments that facilitate the creation of ecologically diverse beaver meadows after ponds washout. The extent to which this happens in peatlands is unknown. Peatlands differ from mineral soils in that they accumulate organic matter over time, storing a vast archive of the environmental conditions that impacted peat development thru history. The goal of this chapter is to interpret this archive in a peatland beaver meadow, as well as other areas of the peatland, to bring insight into how the soils forming factors vary at each location, and to further elucidate the role of beavers in the development of peatland soils.

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[5] Karran, D.J., Loisel, J., Von Ness, K., Westbrook, C.J.,Kohlmeyer, C., Bedard-Haughn, A., 2018 (submitted 6 March). Enduring effects of topographic constraints on peat development in a beaver-inhabited montane fen. Journal of Geophysical Research: Biogeosciences. Daniel Karran is the major contributor and lead author of this manuscript. Julie Loisel helped with the idea formulation, provided guidance with the methodology and the use of her lab, and provided useful comments with regards to the structure and writing of the manuscript. Kate Von Ness helped with the lab work and analyses. Cherie Westbrook helped with the idea formulation, and provided useful comments with regards to the content of the manuscript. Collin Kohlmeyer helped with the lab work and analyses. Angela Bedard-Haughn was the primary supervisor for this piece and provided useful comments with regards to the content, structure and writing of the manuscript.

6.2 Abstract

Carbon storage estimates from multi-proxy, paleo-reconstruction typically assume a uniform peatland represented by a solitary core. Rarely are multiple cores extracted from separate locations in the same peatland, where peat evolution varies because of different external pressures. Our goal was to bring insight into why peat accumulates more in some areas than in others, and describe the soil-forming factors and processes responsible for such spatial complexity. We extracted three cores from a montane fen, each representing different local environments in terms of plant community, hydrology, and peat depth. The cores were extracted from a beaver meadow, a riparian area, and a fen, away from a local stream. Testate amoebae were used to group core samples according to different environmental conditions, as interpreted through biotic and abiotic proxies. Topographic position and proximity to surface water features largely explained differences in timing of peat initiation and development of peat between sites. That said, regional climate exerted a primary control on peat properties and its biota, as synchronous shifts between dry and wet intervals were found across all three sites. The lowest amount of peat accumulated in the beaver meadow, where peat initiation was delayed and frequent inundation encouraged sediment deposits that enhanced turnover rates during dry periods. Turnover was also high in the riparian area, where high biogeochemical activity and unstable hydrology favored the growth of herbaceous vegetation that was easily decomposed. Peat accumulation was highest in the fen, where peat initiated sooner and strong internal feedbacks facilitated a relatively stable hydrology over time.

6.3 Introduction

Nearly a third of the global soil carbon pool is stored in peatlands (Gorham, 1991; Loisel et al., 2017; Yu et al., 2010), and whether these ecosystems will continue to do so under a changing climate is a question of scientific debate. The spatial distribution of peat on a landscape is the net-result of hydrological and biogeochemical processes interacting with localized autogenic (internal) and allogenic (external) controls over time (Waddington et al., 2015; Zehe et al., 2014). Such interactions are often interpreted from peat cores by means of multi-proxy analysis and paleo-reconstruction; however, these studies typically assume a uniform peatland represented by a solitary core (Bacon et al., 2017; Gałka et al., 2017). This approach fails to explain the spatial complexity in peat accumulation within peatlands, and experimental designs with such objectives are needed.

Peat development can be thought of in terms of the soil-forming factors, specifically: climate, topography, organisms, parent material, and time (Jenny, 1994; Yu et al., 2009). The climate, topography and parent material are especially important to peatlands as they dictate the water source and quality (Halsey et al., 1997), which in turn influences the makeup of organisms (i.e. flora and fauna) that accumulate into peat (Blodau, 2002). Over time, the balance between net-primary productivity and aerobic/anaerobic decomposition shapes the physical properties of the peat and determines how much carbon is stored (Loisel et al., 2017). The peat properties then act as internal controls, influencing water table behaviour as the peatland matures and/or is exposed to external pressures (Clymo, 1984; Waddington et al., 2015).

The properties of the peat and its prospective function are in a constant state of flux as multiple environmental factors exert varying levels of control. Not all areas of the peatland are exposed to the same external pressures and this is how spatial complexity manifests. For example, riparian areas within peatlands are subject to fluvial processes such as overbank floods (Candel et al., 2017). These areas are also biogeochemical hotspots (Hill, 2012) that are often inhabited by beavers (Gorham et al., 2007; Johnston, 2017; Morrison et al., 2015). Beaver activity in peatlands is still relatively unstudied, but there is strong evidence to suggest that it has enduring effects on peatland development.

Recurrent flooding of a fen by beaver dams in southwestern Quebec resulted in changes to plant community structure (Reddoch and Reddoch, 2005), and in a montane fen in western Canada, beaver dams raised and stabilized the surrounding water tables (Karran et al., 2018). Such changes are strongly linked to the ecological and biogeochemical processes that regulate fluxes of carbon to and from peatlands (Waddington et al., 2015). Furthermore, beaver ponds can trap sediments that alter the physicochemical properties of underlying soils (Correll et al., 2000; Ives, 1942; Maret et al., 1987). Sediment aggradation, coupled with the high carbon emissions reported from peatland beaver ponds (Roulet et al., 1997; Wik et al., 2016), implies that, in these environments, beavers may be agents of soil formation. However, to investigate the validity of this notion requires a methodology that can infer the potentially transformative impacts of beaver activity from the peat itself.

Process signatures associated with the factors controlling peat development are archived in the peat column and can be interpreted with multi-proxy analysis (Charman et al., 2013; Peros et al., 2016). Biotic indicators, such as plant macrofossils and testate amoebae assemblages, are often used to define environmental gradients (Elliott et al., 2012; Marcisz et al., 2016); most commonly, the position of the water table. Further evidence of these processes can be inferred from abiotic proxies, such as bulk density, elemental concentrations and ratios, and isotopic natural abundances of light stable elements (Andersson & Schoning, 2010; Jones et al., 2010; Larsson et al., 2017). When combined, multi-proxy reconstructions of peat cores can offer a unique window into the state of the peatland, including the important factors driving its development over time.

Our goal is to bring insight to why peat accumulates more in some areas of a peatland than in others. To do this we extracted multiple cores from a montane fen in areas where the peat and environmental conditions are different; thus, representing the spatial complexity inherent to the ecosystem. We analyzed each core using a multi-proxy, paleo-reconstruction approach to determine how they vary in terms of the soil forming factors, and what this means with regards to the development of peat in each location over time.

6.4 Methods

6.4.1 Study area, core locations and sampling strategy

Three peat cores were extracted from the Sibbald Research Wetland (Sibbald) for multi-proxy analysis (Fig. 6.1). Sibbald is a rich, flow-through fen that is bisected by Bateman Creek, a small, second-order stream (Westbrook and Bedard-Haughn, 2016). Inputs to the stream originate from a combination of spring snowmelt, rain and groundwater, and aerial photo analysis has verified beaver activity along the stream since the early 1950s. In June 2013, many of the dams were breached by a major flood event (Pomeroy et al., 2015), leaving behind exposed beaver meadows.

The three coring locations were selected to reflect differences in peat depth, plant community, and local hydrology (Table 6.1). The first core (Meadow) was extracted from a beaver meadow that had been inundated for nearly 60 years prior to the flood in 2013 (Karran et al., 2018). The Meadow core contains approximately 1.77 m of continuous peat overtop nearly 2 m of marl interbedded with several thin peat layers. The second core (Riparian) was extracted from the riparian area adjacent to the beaver meadow and contains 2.97 m of continuous peat overtop of clay and alluvium. The third core (Interior) was extracted from the interior of the fen, far from the stream and ponds, and contains 6.8 m of continuous peat overtop of clay and alluvium. Each core location had different dominant plant communities: the Meadow core was dominated by sedges and rushes (e.g. *Carex aquatilis, Carex rostrata, Juncus balticus*); the Riparian core was dominated by grasses (e.g. *Calamagrostis canadensis, Phalaris arundinaceae*); and, the Interior core was dominated by shrubs and brown mosses (e.g. *Betula nana, Drepanocladus uncinatus, Aulacomnium palustre*). The Riparian and Interior cores were extracted near groundwater wells, where summer water tables have been monitored since 2006. The water table near the Riparian core descends deeper and experiences greater magnitude fluctuations than the water table near the Interior core, which is more stable (Table 6.1).

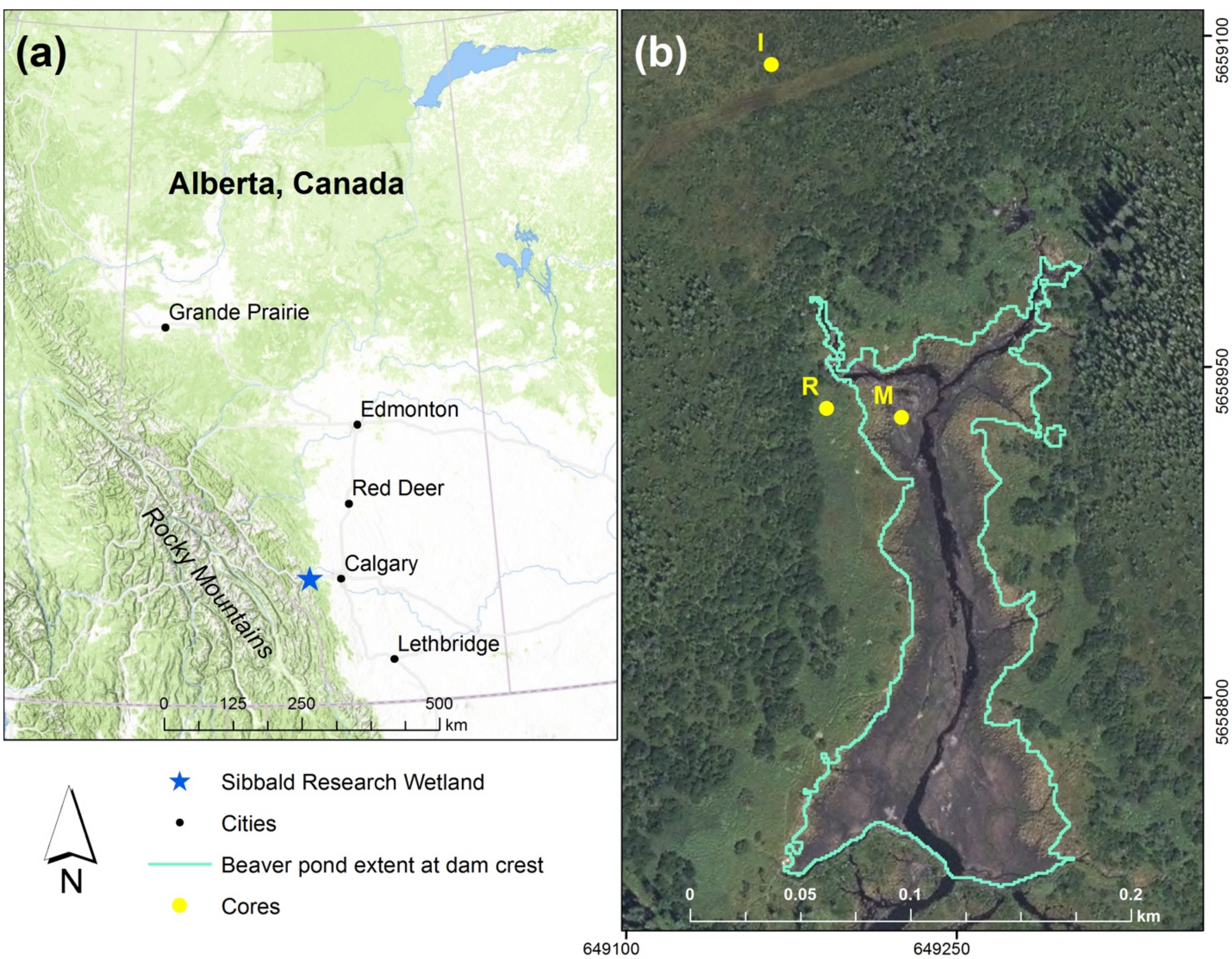

Fig. 6.1 Location of the sampling area (a) and the location within the Sibbald Research Wetland, where the Meadow (M), Riparian (R), and Interior (I) cores were extracted for multi-proxy analysis (b). Aerial photo

in (b) was taken post-flood in August of 2013, two months after the beaver dam breached. The blue line represents the high water mark of the beaver pond when the water surface was at the dam crest. Approximately 15 m south of the Interior core location exists a logging road that was created in late 1980s to cut timber on the nearby hillslopes.

Table 6.1 Characteristics of cores extracted for extensive multi-proxy analysis, where n is the number of measurements used for the calculation of the average water table depth (2006–2015)

Core	UTM coordinates	Surface elevation (amsl)	Continuous peat depth	Dominant vegetation	Average summer water table depth below peat surface (± standard deviation; n=85)
Meadow	649225 E 565892 N	1486.57	1.77 m	Sedges and Rushes	Flooded (no data)
Riparian	649191 E 565893 N	1488.61	2.97 m	Grasses	54.00 cm ± 28.00
Interior	649166 E 565908 N	1492.62	6.80 m	Shrubs and Brown mosses	1.23 cm ± 5.94

Peat cores were collected in August of 2015 with a 50-cm long Russian-type peat corer. Each core segment was placed in a PVC frame and sealed with cellophane. The cores were then placed in a freezer before their transport and analysis at Texas A&M University in 2016. For the Meadow core, with the least amount of continuous peat, a 4-cm resolution resulted in 45 sampling increments. To compare the development of all cores equally, the Riparian and Interior cores were also sampled to the same depth so that there were 45 sampling sites per core. The remainder of the Riparian and Interior cores were not used for this study.

6.4.2 Peat chronology

Peat core chronology was determined using the Accelerator Mass Spectrometry (AMS) radiocarbon (^{14}C) dating method. Most of the peat cores were strongly humified; therefore, dating materials were limited to root-free bulk peat. We sieved fresh peat samples using 125- and 63-μm sieves; the material caught between those sieves was used for ^{14}C dating, thereby limiting the presence of roots (> 150 μm) and fine inorganics (< 63 μm). Three samples were submitted for the Meadow core, one for the Riparian core and five for the Interior core. To get a full history of each core, some of the layers sampled for ^{14}C dating were deeper than what was sampled for multi-proxy analysis (i.e. top 180 cm of each core). In the Meadow core, two of the ^{14}C samples came from peat layers interbedded within the marl. The samples were submitted to the Center for Accelerator Mass Spectrometry (CAMS) at Lawrence Livermore National Laboratory in Livermore, California. Results were calibrated using Bacon (Blaauw and Christen, 2011) and the

INTCAL13 calibration data set (Reimer et al., 2013). Only one sample was available for the Riparian age depth model so ages below 1.06 m were extrapolated to the bottom of the core. AMS ^{14}C results are reported in Table 6.2.

Table 6.2 Radiocarbon dating results and calibration for Sibbald peat cores ....

Core	Sample depth (cm)	^{14}C age (years BP)	Calibrated 2σ age range (cal years BP)	Median age (cal years BP)	Laboratory ID (CAMS#)
Meadow	58	1620 ± 70	1365–1899	1586	176208
	191	8445 ± 50	9091–9578	9417	176207
	298	11130 ± 40	12787–13174	13016	176206
Riparian	106	3955 ± 25	4204–4566	4413	176209
Interior	112	1900 ± 25	1710–1908	1822	176204
	223	2915 ± 30	2975–3312	3107	176203
	405	5750 ± 30	6332–6623	6503	176202
	537	6875 ± 45	7622–7918	7750	176201
	649	8470 ± 130	8683–9498	9124	176200

6.4.3 Plant macrofossils

At 4-cm increments along each peat core, 1 cm^3 was extracted for macrofossil analysis. The fine-particle fraction of each sample was removed by rinsing with distilled water through a 125 µm sieve. Larger fractions were then placed in a Petri dish and investigated with a dissecting microscope at 4 to 10X resolution. Each sample was further defined by their respective percentages of herbaceous, ligneous, moss, inorganic and unidentified organic matter (UOM). The amount of fine particle material that was sieved out was then estimated and added to the UOM percentage. The presence of macrocharcoal and aquatic molluscs were also noted as proxies for fire disturbance and ponding, respectively (Marcisz et al., 2016; Whittington et al., 2015).

6.4.4 Geochemical properties

From each sample, 1 cm^3 was extracted for bulk density, total organic carbon (C), total nitrogen (N), $\delta^{13}C$, $\delta^{15}N$, and C:N analysis (Chambers et al., 2011; Loisel and Yu, 2013). Samples were weighed and dried for 24 hours at 105°C. Once dry, the samples were weighed again, crushed into fine particles by mortar and pestle, and placed in paraffin sealed containers. The dried and crushed samples were used for elemental analysis (i.e. C and N) and isotope analysis at the Stable Isotope Geosciences Research Facility of Texas A&M University. Each sample was weighed and placed in a silver capsule. The samples were then treated with HCl to remove any inorganic carbon. After desiccation, the capsules were inserted into a Carlo Erba NA 1500 Elemental Analyzer with a Costech Zero-Blank Autosampler. Gases were then introduced to a Thermo Scientific DELTA^{plus}XP isotope ratio mass spectrometer for analysis through a Thermo Scientific ConFlo III continuous flow peripheral device. The C:N ratios were calculated by dividing the moles mg^{-1} of C by the moles mg^{-1} of N, as determined by the mass spectrometer. Total C and N content (mg cm^{-3}) were calculated by multiplying the mass of C and N in each sample by the sample's bulk density. The long-term apparent rate of carbon and nitrogen accumulation (LORCA and LORNA, respectively) was calculated by multiplying the C and N content by the peat accumulation rate (cm yr^{-1}) derived from the age-depth models (Turunen et al., 2004). Finally, total organic carbon (TOC; kg m^{-2}) was calculated for each core by summing the product of the C content and the thickness (cm) between each sample.

6.4.5 Testate Amoebae

At the same 4-cm resolution as the other analyses, 1 cm^3 was extracted from each sample for testate amoebae analysis. Samples were prepared for analysis following standard procedures (Booth et al., 2010). The media was spiked with *Lycopodium* spores and stained with safranin. Using a microscope at 400X resolution, a minimum of 50 testates were counted in each sample to provide a sufficient statistical sample size and *Lycopodium* spores were counted to assess testate concentrations. The presence of moss cellular material was also noted during testate analysis.

6.4.6 Statistical analysis

The testate amoebae taxa composition data from all cores were combined and used to order the sampling sites into four different groups. Only the most predominant testate taxa were included in the ordination; taxa that did not occur in at least 5 samples, or that occurred less than 100 times in the entire dataset, were removed (Payne et al., 2006). Distance between samples was measured using the Bray-Curtis dissimilarity and groups were defined with Ward's hierarchical clustering (Borcard et al., 2011; Schwind et al., 2016).

A redundancy analysis (RDA) was performed on the testate taxa composition data set using the macrofossil and abiotic variables to explain the variance. The presence/absence of charcoal, moss, and inorganics were also tested as explanatory variables. All data were standardized so that all values ranged between 0 and 1. Testate data and presence/absence data were transformed with the Hellinger transformation (Legendre and Gallagher, 2001) and abiotic variables were transformed by dividing each by their respective maximum. To avoid negative numbers, an integer was added to the concentrations of $\delta^{13}C$ and $\delta^{15}N$ to bring all values above zero before transformation. Only those variables that were significant and that were not collinear with other variables were kept in the analysis. The null hypothesis in RDA is that no linear relationship exists between the response data (i.e. testates) and explanatory variables (i.e. macrofossil and abiotic variables). To test this hypothesis a *pseudo-F* statistic (Borcard et al., 2011) was generated by permutation 1000 times and the distribution of values was compared to the true value of *pseudo-F*. The probability was calculated as the proportion of $pseudo\text{-}F_{perm}$ that is larger than or equal to the true *pseudo-F*, and significance was when this probability was less than 0.05. Whether a variable has strong collinearity with other variables was determined by looking at Variance Inflation Factors (VIF), and those with VIFs greater than five were discarded (Borcard et al., 2011).

6.4.7 Group characterization and core phase delineation

Correlations among explanatory variables (i.e. macrofossil compositions and abiotic variables) were examined for each core, and the Mann-Whitney U test was used to determine significant differences between variable distributions. The same procedure was used for correlations and variable distributions in the testate ordered groups. Correlations that yielded Pearson's r values greater than 0.7 (i.e. $r^2 > 0.5$) were noted for discussion and significant differences were identified at p-values less than 0.05. The properties and processes of each group were then characterized based on their position within the RDA plot, and the correlations and similarities/dissimilarities among variable distributions.

The variation in testate assemblages is best described in most studies by the peatland water table depth (Van Bellen et al., 2014). Climate is the major external control on peatland water tables (Waddington et al., 2015); therefore, if other external factors (e.g. beavers) are not affecting water tables, group assignments should reflect the climatic conditions of the time. Based on this assumption, we further divided the cores into wet and dry phases using the predominance of the various groups as a guide. Within these phases, we looked at the median values of the biotic and abiotic explanatory variables, and we also looked at correlations that show evidence of diagenesis. More specifically, we focused on the relationship between the C:N ratio and $\delta^{13}C$ and $\delta^{15}N$ concentrations, which describe the significance of anaerobic and aerobic decomposition processes on the peat, respectively (Jones et al., 2010; Larsson et al., 2017; Lehmann et al., 2002; Sharma et al., 2005).

6.5 Results

6.5.1 Plant macrofossil composition

There was considerable variability in the macrofossil composition of each core (Fig. 6.2). Most of the peat was comprised of herbaceous, ligneous, and UOM fractions. Moss was found in every core, but inorganics were only found in the Meadow core (median % inorganic = 4.64). Trace amounts of inorganics were likely present in the Riparian and Interior cores, but their identification was below the detection limit of our analytical method.

The Meadow core had the least herbaceous content and the greatest ligneous content, both significantly different from the other two cores. The Riparian core had significantly less ligneous content and significantly more UOM. Finally, the Interior core had the most moss, but the distribution was only significantly different from the Riparian core, which had the least. Macrocharcoal (> 125 um) was found in 31% of the Meadow core samples, 9% of the Riparian core samples, and in 11% of the Interior core samples. Mollusks were only found in four samples of the Meadow core.

6.5.2 Peat geochemical properties

The three cores were most different from each other (i.e. $p<0.01$) in %C, bulk density, and N content (Fig. 6.2). For %C, Meadow < Riparian < Interior, but because the order is reversed for bulk density, there is a higher mass of C in the Meadow and Riparian cores. The same is true for N content, even though the %N is not significantly different in any of the cores. These relationships are further expressed in the Meadow core by strong negative correlations between bulk density and %C ($r = -0.84$, $p<0.001$) and %N ($r = -0.79$, $p<0.001$), but a strong positive correlation between the bulk density and the percentage of inorganics ($r = 0.78$, $p<0.001$). Furthermore, %C is strongly correlated to %N ($r = 0.91$, $p<0.001$) in the Meadow core, which is also significantly more enriched in $\delta^{15}N$ ($p<0.05$) and has a significantly lower C:N ratio ($p<0.001$).

Whereas bulk density is a function of the percentage of inorganics in the Meadow core, it is a function of C and N content in the Riparian core (denoted by strong positive correlations of *r*

= 0.87, $p<0.001$ and $r = 0.81$, $p<0.001$, respectively). The Riparian core is also different from the Meadow core in terms of N. The %N is strongly positively correlated to the concentration of $\delta^{15}N$ ($r = 0.71$, $p<0.001$), and the C:N ratio is strongly negatively correlated to both the %N and N content ($r = –0.89$, , $p<0.001$ and $r = –0.85$, $p<0.001$, respectively).

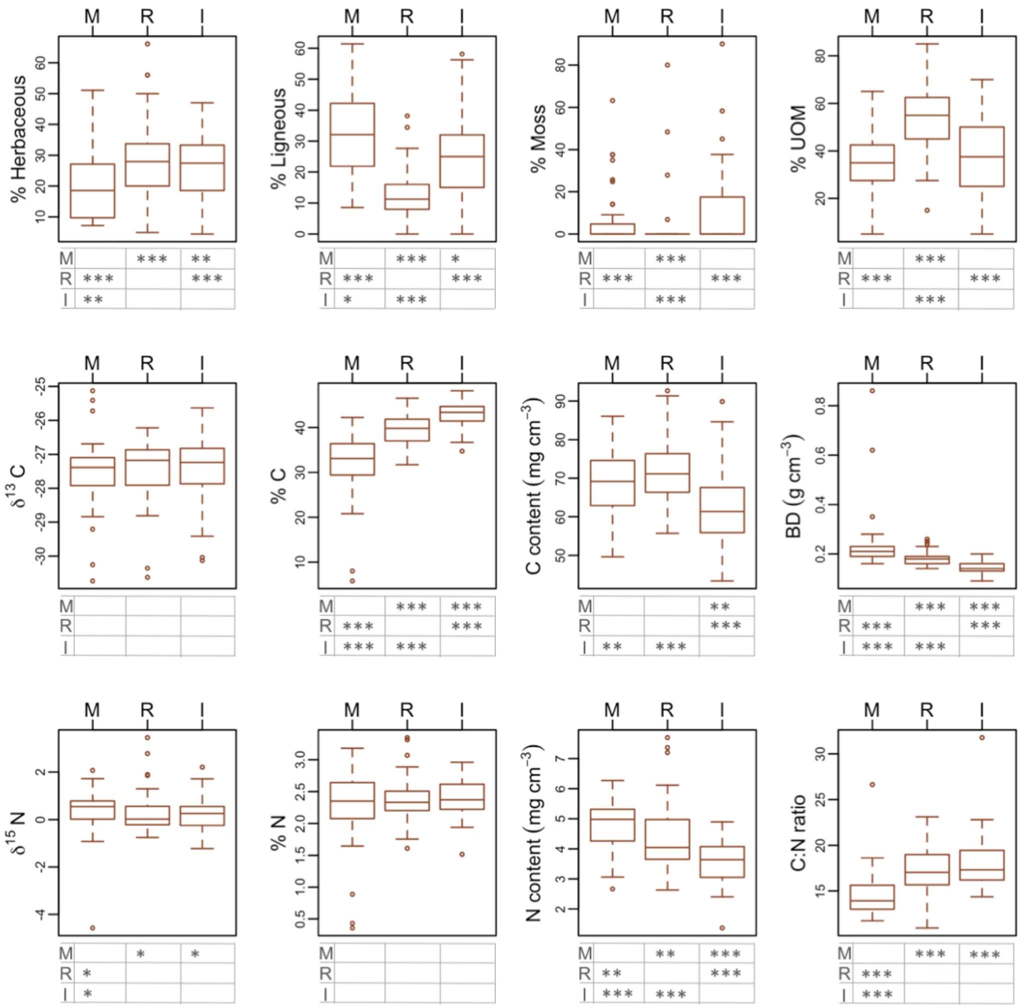

Fig. 6.2 Variable distributions in the Meadow (M), Riparian (R), and Interior (I) cores. Significant differences with other groups are shown below each distribution, where "*" is p<0.05, "**" is p<0.01, and "***" is p<0.001.

The Interior core has the lowest bulk density ($p<0.001$), C content ($p<0.01$), and N content ($p<0.001$) of all three cores. Like the Riparian core, bulk density in the Interior core shows strong positive correlations with C and N content ($r = 0.91$, $p<0.001$ and $r = 0.81$, $p<0.001$, respectively), and the C:N ratio is negatively correlated with the %N and N content ($r = –0.87$, $p<0.001$ and $r = –0.74$, $p<0.001$, respectively). Unlike the two other cores, however, C and N content are strongly positively correlated with one another ($r = 0.76$, $p<0.001$), and the concentration of $\delta^{13}C$ is strongly negatively correlated with the percentage of moss ($r = -0.70$, $p<0.001$).

6.5.3 Redundancy analysis and core sample grouping

Coupling testate amoebae-ordered core samples with RDA was an effective approach to define groups based on environmental gradients (Fig 6.3). After removing outliers, nine predominant testate amoebae taxa were used to cluster the four groups: *Arcella artocrea*, *Arcella catinus*, *Centropyxis aculeata*, *Centropyxis cassis*, *Centropyxis pontigulasiformis*, *Cyclopyxis arcelloides*, *Cyclopyxis ecornis*, *Heleopera petricola*, and *Phryganella acropodia*. Of the 135 core samples, 41 were assigned to Group 1, 36 to Group 2, 39 to Group 3, and 19 to Group 4.

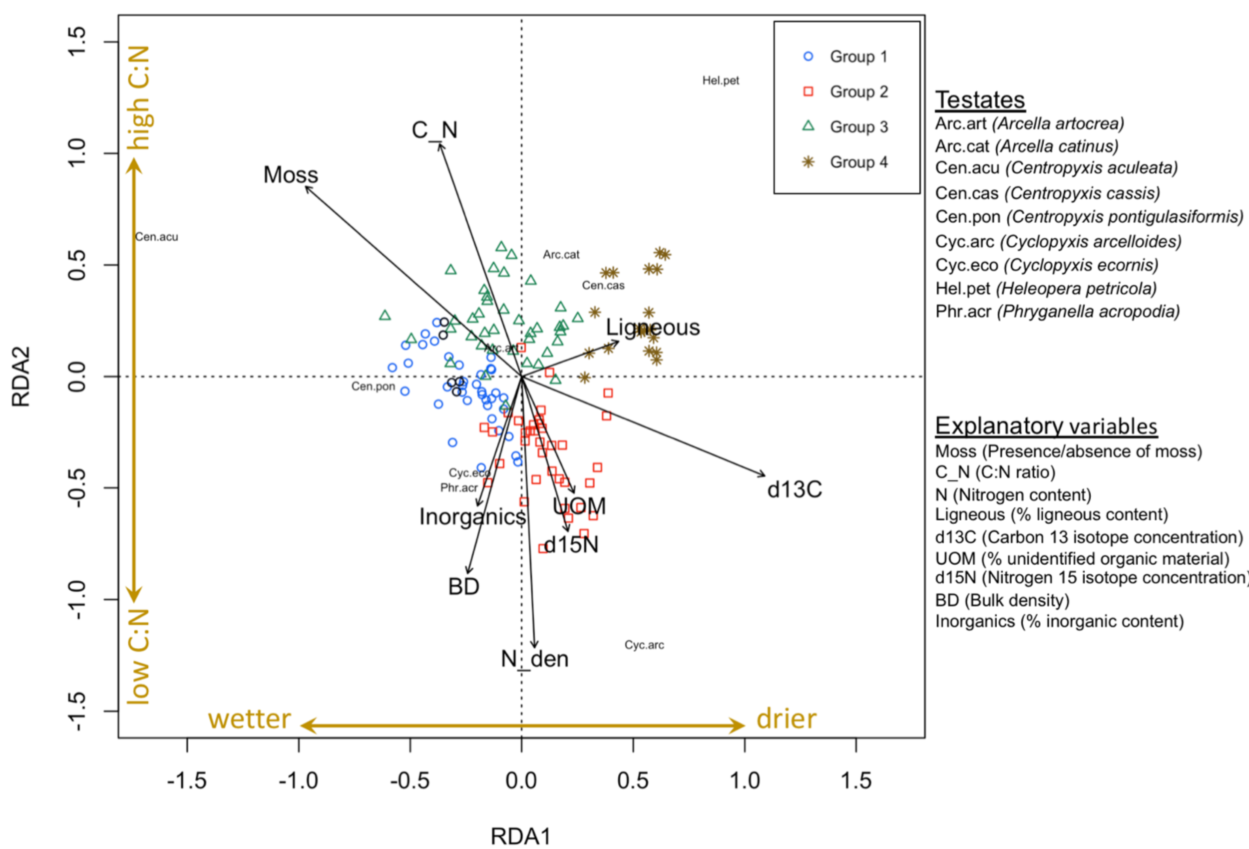

Fig. 6.3 Redundancy analysis shown with significant vectors. Core samples are symbolized by their respective groups and black circles are sites from Group 1 where mollusc macrofossils were found.

The RDA produced a model with three significant axes and nine significant explanatory variables that explained 25.19% of the total variance (i.e. inertia) in the data (Fig 6.3). Both the percentage of moss and the presence/absence of moss were significant in explaining the variance, but due to high VIFs, the percentage of moss was discarded along with the percentage of carbon, the percentage of nitrogen, and the carbon content, which exerted high collinearity with the C:N ratio and nitrogen content. The results of the RDA are shown in Table 6.3. Since most of the variance (~ 88%) is explained by RDA axis 1 and 2, we focus on these axes for the remainder of our analysis.

Table 6.3 Summary of the redundancy analysis results

	Significance (Pr (>F))	Variance explained (%)	Proportion of explained variance (%)
Entire model	0.001***	25.19	100
RDA axis 1	0.001***	14.52	57.64
RDA axis 2	0.001***	7.67	30.45
RDA axis 3	0.009**	1.7	6.75

The environmental gradients represented by RDA axes 1 and 2 are defined by their correlation with the explanatory variables, the variable distributions within each group, and the ordination of the testate species (i.e. scores). RDA axis 1 is most correlated with the concentration of $\delta^{13}C$ (r = 0.71) and the presence of moss (r = –0.63), whereas RDA axis 2 is most correlated with the C:N ratio (r = 0.69) and N content (r = –0.80) As each of the four groups is dominant in one of the four quadrants of the RDA, the differences in variable distributions within the groups show how they are separated (Fig. 6.4). For example, Groups 1 and 3 (left side of RDA) are different from Groups 2 and 4 (right side of RDA) in terms of $\delta^{13}C$ and the percentage of nitrogen. Groups 1 and 2 (bottom of RDA) are most different from Groups 3 and 4 (top of RDA) in terms of the percentage of carbon, C:N ratio, and bulk density. From the differences, we deduce that RDA axis 1 represents a wetness gradient and RDA axis 2 represents a trophic gradient. The testate amoebae species scores and the location of core samples containing mollusks also support a wetness gradient along RDA axis 1; unambiguous wet and dry testate taxa (i.e. *Centropyxis aculeata* and *Cyclopyxis arcelloides*, respectively) are positioned opposite to one another along RDA 1, and all core samples with mollusks are grouped on the left side of the plot. Based on the clustering and RDA analysis, we characterize the groups as follows (Table 6.4): Group 1 – marsh; Group 2 – dry meadow; Group 3 – semi-aquatic moss dominated peat; and, Group 4 – shrub dominated peat.

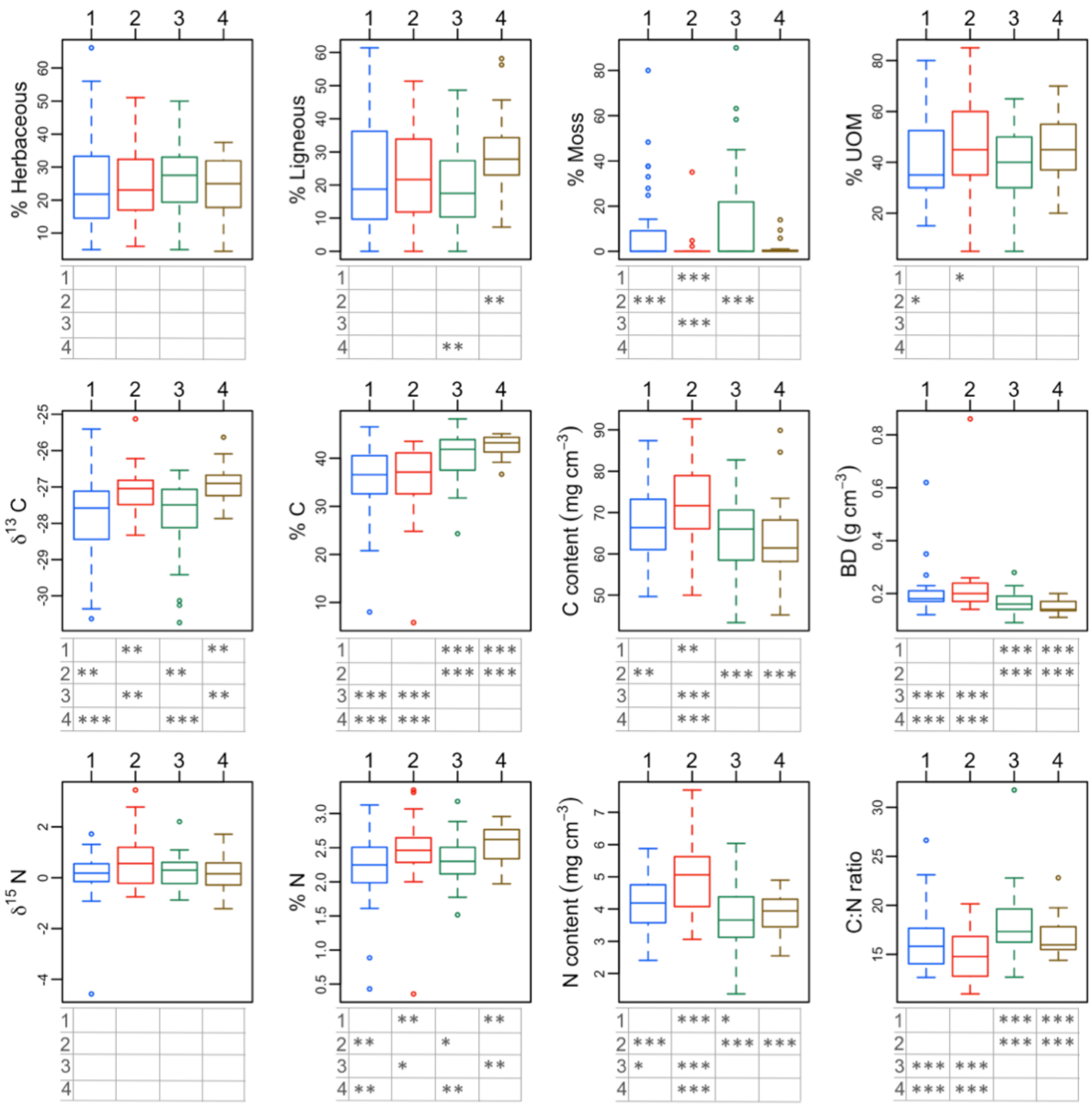

Fig. 6.4 Variable distributions in Group 1 (n = 41), Group 2 (n = 36), Group 3 (n = 39), and Group 4 (n = 19). Significant differences with other groups are shown below each distribution, where "*" is p<0.05, "**" is p<0.01, and "***" is p<0.001.

Table 6.4 Characterization of the four groups created via testate amoebae communities, and the number of samples in each core assigned to each group

Group	Description	Properties and processes	Associated testate taxa	# of samples in Meadow core	# of samples in Riparian core	# of samples in Interior core
1	Marsh	-methanogenesis from ponding -low C:N ratio -high bulk density	*C. ecornis* *C. pontigulasiformis* *P. acropodia*	24	16	1
2	Dry Meadow	-low and unstable water table -low C:N ratio -high N and C content -increased UOM -high bulk density	*C. arcelloides*	15	20	1
3	Semi-aquatic moss dominated peat	-high and stable water table - low $\delta^{13}C$ signature from methanogenesis and methane oxidation (high water table) -high moss content -high C:N ratio -low bulk density	*A. artocrea* *C. aculeata*	6	9	24
4	Shrub dominated peat	-low and unstable water table -high ligneous content -high C:N ratio -low bulk density	*A. catinus* *C. cassis* *H. petricola*	0	0	19

6.5.4 Core chronology, peatland development, and carbon accumulation

The proportion of samples in each core assigned to the various groups (Table 6.4) shows how differently they accumulated peat and developed over time. Therefore, core sections were further divided into phases, reflecting periods that are wetter (i.e. majority of samples in Groups 1 and 3) or drier (i.e. majority of samples in Groups 2 and 4). The Meadow core (Fig. 6.5) accumulated the lowest amount of peat (median LORCA = 1.23 mg cm^{-2} yr^{-1}; TOC =123 kg m^{-2}) and had the highest proportion of samples in Group 1 (53%), suggesting that it was likely inundated more often than the other two cores. The basal layer of the continuous peat in the Meadow core was assigned to Group 2, but immediately thereafter wet conditions set in. Ponded conditions prevail in the core until ~4330 cal yrs BP, at which time a drier phase (with infrequent flooding) commences and remains until ~1092 cal yrs BP. In the years following, marsh-like conditions remain with a few dry periods in between.

The Riparian core accumulated more peat (median LORCA = 1.58 mg cm^{-2} yr^{-1}; TOC = 130 kg m^{-2}) than the Meadow core over time. Samples grouped similarly in both cores, but there was less of Group 1 and more of Group 2 and 3 in the Riparian core (Fig 6.6). More samples in Group 2 suggests drier conditions overall, and more samples in Group 3 suggests semi-aquatic conditions that promotes moss growth. Trends at longer time-scales in the Riparian core are closely aligned with the Meadow core, but the early wet period ends sooner (i.e. ~5540 cal yrs BP) and the dry phase persists until present day.

The Interior core accumulated the most peat (median LORCA = 4.31 mg cm^{-2} yr^{-1}; TOC = 112 kg m^{-2}) and its development was very different from both the Meadow and Riparian cores (Fig 6.7). Group 4 is entirely unique to the Interior core and almost all the other samples are in Group 3, except for one in both Groups 1 and 2. Samples in Group 3 dominated the core from the earliest date of 2620 cal yrs BP until ~1315 cal yrs BP, at which time the core becomes dominated by samples in Group 4. This transition suggests a lowering and/or destabilizing of the water table, a condition that has lasted until present day.

6.5.5 Statistical relationships between proxies

Notable correlations between biotic and abiotic variables within the wet and dry phases of each core, reveal important processes operating on the peat (Table 6.5). In the Meadow core, the correlation between the C:N ratio and the $\delta^{13}C$ concentration is weakly positive during the wet phase, but strongly negative during the wet phases of the Riparian and Interior cores. However, during the wet phase in both the Riparian and Interior cores, the $\delta^{13}C$ concentration shows strong negative correlation to the percentage of moss remains ($r = -0.81$, $p<0.001$ and $r = -0.68$, $p<0.001$, respectively), and in the Interior core, the $\delta^{13}C$ concentration shows strong positive correlation to the percentage of ligneous material ($r = 0.78$, $p<0.001$). The percentage of moss also shows strong positive correlation to the C:N ratio in the Riparian core during the wet phase ($r = 0.71$, $p<0.01$).

There is little correlation between C:N ratio and $\delta^{13}C$ concentration during the dry phase of the cores, except for a moderate correlation in the Interior core. Strong correlations between C:N ratio and $\delta^{15}N$ concentrations are present in all cores during the dry phase, but not the wet phase. Also during the dry phase: the $\delta^{15}N$ concentration shows strong negative correlation to the %C and C:N ratio ($r = -0.85$, $p<0.001$ and $r = -0.82$, $p<0.001$, respectively) in the Meadow core; the $\delta^{15}N$ concentration shows strong positive correlation to the %N ($r = 0.81$, $p<0.001$) in the Riparian core;

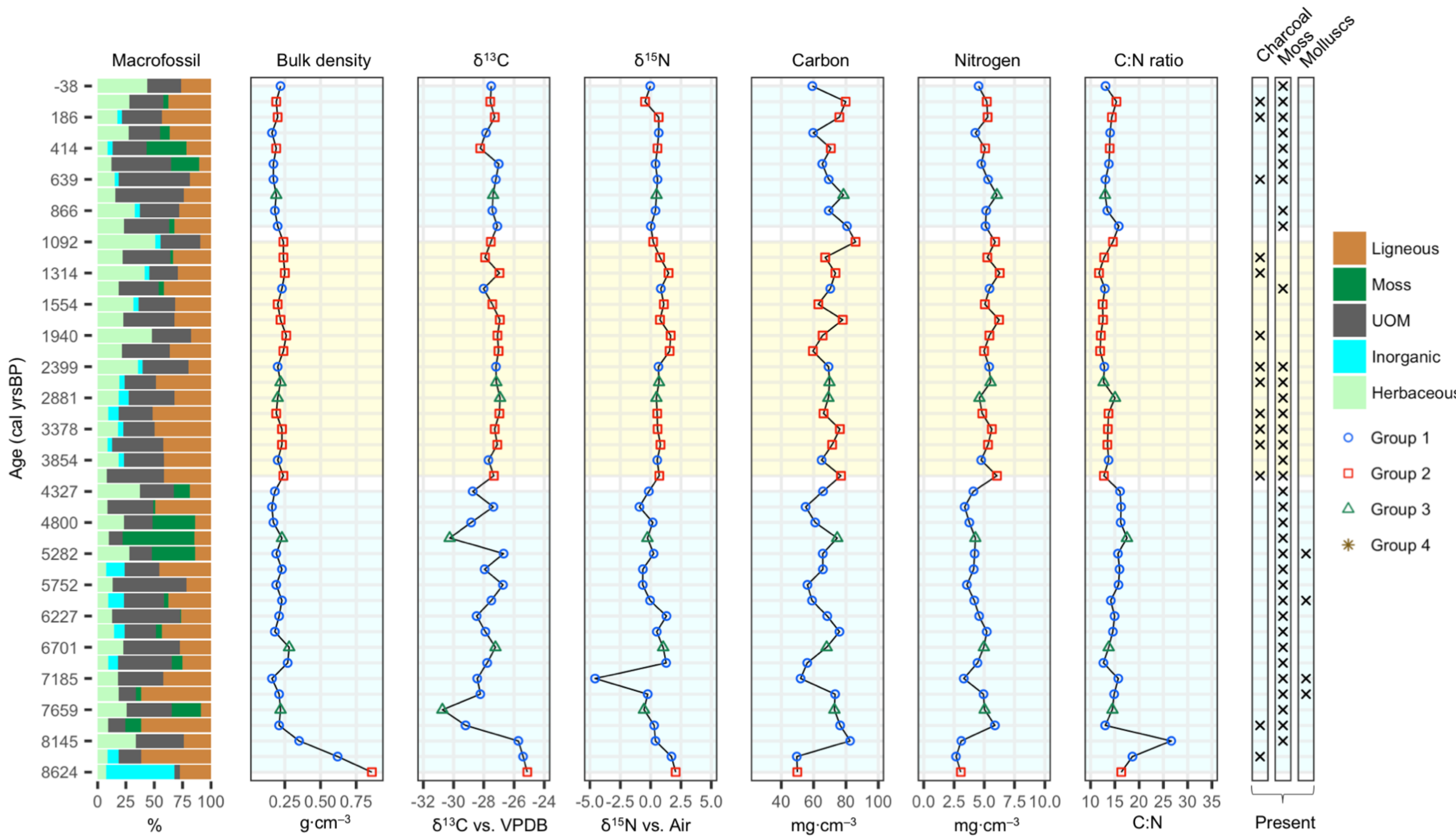

Fig. 6.5 Meadow core paleo reconstruction of macrofossil composition, abiotic variables, and presence/absence data. Core sample symbols reflect their assigned groups. Shaded time periods show the separation between wet (light blue) and dry (yellow) phases of the core.

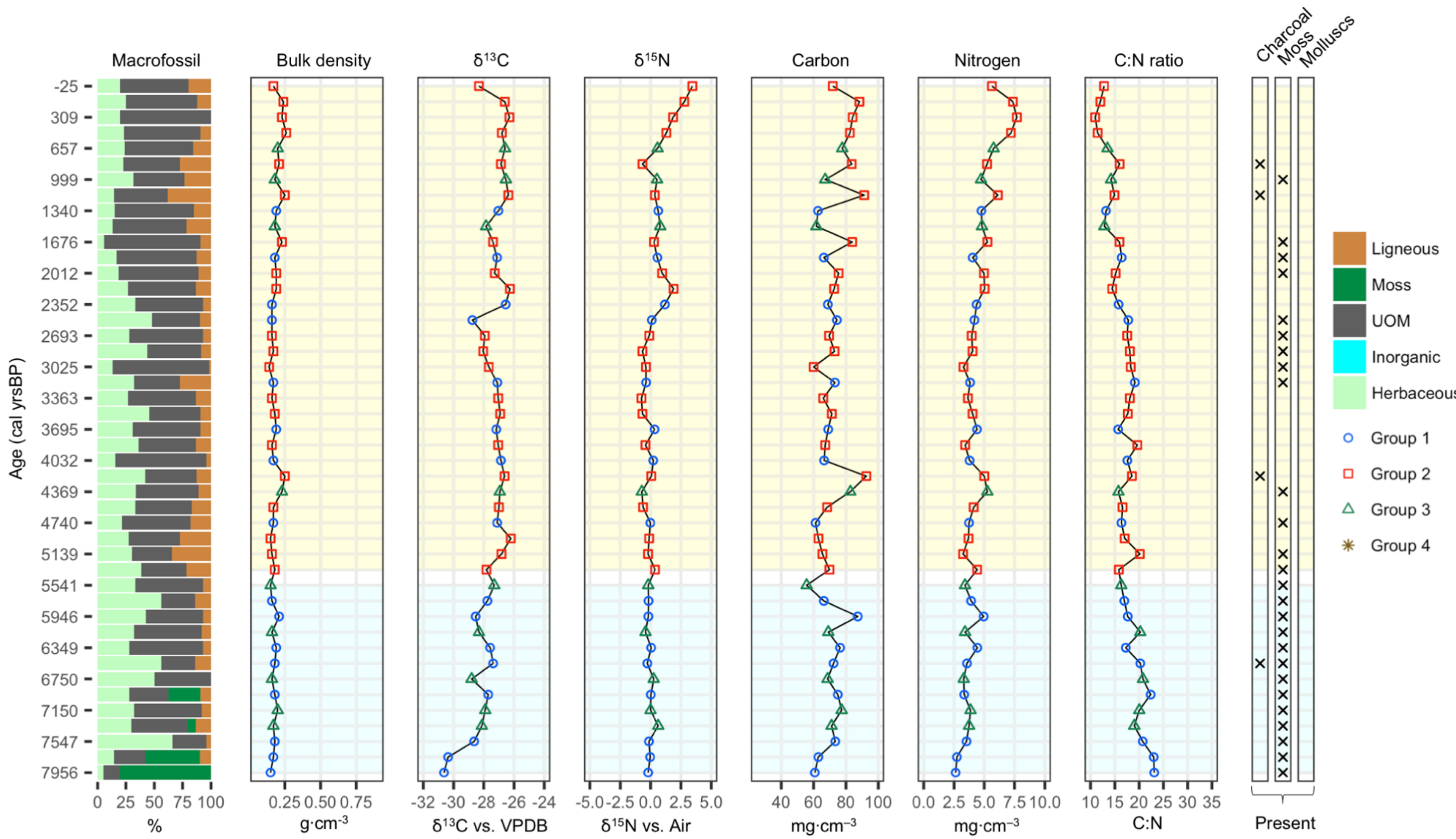

Fig. 6.6 Riparian core paleo reconstruction of macrofossil composition, abiotic variables, and presence/absence data. Core sample symbols reflect their assigned groups. Shaded time periods show the separation between wet (light blue) and dry (yellow) phases of the core.

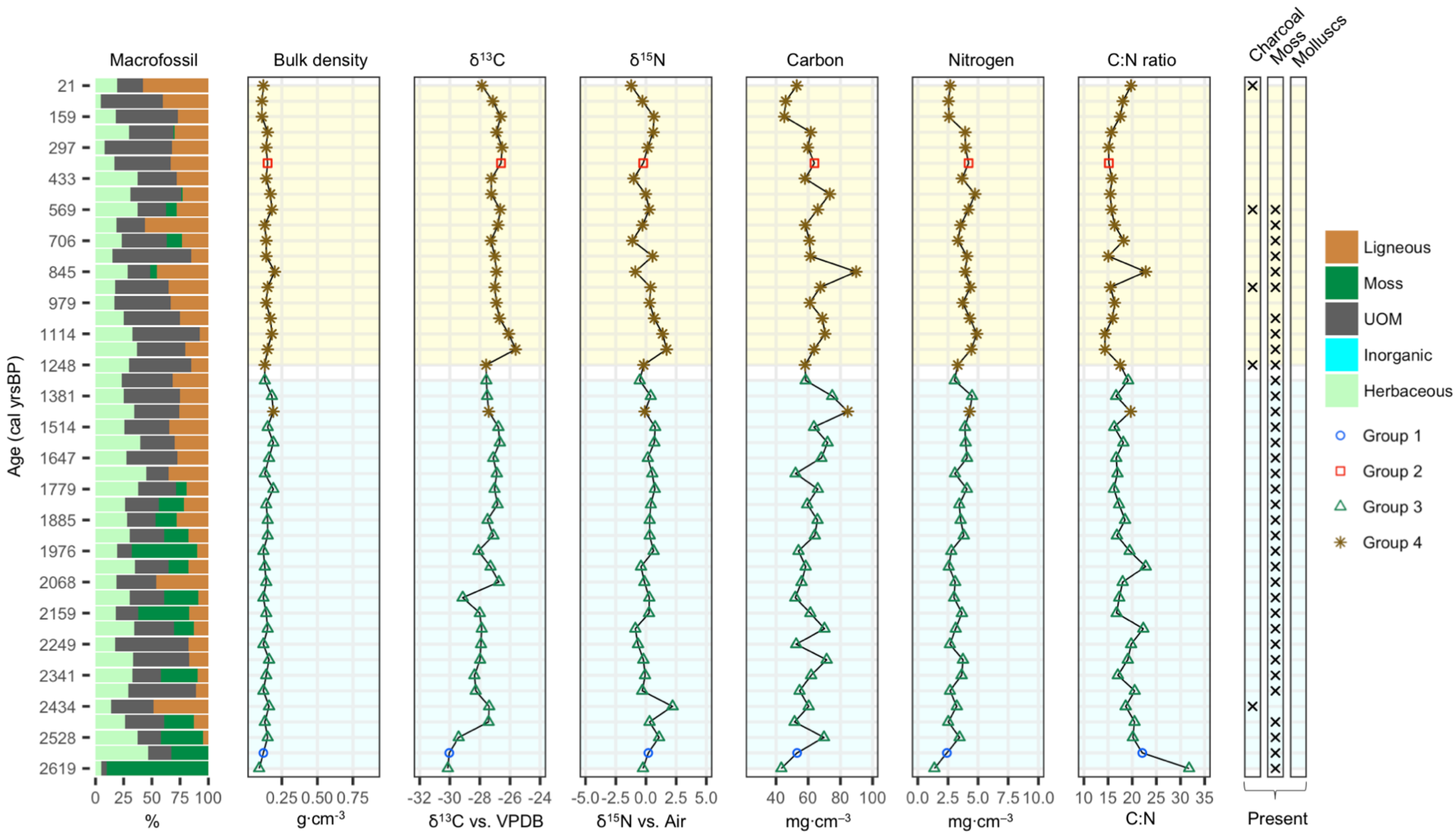

Fig 6.7 Interior core paleo reconstruction of macrofossil composition, abiotic variables, and presence/absence data. Core sample symbols reflect their assigned groups. Shaded time periods show the separation between wet (light blue) and dry (yellow) phases of the core.

the $\delta^{15}N$ concentration and the $\delta^{13}C$ concentration also show strong positive correlation with each other (r = 0.79, p<0.001) in the Interior core. Finally, during the dry phase of the Riparian core, the percentage of UOM shows a strong negative correlation to the herbaceous content (r = – 0.75, p<0.001).

Table 6.5 Pearson's r correlation between the C:N ratio and $\delta^{13}C$ and $\delta^{15}N$ concentrations within the wet and dry periods of each core.

Core	Phase	C:N vs $\delta^{13}C$	C:N vs $\delta^{15}N$
Meadow	Wet	0.31	–0.04
	Dry	–0.09	–0.82***
Riparian	Wet	–0.68*	0.01
	Dry	–0.19	–0.75***
Interior	Wet	–0.62***	–0.35
	Dry	–0.50*	–0.66**

Statistical significance, where "" is p<0.05, "**" is p<0.01, and "***" is p<0.001.

There are notable differences in the peat properties in each core during the wet and dry phases (Table 6.6). For biotic variables, the transition from wet to dry phases sees more herbaceous material in the Meadow core, and less in the Riparian and Interior cores. There is more Ligneous material in every core, whereas there is less moss (i.e. macrofossils) in every core. The amount of UOM is unchanged in the Meadow core, but is higher in both the Riparian and Interior cores during the dry phases.

Table 6.6 Median values of biotic and abiotic variables within the wet and dry phases of each core

Core	Meadow		Riparian		Interior	
Phase	Wet	Dry	Wet	Dry	Wet	Dry
% Herbaceous	16.00	20.31	32.00	26.67	28.61	23.08
% Ligneous	27.22	34.69	8.00	13.10	17.50	28.13
% Moss†	9.13	3.43	38.10	0.00	28.31	5.74
% UOM	35.00	35.00	50.00	60.00	31.75	47.00
Bulk density (g cm^{-3})	0.20	0.23	0.17	0.18	0.14	0.14
% Nitrogen	2.22	2.45	2.06	2.45	2.31	2.62
Nitrogen (mg cm^{-3})	4.53	5.41	3.54	4.41	3.34	3.94
LORNA (mg cm^{-2} yr^{-1})	0.08	0.09	0.07	0.10	0.26	0.23
$\delta^{15}N$ vs. Air	0.29	0.75	-0.14	0.25	0.26	0.15
% Carbon	34.59	31.90	40.79	38.99	43.82	42.69
Carbon (mg cm^{-3})	68.10	69.53	71.13	70.56	60.86	61.41
LORCA (mg cm^{-2} yr^{-1})	1.23	1.24	1.42	1.70	4.75	3.57
$\delta^{13}C$ vs. VPDB	–27.51	–27.18	–28.13	–27.01	–27.50	–26.90
C:N ratio	14.86	12.81	20.24	15.97	18.57	15.79

†Median moss percentages exclude samples without moss macrofossils

For abiotic variables, the transition from wet to dry phases sees a higher bulk density in the Meadow and Riparian cores but no change in the Interior core. The LORNA and LORCA are also higher in the Meadow and Riparian cores, but lower in the Interior core. The C:N ratio is lower in every core during the transition from wet to dry phases.

6.6 Discussion

6.6.1 Regional climate as the primary driver of community shifts over millennial timescales

The regional climate is the major factor forcing the transition between wet and dry phases in each core. The oldest age of all samples (~8620 cal yrs BP), from the basal layer of the continuous peat in the Meadow core, dates back to the early Holocene, when mild and arid conditions caused rapid glacial ablation and severe drought (Beierle et al., 2003; Kubiw et al., 1989). This is evident by the large marl deposit (i.e. basal layer inorganics), which is a remnant of a groundwater-fed pond that completely dried up (Beierle & Smith, 1998). However, shortly after peat began to form, wet conditions returned to the site and lasted for over four millennia. The presence of peat and absence of marl during this time suggests that wet conditions resembled that of peat-accumulating marsh rather than an open water pond.

Like the Meadow core, the earliest dates in the Riparian core are assigned to Groups 1 and 3, reaffirming the wetness of the area during this period. However, because the Riparian core is upslope from the Meadow core, the dry phase begins sooner as the pond stage receded over time. The transition from wet to dry conditions in both the Meadow and Riparian cores happens during an early-middle Neoglacial period (i.e. 7500 – 3000 yrs BP), when temperatures were colder than the early Holocene and glaciers were once again advancing in the region (Menounos et al., 2009). The Neoglacial conditions are a likely reason for a lowered water table as there was no longer sufficient runoff and groundwater to sustain the prolonged ponding of the early Holocene (Jones & Yu, 2010; Lemieux et al., 2008). Dry conditions mostly prevail in the Meadow and Riparian cores until a brief wet period between ~2880 – 2400 cal yrs BP. The earliest samples in the Interior core are also from this period and, given the high percentage of moss and the sole Group 1 assignment, they also indicate exceptionally wet conditions.

Sometime around ~1300-1000 cal yrs BP, the regional climate warms and glacial ablation begins again (Beierle et al., 2003). This returns wet conditions to the Meadow core but not the Riparian core, suggesting that enough peat had accumulated such that the surface of the Riparian core was no longer in a zone of regular inundation. Conditions in the Interior core also become drier as less moss and more shrubby vegetation begins to colonize the site. A likely explanation for this is that the Interior core is more dependent on atmospheric water inputs rather than ground and surface water inputs. Wet conditions prevail in the Meadow core until ~300 cal yrs BP, at which time a brief dry period begins and conditions in the Interior core become even drier. This period is synchronous with the Little Ice Age period (~ 1450-1850 AD), when cooler conditions and glacial advances are reported in the region (Menounos et al., 2009).

6.6.2 Topographical constraints on peat initiation timing and development

The timing and pathway of peat initiation in each core was controlled by its topography and parent material. The continuous peat stratigraphy in the Riparian and Interior cores developed overtop clay layers at nearly the same elevation (i.e. 1485.6 m and 1485.8 m, respectively). In the Meadow core, the continuous peat stratigraphy developed overtop a layer of marl in a topographic depression (1484.8 m). While peat accumulation had already initiated in the Riparian and Interior sites through the process of paludification (Kroetsch et al., 2011; Lavoie et al., 2005b), the Meadow site was inundated by a shallow pond. Later, as the climate dried and the pond level lowered, peat began to accumulate at the Meadow site through the process of terrestrialization (Kroetsch et al., 2011; Kuhry and Turunen, 2006), supported by the enriched $\delta^{13}C$ values in the earliest samples (Andersson & Schoning, 2010).

6.6.3 Key biogeochemical processes dominating peatland beaver meadow soils

Peat-accumulating marshes and similar ecosystems are associated with high rates of denitrification because of their anaerobic conditions and the production of labile substrates (Hill & Cardaci, 2004; Pihlatie et al., 2004; Wang et al., 2017). Those characteristics are inferred for our Meadow core. With its topographically low position, which had clear and enduring impacts on peat development, including its late inception at 8620 cal yrs BP and its relatively shallow deposit (177 cm), the core's proximity to an area of groundwater discharge explains why it was ponded more often than the other two sites. That this site is indeed ponded during the wet phases is not only supported by the testate groupings, but also by the C:N ratio and lower LORNA. The median

C:N ratio (during both wet and dry phases) is considerably lower than that of other cores and near the 15.8 average reported for peatland marshes in Alberta (Whitehouse and Bayley, 2005).

Numerous inorganic layers along the Meadow core indicate that, in addition to groundwater, this area was receiving surface water inputs via overland flow or flood events. It is fair to assume that most of these inorganics are of fluvial origin and not from atmospheric deposition given their size and absence from the other two cores. Furthermore, similar deposits were found in many of the peatland beaver meadows sampled in the region (see Supporting information). During the dry phase (4330-1090 cal yrs BP), the Meadow core recorded intermittent ponding, indicated by samples in Groups 1 and 3 that tend to correspond with inorganic deposits. Some inorganic deposits are found in Group 2, which may be deposits from overbank floods or intermittent ponding that occurred at shorter time scales than what could be observed within the 4-cm sampling resolution.

Peat biota (i.e. flora and fauna) has played a major role in the development of the Meadow core and reflects multiple feedbacks and interactions with the local hydrology. For example, the dry conditions at the onset of peat accumulation seem to encourage the early colonization of woody species (e.g. *Salix* spp.), indicated by high ligneous contents and the presence of macrocharcoal (> 125 um) in the first few layers. It is possible that this incursion of shrubs is why the site becomes progressively wetter thereafter, as increased vegetation density and leaf area index reduced the energy available to evaporate the groundwater discharge (Waddington et al., 2015). Furthermore, the low C:N ratio is likely due to the proportion of algae incorporated into the carbon pool during ponding (Herczeg et al., 2001; Jones et al., 2010), and ponding is likely responsible for the presence and preservation of mollusc and moss macrofossils. That the C:N ratio drops even further during the dry phase is attributed to the higher herbaceous and lower moss content comprising the peat (Andersson & Schoning, 2010), and may reflect a higher organic nitrogen supply relative to that being lost to denitrification.

The Meadow core accumulated the least amount of peat of all three sites. Although wet conditions prevailed for most of the Meadow core's history, there is no evidence of anaerobic diagenesis. If there was, we would expect to see a negative correlation between the C:N ratio and the $\delta^{13}C$ concentration (Sharma et al., 2005). Decomposition favours labile substrates (i.e. carbohydrates and proteins) enriched in ^{13}C and, in anaerobic environments, the pool of organic matter resistant to decay is much larger, leaving a more depleted $\delta^{13}C$ signature than during aerobic decomposition (Larsson et al., 2017; Lehmann et al., 2002). Methanogenesis was likely enhanced by the warm temperatures of the early Holocene (Jones et al., 2010; Yu et al., 2013), and may have been aided by an extra supply of electron acceptors provided by the marl (Boomer and Bedford, 2008). However, the $\delta^{13}C$ lows during this period also correspond with higher moss contents, which is a sign that bryophyte-mediated methane oxidation was likely occurring. Methane oxidation (methanotrophy) by bacteria, living in close association with mosses, discriminates against the heavier isotope, leaving the methane more enriched and further depleting the peat $\delta^{13}C$ signature (Liebner et al., 2011; Nichols et al., 2009). Thus, given the evidence presented here, we cannot be conclusive that anaerobic processes were significant to shaping the peat properties in this core.

The strong negative correlation between the $\delta^{15}N$ concentration and the C:N ratio during the dry phase suggests that aerobic decomposition was high, with a preferential loss of ^{14}N from the bulk peat. Both plant N uptake and decomposition discriminate against ^{15}N (Jones et al., 2010; Larsson et al., 2017), and the lowered water table would facilitate denitrification (Regina et al., 1999), removing ^{14}N from the peat and enriching the $\delta^{15}N$ signature (Andersson et al., 2012). High aerobic decomposition would also explain the absence of moss macrofossils even though cellular material was present at higher microscope resolutions. Ligneous content increases by 27% during the dry phase, but this may stem from the increased decomposition of more labile carbon substrates rather than a change in plant community composition. Increases in decomposition would partially explain the higher bulk density during the dry phase, but there was also an increase in the prevalence of fire, which can further densify peat bulk volumes (Sherwood et al., 2013).

High decomposition in the Meadow core may be explained by the high bulk density and the deposition of inorganics. Bulk density has been found to be an important predictor of carbon and nitrogen mineralization as it controls the size of the nutrient pool within a given soil volume (Bridgham et al., 1998). When bulk density increases, diffusion pathways get shorter, allowing plant and microbes greater access (Barko and Smart, 1986; Long and Or, 2005). Inorganic deposits enhance this by increasing both the bulk density and the effective porosity through which solutes can move (Rezanezhad et al., 2016b). Furthermore, inorganics may also provide extra electron acceptors that enhance nitrogen (Wang et al., 2016b) and carbon mineralization processes (Broder et al., 2012; Wang et al., 2016a).

Wet phase conditions would have been ideal for beaver habitation, and it is possible that they colonized the area early on and are partly responsible for the inorganics and abrupt declines in ligneous content. Beavers cultivate large amounts of woody biomass (Johnston & Naiman, 1990) and removal of the shrubs would reduce light competition and make the environment more favorable for fen bryophytes (Kotowski et al., 2001), explaining why moss content tends to increase when ligneous content declines ($r = -0.51$). Other explanations for declines in ligneous content, such as fire and flood-induced mortality, are less probable because there is no evidence of local fire (Kuhry, 1994), and it is assumed that tolerance to inundation would be a prerequisite for shrubs colonizing a perennially saturated area (Amlin and Rood, 2001). Beavers, or the lack thereof, may have influenced other external factors as well. Fire, for example, is much more prevalent during the dry phase as there is significantly more ligneous material to ignite.

6.6.4 Riparian peat soils are nitrogen hotspots

The higher elevation of the Riparian core, relative to the meadow, and its proximity to the stream/pond are major factors for peat development. Peat began to accumulate earlier as the core was nearer to the pond margin. The pond stage was often above the peat surface during the wet phase of the early Holocene, but inundation was shallower explaining the higher prevalence of samples assigned to Group 3. As such, when the pond stage receded during the early Neoglacial, this location dried sooner than the Meadow core location, and mostly dry conditions have prevailed since. However, samples assigned to Groups 1 and 3 within the dry phase suggest the continued influence of the stream as they indicate periods with ponding and high water tables, respectively.

The higher C:N ratios are nearer the average reported for open fens by Whitehouse and Bayley (2005), and reflect the distinct vegetative characteristics of the peat. High moss content explains the higher C:N ratio during the wet phase and the dry phase is characterized by a high percentage of UOM. The UOM originated mostly from herbaceous substrates, given the strong negative correlation between the two. This core also had the least amount of ligneous material, which may be a result of the increasing nitrogen content observed through time. Fertilization studies have shown that graminoids outcompete other fen species, and that shrub biomass is reduced in bogs when nitrogen is added (Granberg et al., 2001; Pauli et al., 2002; Thormann and Bayley, 1997).

The Riparian core accumulated slightly more peat than the Meadow core, but just over a third of the peat that the Interior core accumulated. Where bulk density is strongly correlated to the percentage of inorganics in the Meadow core, it is strongly correlated to the C and N content in the Riparian core, suggesting that the physical properties of the peat are being shaped by decomposition. This notion is supported by the strong diagenetic correlations. That the $\delta^{13}C$ concentration becomes more depleted as the C:N ratio increases during the wet phase is evidence of both anaerobic decomposition and methane oxidation from high water tables and moss contents, respectively (Jones et al., 2010; Liebner et al., 2011; Nichols et al., 2009). This assertion is supported by the strong negative correlation between $\delta^{13}C$ concentration and the percentage of moss. Similar to the Meadow core, aerobic decomposition during the dry phase was high and, given that it is a much more efficient process than anaerobic decomposition (Kroetsch et al., 2011), it was more significant to soil carbon depletion in this core.

High decomposition in the Riparian core may have a lot to do with a highly fluctuating water table and nitrogen content. Contrary to what is expected with diagenesis (i.e. Kuhry and Vitt, 1996), the nitrogen profile increases with time and is a near mirror image of the C:N ratio. Anderson (2002) had similar findings in three Scottish bogs and explained this phenomenon as a function of alternating wet and dry cycles. Peatland riparian areas are hotspots for the removal of nitrates from groundwater via biotic retention (Hill, 2012), and it is possible that when water tables are high, the upper layer of the peat is enriched with a surplus of dissolved organic N that becomes mineralized when water tables descend and aerobic decomposition proceeds (Patrick and Wyatt, 1964). Over time, the amount of nitrogen mineralized exceeds the amount lost through denitrification, resulting in a net-gain. Furthermore, the local hydrology in the Riparian core would have surely been influenced by nearby ponds (Ferone and Devito, 2004; Janzen and Westbrook, 2011), and recent work has shown that peatland beaver ponds can flush nitrogen into riparian areas along lateral hyporheic flow paths (Wang et al. 2018; submitted). This may explain why nitrogen becomes especially enriched during the late Holocene, when ponded conditions prevailed in the Meadow core.

Unstable water tables and high nitrogen conditions favour graminoid vegetation (Granberg et al., 2001; Pauli et al., 2002; Potvin et al., 2014), the litter of which has been linked to increased ecosystem respiration in peatlands (Jassey et al., 2017) as it is easier for microbes to decompose (Ward et al., 2015). This explains the strong positive correlations between the $\delta^{15}N$ values and N content, and the high percentage of UOM. Humified peat is a better sink for nitrogen (Cabezas et al., 2012), which may be why the LORNA sees a greater increase during the dry phase than in the Meadow core.

6.6.5 Fen soils characterized by stable hydrology and greater carbon stocks

Given its distance from the stream, peat development in the fen (Interior core) is more reflective of hydrological inputs coming from the ground and atmosphere. The basal layer of Interior core is only 18 cm higher in elevation than the basal layer of the Riparian core and the two cores are separated by 160 m distance. Therefore, peat began accumulating overtop clay on a nearly flat surface, which are the ideal conditions for paludification (Kroetsch et al., 2011; Lavoie et al., 2005b). This explains the more stable hydrology that is apparent in the roughly singular group assignments of each phase, and in recent water table measurements from the area.

The Interior core has the highest percentage of moss and a similar C:N ratio to the Riparian core in both the wet and dry phases. The enrichment of $\delta^{13}C$ and $\delta^{15}N$ concentrations during the dry phase indicates a drop in the water table. Similar to the Meadow core, the ligneous content increases during the dry phase, which should elicit an increase in the C:N ratio as more ericaceous biomass is expected (Hornibrook et al., 2000). However, the C:N ratio goes down, which indicates increased turnover rather than a drastic change in plant community structure. This notion is supported by the decrease in herbaceous content and the increase in UOM. In all of the cores, it may be that the UOM represents the proportion of microbial biomass and, as decomposition increases, the peat C:N ratio becomes closer to that of the microbes (Wang & Moore, 2014). Nevertheless, the increased prevalence of fire during the dry phase supports an increase in shrub density and it is possible that ericaceous biomass was not well represented by the sampling methodology as large woody fragments were avoided.

The total carbon stored in the Interior core is over three-fold that stored in the Meadow core. Similar to the Riparian core, decomposition is driving changes to the physical properties of the peat as bulk density shows strong positive correlation to the C and N content. Strong negative correlations between the C:N ratio and $\delta^{13}C$ and $\delta^{15}N$ values suggest evidence of anaerobic and aerobic decomposition during the wet phase and dry phases, respectively (Jones et al., 2010; Larsson et al., 2017), and methane oxidation is likely occurring as low $\delta^{13}C$ values show a strong negative correlation to the percentage of moss (Liebner et al., 2011; Nichols et al., 2009). Unlike the other two cores, however, a relatively strong correlation exists between the $\delta^{13}C$ values and C:N ratio during the dry phase, suggesting that during the transition from wet to dry conditions, the water table did not lower too far or become much more unstable. This notion is consistent with recent water table measurements that show a high and stable water table (Table 1). Such hydrological conditions explain the higher accumulation of peat in the Interior core (Menberu et al., 2016); although, the slight water table drop during the dry phase saw a ~25% decrease in the carbon accumulation rate.

6.6.6 Topographic constraints impact spatial complexity and carbon storage

As other studies have shown, the interaction between topography and climate dictates wetland type and distribution (Halsey et al., 1997), and the timing and pathway of peat initiation (Belyea and Baird, 2006). In this study, however, we show that topography has enduring effects on peatland development as it determines to what extent the peat is exposed to other external controls over time. Thus, rather than solely acting as a boundary condition, topography is ultimately responsible for much of the spatial complexity observed. This idea is exemplified by the distance of each core to surface water features (i.e. groundwater discharge zone, stream, and beaver ponds), as more carbon accumulated in cores that were further away.

Peatland beaver meadows and other riparian areas are exposed to external pressures that areas further away from the stream are not. The most obvious difference between the cores was the time spent inundated by water. We cannot be conclusive as to what caused the marsh-like conditions, but it is reasonable to assume that some of it was from the activities of beavers. Gnawed wood has been found deep in numerous peat profiles in other mountain peatlands (Gorham et al., 2007; Kaye, 1962), and we know from historic aerial photos that the Meadow site was inundated by a beaver pond for the past seven decades.

The Meadow core was closest to the stream and it accumulated the least amount of peat, which is consistent with other studies that have reported low carbon contents in beaver meadow peat in Voyageurs National Park, Minnesota USA (Bridgham et al., 1998; Johnston, 2017; Updegraff et al., 1995). Furthermore, this finding suggests that the peatland beaver meadows studied in the same region as Sibbald (Fig. 4.1) may also be depleted in carbon, given that they had a lower percentage of organic matter than peat in adjacent areas (Fig. 4.2). In mineral soil environments, the cyclic construction and abandonment of beaver ponds is associated with an accumulation of carbon (Johnston, 2014; Wohl et al., 2012); however, this does not seem to be the case in peatlands. Our results show that these areas produce labile substrates that are quickly decomposed, leaving behind a higher fraction of refractory material (i.e. ligneous). Furthermore, similar to the findings of Bridgham et al. (1998), carbon accumulation tends to decrease as bulk density increases, and in the Meadow core, bulk density is largely controlled by inorganic deposits. Inorganic sediments can be deposited by overbank floods (Candel et al., 2017) but they can also be trapped by beaver ponds in both mineral soil (Correll et al., 2000; Maret et al., 1987) and peatland environments (Supporting information). Such additions may aid aerobic decomposition when ponds wash out as there was little evidence of anaerobic diagenesis. This would seem to contradict the fact that peatland beaver ponds are hotspots for methane release (Bubier et al., 1993; Roulet et al., 1997; Wik et al., 2016), but the carbon released may not originate from the peat itself; instead, it may have been introduced by fluvial means as storm events flush waters into the stream that are enriched in organic carbon (Elder et al., 2000; Limpens et al., 2008; Stimson et al., 2017). This notion is supported by the regional sampling of peatland beaver ponds, where over half of the sediments trapped by ponds were organic (Table 4.1).

As distance from the stream increased, so too did the carbon accumulation rate. Although the Riparian core was still influenced by the nearby stream, its higher base elevation buffered the magnitude of impacts and left the peat surface free from inundation more often. However, the core's near proximity to the stream and unstable hydrology made it a hotspot for nitrogen mineralization (Hill, 2012), which dictated the plant community structure and subsequent turnover rate. The possibility that the beaver pond could have also been a source of nitrogen to this location (Wang et al. 2018; submitted) is another way in which beavers may be agents of soil formation in peatlands.

The Interior core was not exposed to the pressures exerted by the stream, allowing it to accumulate nearly three times as much carbon as the other two cores. The peat in this core developed overtop a relatively flat surface with a relatively stable hydrology. As the peat accumulated, internal controls raised the water table with it (Clymo, 1984), which after time made it more susceptible to perturbations in the local climate (Glaser et al., 1996). The warmer conditions of the late Holocene caused a slight drop in the water table that amounted to a 25% reduction in the carbon accumulation rate. Such a response indicates the peatland's sensitivity to climate and provides useful insight into how peatlands may adapt to further changes. Although the carbon accumulation rate was decreased, this location was still an efficient carbon sink, further challenging the notion that carbon stores in northern peatlands will shrink under a warming climate (Bacon et al., 2017).

6.7 Conclusions

Our results show how soil forming factors come together within different areas of a peatland, creating differential rates of carbon accumulation. Carbon storage estimates typically rely on cores collected from the center of peatlands or where the thickest peat is found (Bacon et al., 2017; Loisel et al., 2017). It is rare that multiple cores are used for carbon storage estimates at the peatland scale, and almost never is the spatial complexity within the peatland accounted for. This research provides insight into how such complexity manifests in terms of the processes elicited. We found that the exposure of each core to different external pressures over time is strongly mediated by its topographic position and proximity to surface water features. Such pressures are partially responsible for the current state of the peatland at each location in terms of the plant community characteristics, peat properties, and total carbon accumulated. The lowest amount of peat accumulated in the beaver meadow, where peat initiation was delayed and frequent inundation encouraged sediment deposits that enhanced turnover rates during dry periods. There was a slight decrease in turnover in the riparian area, where high biogeochemical activity and unstable hydrology favored the growth of herbaceous vegetation that was easily decomposed. Peat accumulation was highest in the interior of the peatland, away from the stream, where peat first began to accumulate and where strong internal feedbacks facilitated a relatively stable hydrology over time.

Few studies link topography to spatially complex areas within peatlands such as fens, and models that estimate carbon budgets in peatlands are generally limited to ombrotrophic bogs as they rely on predictable internal feedbacks with low external forcing (Malhotra et al., 2016). This work furthers our understanding of the types of external forcing, and associated impacts, that can be expected given a certain topographic position and proximity to different features. Furthermore, we add insight to the potential legacy of beaver activity in peatlands. Future work should focus on validating whether processes are consistent in peatland areas that exhibit similar properties and surface characteristics, and whether predictable relationships exist between them. Establishing such may support the meaningful inclusion of external factors in models that are currently limited to the interaction between climate and internal peatland controls.

7. SYNTHESIS AND CONCLUSIONS

Previous studies on beaver-mediated hydrological and biogeochemical impacts have been primarily focused in riverine/mineral soil environments, where the ecosystem engineering activities of beavers are more clearly defined (Naiman et al., 1986). The goal of this dissertation was to extend this knowledge to the organic soil landscapes beaver inhabit, such as peatlands. In Canada alone, peatlands cover 12% of the land surface and store approximately 56% of the country's terrestrial carbon (Tarnocai, 2009). Peat formation depends on the relative importance and interaction of a host of internal and external factors (Waddington et al., 2015). To what extent beavers are a factor is largely unknown; therefore, the following research objectives were pursued: 1) characterize beaver pond morphometry and surface water storage in a variety of different physiographic settings in North America; 2) determine if beaver-mediated sediment aggradation occurs in peatlands at a regional scale and assess the potential impact of such on beaver meadow soils; 3) determine the impact of beaver activity on water table dynamics at the peatland scale; and, 4) disentangle the drivers of peat accumulation in a beaver meadow over time to further elucidate the legacy impacts of beaver activity in these environments.

This study analyzed numerous spatial beaver pond models to characterize general beaver pond morphometry with regards to surface water storage capacity, and to test whether simple tools could be developed to estimate this capacity (Chapter 3). The research then focuses in on montane peatland environments, where soil and water samples were collected to test the properties of beaver meadow soils and test whether sediment aggradation occurs in these environments (Chapter 4). Groundwater is the focus of the next study, where a multi-year water table dataset is analyzed to determine how beaver impact water table dynamics at the peatland scale (Chapter 5). Finally, three peat cores were collected from areas of the peatland that represent its inherent spatial complexity (e.g. beaver meadow). Multi-proxy analysis was employed on each core to determine the soil forming factors that best explain the peat properties and differential rates of accumulation in each area (Chapter 6). The main findings of this research are summarized in the following section.

7.1 Summary of findings

The activities of beavers have profound impacts on peatland landscapes that endure through time. Beavers alter many of the same geomorphological and ecohydrological processes that they do in riverine/mineral soil environments, but with different outcomes. Beaver-mediated impacts in peatlands can be divided into those within the zone inundated by the dam and those outside of it.

Within the area inundated by the dam, the impacts of beavers are more pronounced as changes mostly occur above the surface. In all of the different landscapes studied, beavers tended to build ponds that have a convex bathymetry as dams would often extend past a narrow stream channel and inundate the adjacent area that was, in many cases, more gradual (Chapter 3). This was especially true in the SRW, where beavers were observed to build dams in a different way than what is reported (Chapter 5). Peat was a primary dam-building material that beavers excavated to create berm-like structures above the land surface. This building style allowed dams to extend far beyond the stream channel, inundating much greater surface areas. Furthermore, the immovable nature of these structures combined with the relatively low streamflow energy characteristic of peatland streams, allowed beaver ponds to persist for time periods of up to 70 years. Even after dams breached and ponds were abandoned by beavers, the berm-like structures remained and maintained some function. Peat excavation by beavers also changed the physical shape of the peatland and de-anchored peat that may have otherwise remained stationary for many millennia.

Contrary to what has been found in riverine/mineral soil environments (e.g. Johnston, 2014; Polvi and Wohl, 2012), the presence of beaver ponds did not result in an increase in organic matter within the ponded area. Instead, the beaver meadow accumulated the least amount of peat over time compared to peat in areas not subject to inundation (Chapter 6). Loss on ignition tests of peat from beaver-impacted peatlands within the region further support this notion (Chapter 4), and the main findings that explain this are summarized by the system dynamics model shown in Figure 7.1. As the beaver population increases, so does the number of ponds. An increase in ponds results in an overall decrease in NPP (Reddoch and Reddoch, 2005), as aquatic production does not exceed that lost from the inundation of highly productive riparian areas and the consumption of shrubby biomass by beaver. Anaerobic conditions, however, slows the decomposition of organic matter that is either produced locally or introduced by fluvial means. While the dams are functional, the ponds aggrade both organic and inorganic sediments (Chapter 4). Such additions to the peat matrix change the physicochemical properties of the peat by increasing the bulk density and introducing nutrients and electron acceptors (Chapter 6; Naiman et al., 1994). When the beaver ponds washout and the meadow is exposed, the aggraded sediments facilitate the enhanced production of graminoid plant species as they outcompete ericaceous shrubs and mosses in highly trophic conditions (Pauli et al., 2002). However, the plant material produced is quickly decomposed because it is more labile than ericaceous biomass and because aerobic decomposition is also amplified by the abundant supply of electrons and shorter diffusion pathways from the increased bulk density (Rezanezhad et al., 2016a). Thus, the full cycle of beaver-pond creation and washout produces an overall net-loss of carbon from within the ponded area.

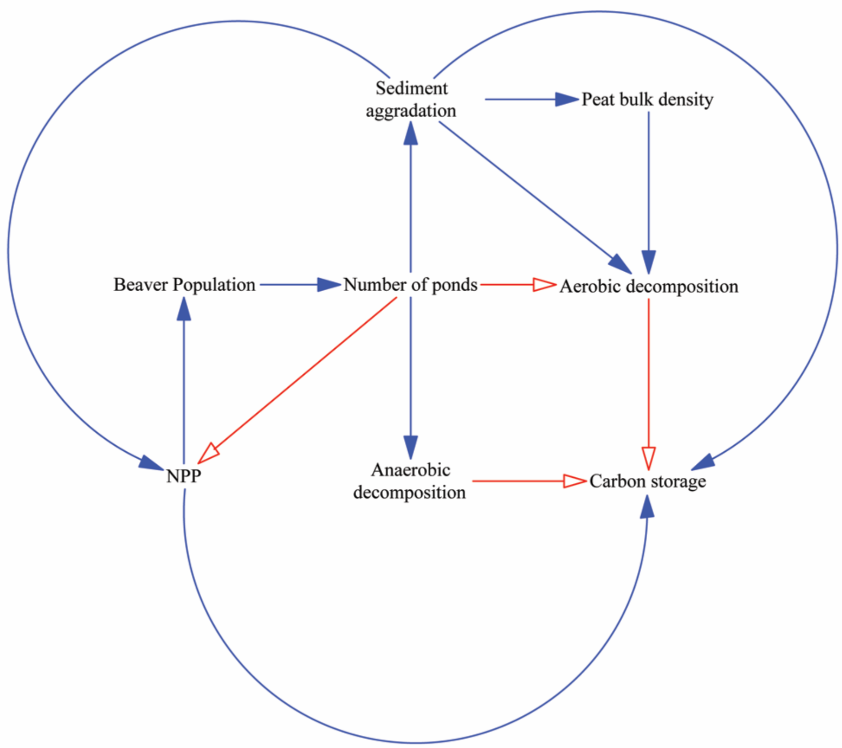

Fig. 7.1 System dynamics model describing positive and negative feedbacks between beaver populations and peat accumulation/carbon storage within areas inundated by beaver ponds. Blue solid arrows represent positive feedbacks, whereas red open arrows represent negative feedbacks.

Although beaver activity was found to decrease carbon stocks in the zone of inundation, its impact may have the opposite effect in areas beyond the pond. Within a 150-m proximity, beaver dams exerted control over water table dynamics in the SRW by rerouting groundwater away from the stream and into longer down-valley flow paths (Chapter 5). With the dams intact, the water table was ~13 cm higher and nearly twice as stable, constituting an increase in groundwater storage and buffering against climate induced variation, respectively. The higher and more stable water table may also have significant implications for peat accumulation as described by the system dynamics model shown in Figure 7.2. Plant community composition in peatlands is extremely sensitive to water table dynamics (Menberu et al., 2016); high and stable water tables produce a moss-dominated ecosystem, whereas the reverse produces a shrub-grass dominated ecosystem (Chapter 6; Kettridge et al., 2015). Anaerobic and aerobic decomposition also increases and decreases, respectively, but not nearly to the same magnitude as complete inundation. Instead, terrestrial and semi-aquatic plants are still produced, but their decomposition is slowed, as described by most peatland models (Baird et al., 2012; Belyea and Clymo, 2001). Furthermore, the reduction of shrubby biomass via changing water table dynamics and harvesting by beavers would likely reduce the prevalence of fire (Kettridge et al., 2015). Overall, the impact of beaver activity on peatland water tables likely produces a net-gain of carbon within affected areas. Where previous studies have anecdotally linked the creation of beaver ponds to the emergence of new plant communities (Mitchell and Niering, 1993; Walbridge, 1994), this research confirms a mechanism by which this can happen.

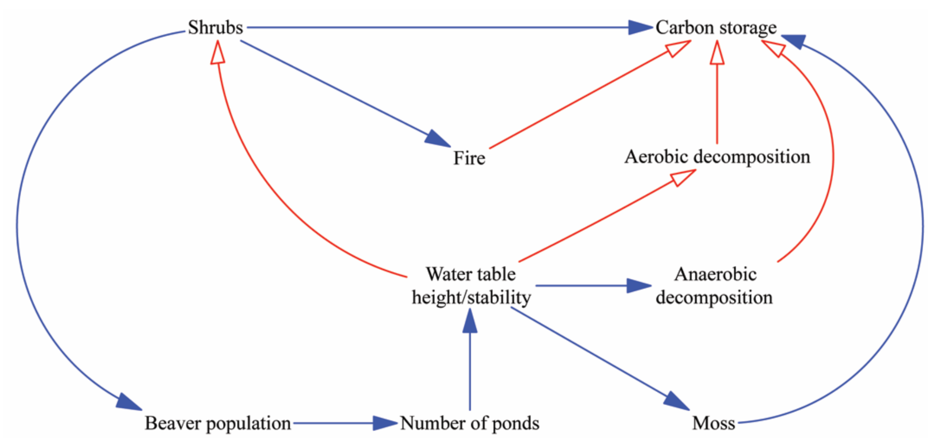

Fig. 7.2 System dynamics model describing positive and negative feedbacks between beaver populations and peat accumulation/carbon storage in areas beyond the pond (i.e. within 150-m proximity of beaver dams). Blue solid arrows represent positive feedbacks, whereas red open arrows represent negative feedbacks.

At the very least, this research shows that beaver activity can alter the appearance of peatlands and exert control over processes fundamental to their function as a carbon sink. This activity leaves a legacy beyond cyclic pond creation and abandonment that contributes to the spatial complexity of the peatland. Beavers deserve greater inclusion in peatland conceptual models and deeper investigation is required in the peatlands they are known to inhabit.

7.2 Future research

This research shows how beaver activity can manipulate peatland processes and how peat develops in beaver-impacted areas. However, definitive links between what beavers do and what happens to the peat as a result have not been established. A logical first step in future research is to investigate the hypothesized outcomes from beaver-mediated process manipulation, particularly as they relate to broader questions about carbon cycling, catchment hydrology, and climate change.

Many questions still exist regarding carbon cycling in beaver-inhabited peatlands. For example, beaver ponds are well known hotspots for methane emissions (Bubier et al., 1993; Wik et al., 2016), but the source of these emissions has never been determined. Roulet et al. (1997) argued that emissions likely originated from the underlying peat because the pond did not constitute a net source of dissolved organic carbon and because much of the woody biomass introduced by beaver is hard to decompose. However, the research presented here did not find clear evidence that anaerobic processes were significant to shaping the physicochemical properties of peat, and over half of the suspended sediments deposited in the beaver ponds were organic. It is possible that, in addition to methane release, beaver ponds are also hotspots for the deposition of labile organic sediments from the surrounding landscape. If true, this would comprise an important find for exported carbon from these environments, but finding answers requires a deeper investigation of the quantity and quality of organics imported/exported to/from peatland beaver ponds by both beavers and hydrological processes. Also, it is important to ask - how much carbon does a peatland beaver pond produce? The amount of biomass from aquatic macrophytes and algae that grows in a typical beaver pond is currently unclear, as is its fate. Questions such as - does biomass accumulate in the pond over time (?), or is it entirely decomposed (?), need answering.

Similar questions also arise beyond the pond. A limitation of this research is that links between the water table and the surrounding plant community could not be established. Future studies should remedy this by characterizing both the plant community (to the species level) and water table dynamics, while beaver dams are intact and after they are breached. Such research would further benefit from additional instrumentation that measures other important ecohydrological variables like vertical hydraulic gradients and soil moisture, to name a few.

Finally, the link between deposition in beaver ponds and enhanced decomposition in beaver meadows requires more investigation as much of the previous literature on peat decomposition/mineralization (e.g. Bridgham et al., 1998; Rezanezhad et al., 2016) has relied on findings from lab incubations. In-situ experimental designs are needed, where peat properties and production/decomposition rates are measured along meaningful spatial gradients in ponds (before and after they washout). High resolution (i.e. ≤ 1–cm) multi-proxy core reconstructions of beaver meadow soils would also be useful for looking at peat development over timescales closer to a lifespan of a beaver pond. Without these insights (both inside and outside the pond), it is not possible to determine to what extent soil formation in peatlands is influenced by beavers, nor is it possible to reasonably estimate and/or forecast carbon budgets in peatlands that beavers inhabit.

The impact of beavers on hydrological processes at the pond and catchment scale also needs more probing. This research developed, and tested pre-existing, approaches for estimating reliable surface water volumes in beaver ponds with a variety of data limitations. Such tools should be adapted into new and pre-existing models to help elucidate surface water contributions to local and regional water balances from beaver ponds. More work is also needed to characterize the impact of ponds on groundwater in both the peat and alluvial aquifers, and determine if there is an impact to baseflow. This research showed how beaver dams can impact water tables in the adjacent peatland, but how flow paths and hydraulic gradients change within the pond itself is still unstudied. A practical approach to answer such questions would be to create physically-based models and run them with empirically derived variables - bringing insight into how interactions between beaver-mediated hydrological processes and underlying soil properties control groundwater flow in and around ponds. Lastly, In all of the beaver-inhabited montane peatlands studied, relic dams, more akin to berms, were present in the riparian areas. Their presence suggests that, even after washout, peatland beaver dams may maintain some hydrological function. In periods of high runoff (e.g. spring snowmelt and extreme precipitation events), these dams may act as natural stormwater ponds, extending the floodplain and attenuating stormflow release downstream. As most montane peatlands form near low order streams, the cumulative impact on regional stormflow may be significant.

The study of beaver-mediated impacts in peatlands needs broadening out beyond the montane peatlands studied here. For example, vast areas of the boreal forest and Hudson Bay Lowlands, are covered by peat and, in these environments, beavers are well-documented inhabitants (Turetsky and St. Louis, 2006). The different physiographic conditions of these areas presents an opportunity for further insight, as does the fact that beavers are reclaiming most of this territory after removal from the fur trade. Moreover, as the climate warms, beaver populations are expanding northwards and densifying (Jarema et al., 2009). Peatlands within these areas should be evaluated for their capacity to support beaver in an effort to predict how these natural engineers may transform these landscapes and contribute to climate change over time.

REFERENCES

ACECSS, 1998. The Canadian System of Soil Classification, 3rd ed. Ottawa.

Admiral, S.W., Lafleur, P.M., 2007. Partitioning of latent heat flux at a northern peatland. Aquat. Bot. 86, 107–116. doi:10.1016/j.aquabot.2006.09.006

Amlin, N.A., Rood, S.B., 2001. Inundation tolerances of riparian willows and cottonwoods. J. Am. Water Resour. Assoc. 37, 1709–1720. doi:10.1111/j.1365-2028.1969.tb01201.x

Anderson, D.E., 2002. Carbon accumulation and C/N ratios of peat bogs in north-west scotland. Scottish Geogr. J. 118, 323–341. doi:10.1080/00369220218737155

Andersson, R.A., Meyers, P., Hornibrook, E., Kuhry, P., Mörth, C.M., 2012. Elemental and isotopic carbon and nitrogen records of organic matter accumulation in a holocene permafrost peat sequence in the east European Russian arctic. J. Quat. Sci. 27, 545–552. doi:10.1002/jqs.2541

Andersson, S., Schoning, K., 2010. Surface wetness and mire development during the late Holocene in central Sweden. Boreas 39, 749–760. doi:10.1111/j.1502-3885.2010.00157.x

Bacon, K.L., Baird, A.J., Blundell, A., Bourgault, M.-A., Chapman, P.J., Dargie, G., Dooling, G.P., Gee, C., Holden, J., Kelly, T., McKendrick-Smith, K.A., Morris, P.J., Nobel, A., Palmer, S.M., Quillet, A., Swindles, G.T., Watson, E.J., Young, D.., 2017. Questioning ten common assumptions about peatlands. Mires Peat 19, 1–23. doi:10.19189/MaP.2016.OMB.253

Baird, A., 1997. Field estimation of macropore functioning and surface hydraulic conductivity in a fen peat. Hydrol. Process. 11, 287–295.

Baird, A.J., Morris, P.J., Belyea, L.R., 2012. The DigiBog peatland development model 1: rationale, conceptual model, and hydrological basis. Ecohydrology 5, 242–255. doi:10.1002/eco.230

Baird, A.J., Waldron, S., 2003. Shallow horizontal groundwater flow in peatlands is reduced by bacteriogenic gas production. Geophys. Res. Lett. 30, 2043. doi:10.1029/2003GL018233

Baker, B.W., Hill, E.P., 2003. Beaver (Castor canadensis), in: Feldhamer, G., Thompson, B., Chapman, J. (Eds.), Wild Mammals of North America: Biology, Management, and Conservation. The John Hopkins University Press, Baltimore, Maryland, pp. 288–310.

Baldini, A., Oltremari, J., Ramírez, M., 2008. Impact of american beaver (Castor canadensis , Rodentia) in lenga (Nothofagus pumilio) forests of Tierra del Fuego , Chile. Bosque 29, 162–169.

Ballantyne, D.M., Hribljan, J. a., Pypker, T.G., Chimner, R. a., 2014. Long-term water table manipulations alter peatland gaseous carbon fluxes in Northern Michigan. Wetl. Ecol. Manag. 22, 35–47. doi:10.1007/s11273-013-9320-8

Barko, J.W., Smart, M.R., 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. Ecology 67, 1328–1340.

Bauer, I.E., 2004. Modelling effects of litter quality and environment on peat accumulation over different time-scales. J. Ecol. 92, 661–674. doi:10.1111/j.0022-0477.2004.00905.x

Beckwith, C.W., Baird, A.J., 2001. Effect of biogenic gas bubbles on water flow through poorly decomposed blanket peat. Water Resour. Res. 37, 551–558. doi:10.1029/2000WR900303

Beckwith, C.W., Baird, A.J., Heathwaite, a. L., 2003. Anisotropy and depth-related heterogeneity of hydraulic conductivity in a bog peat. II: modelling the effects on groundwater flow. Hydrol. Process. 17, 103–113. doi:10.1002/hyp.1117

Beer, J., Blodau, C., 2007. Transport and thermodynamics constrain belowground carbon turnover in a northern peatland. Geochim. Cosmochim. Acta 71, 2989–3002. doi:10.1016/j.gca.2007.03.010

Beierle, B., Smith, D., Hills, L., 2003. Late Quaternary Glacial and Environmental History of the Burstall Pass Area , Kananakis Country, Alberta, Canada. Arctic, Antarct. Alp. Res. 35, 391–398.

Beierle, B., Smith, D.G., 1998. Severe drought in the early Holocene (10,000 – 6800 BP) interpreted from lake sediment cores, southwestern Alberta, Canada. Palaeogeogr. Palaeoclimatol. Palaeoecol. 140, 75–83.

Belyea, L.R., Baird, A.J., 2006. Beyond "The Limits to Peat Bog Growth": Cross-Scale Feedback in Peatland Development. Ecol. Monogr. 76, 299–322.

Belyea, L.R., Clymo, R.S., 2001. Feedback control of the rate of peat formation. Proc. R. Soc. Biol. Sci. 268, 1315–21. doi:10.1098/rspb.2001.1665

Belyea, L.R., Lancaster, J., 2002. Inferring landscape dynamics of bog pools from scaling relationships and spatial patterns. J. Ecol. 90, 223–234. doi:10.1046/j.1365-2745.2001.00647.x

Binnema, T., Niemi, M., 2006. Let the Line Be Drawn Now. Environ. Hist. Durh. N. C. 11, 724–

750.
Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474. doi:10.1214/11-BA618
Blodau, C., 2002. Carbon cycling in peatlands - A review of processes and controls. Environ. Rev. 10, 111–134. doi:10.1139/a02-004
Boomer, K.M.B., Bedford, B.L., 2008. Influence of nested groundwater systems on reduction-oxidation and alkalinity gradients with implications for plant nutrient availability in four New York fens. J. Hydrol. 351, 107–125. doi:10.1016/j.jhydrol.2007.12.003
Booth, R.K., Lamentowicz, M., Charman, D.J., 2010. Preparation and analysis of testate amoebae in peatland palaeoenvironmental studies. Mires Peat 7, 1–7.
Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R, Media. Springer New York, New York, NY. doi:10.1007/978-1-4419-7976-6
Breeuwer, A., Robroek, B.J.M., Limpens, J., Heijmans, M.M.P.D., Schouten, M.G.C., Berendse, F., 2009. Decreased summer water table depth affects peatland vegetation. Basic Appl. Ecol. 10, 330–339. doi:10.1016/j.baae.2008.05.005
Bridgham, S., Johnston, C., Pastor, J., Updegraff, K., 1995. Potential Feedbacks of Northern Wetlands on Climate Change. Bioscience 45, 262–274.
Bridgham, S.D., Updegraff, K., Pastor, J., 1998. Carbon, nitrogen, and phosphorous mineralization in northern wetlands. Ecology 79, 1545–1561.
Briggs, M.A., Lautz, L.K., McKenzie, J.M., Gordon, R.P., Hare, D.K., 2012. Using high-resolution distributed temperature sensing to quantify spatial and temporal variability in vertical hyporheic flux. Water Resour. Res. 48, n/a-n/a. doi:10.1029/2011WR011227
Broder, T., Blodau, C., Biester, H., Knorr, K.H., 2012. Peat decomposition records in three pristine ombrotrophic bogs in southern Patagonia. Biogeosciences 9, 1479–1491. doi:10.5194/bg-9-1479-2012
Brooks, R.T., Hayashi, M., 2002. Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. Wetlands 22, 247–255. doi:10.1672/0277-5212(2002)022[0247:DAVAHR]2.0.CO;2
Bubier, J., Moore, T., Roulet, N., 1993. Methane emissions from wetlands in the midboreal region of Northern Ontario, Canada. Ecology 74, 2240–2254.
Bubier, J.L., Crill, P.M., Moore, T.R., Savage, K., 1998. Seasonal patterns and controls on net

ecosystem CO2 exchange in a boreal peatland complex. Global Biogeochem. Cycles 12, 703–714.

Burns, D. a., McDonnell, J.J., 1998. Effects of a beaver pond on runoff processes: comparison of two headwater catchments. J. Hydrol. 205, 248–264. doi:10.1016/S0022-1694(98)00081-X

Butler, D.R., Malanson, G.P., 2005. The geomorphic influences of beaver dams and failures of beaver dams. Geomorphology 71, 48–60. doi:10.1016/j.geomorph.2004.08.016

Butler, D.R., Malanson, G.P., 1995. Sedimentation rates and patterns in beaver ponds in a mountain environment. Geomorphology 13, 255–269.

Cabezas, A., Gelbrecht, J., Zwirnmann, E., Barth, M., Zak, D., 2012. Effects of degree of peat decomposition, loading rate and temperature on dissolved nitrogen turnover in rewetted fens. Soil Biol. Biochem. 48, 182–191. doi:10.1016/j.soilbio.2012.01.027

Cabin, R.J., Mitchell, R.J., 2000. To Bonferonni or not to Bonferonni: When and how are the questions. Bull. Ecoloical Soc. Am. 81, 246–248. doi:10.2307/20168454

Cain, S., 1939. Pollen analysis as a paleo-ecological research method. Bot. Rev. 5, 627–654.

Candel, J.H.J., Makaske, B., Storms, J.E.A., Wallinga, J., 2017. Oblique aggradation: a novel explanation for sinuosity of low-energy streams in peat-filled valley systems. Earth Surf. Process. Landforms. doi:10.1002/esp.4100

Chambers, F.M., Beilman, D.W., Yu, Z., 2011. Methods for determining peat humification and for quantifying peat bulk density , organic matter and carbon content for palaeostudies of climate and peatland carbon dynamics. Mires Peat 7, 1–10. doi:Chambers, Frank M and Beilman, D W and Yu, Z and others, (2011) Methods for determining peat humification and for quantifying peat bulk density, organic matter and carbon content for palaeostudies of climate and peatland carbon dynamics. Mires and Peat, 7 (7). pp. 1-10. ISSN 1819-754X

Chambers, F.M., Booth, R.K., De Vleeschouwer, F., Lamentowicz, M., Le Roux, G., Mauquoy, D., Nichols, J.E., van Geel, B., 2012. Development and refinement of proxy-climate indicators from peats. Quat. Int. 268, 21–33. doi:10.1016/j.quaint.2011.04.039

Chanton, J., Bauer, J., Glaser, P., 1995. Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands. Geochim. Cosmochim. Acta 59, 3663–3668.

Chanton, J.P., Glaser, P.H., Chasar, L.S., Burdige, D.J., Hines, M.E., Siegel, D.I., Tremblay, L.B., Cooper, W.T., 2008. Radiocarbon evidence for the importance of surface vegetation on fermentation and methanogenesis in contrasting types of boreal peatlands. Global Biogeochem. Cycles 22, n/a-n/a. doi:10.1029/2008GB003274

Charman, D., 2002. Peatlands and environmental change. John Wiley and Sons Ltd., West Sussex.

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J. a., Gallego-Sala, a., Harrison, S.P., Hughes, P.D.M., Jackson, S.T., Korhola, a., Mauquoy, D., Mitchell, F.J.G., Prentice, I.C., van der Linden, M., De Vleeschouwer, F., Yu, Z.C., Alm, J., Bauer, I.E., Corish, Y.M.C., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Sillasoo, Ü., Swindles, G.T., Tuittila, E.-S., Ukonmaanaho, L., Väliranta, M., van Bellen, S., van Geel, B., Vitt, D.H., Zhao, Y., 2013. Climate-related changes in peatland carbon accumulation during the last millennium. Biogeosciences 10, 929–944. doi:10.5194/bg-10-929-2013

Charman, D.J., West, S., Kelly, A., Grattan, J., 1995. Environmental change and tephra deposition: The strath of Kildonan, Northern Scotland. J. Archaeol. Sci. 22, 799–809. doi:10.1016/0305-4403(95)90009-8

Chasar, L.S., Chanton, J., Glaser, P., Siegel, D., 2000. Methane Concentration and Stable Isotope Distribution as Evidence of Rhizospheric Processes: Comparison of a Fen and Bog in the Glacial Lake Agassiz Peatland Complex. Ann. Bot. 86, 655–663. doi:10.1006/anbo.2000.1172

Chasar, L.S., Chanton, J.P., Glaser, P.H., Siegel, D.I., Rivers, J.S., 2000. Radiocarbon and stable carbon isotopic evidence for transport and transformation of dissolved organic carbon, dissolved inorganic carbon, and CH4 in a northern Minnesota peatland. Global Biogeochem. Cycles 14, 1095–1108. doi:10.1029/1999GB001221

Chen, Y. Te, Borken, W., Stange, C.F., Matzner, E., 2012. Dynamics of nitrogen and carbon mineralization in a fen soil following water table fluctuations. Wetlands 32, 579–587. doi:10.1007/s13157-012-0295-7

Chimner, R. a., Cooper, D.J., Parton, W.J., 2002. Modeling carbon accumulation in Rocky Mountain fens. Wetlands 22, 100–110. doi:10.1672/0277-5212(2002)022[0100:MCAIRM]2.0.CO;2

Clement, S., 2005. The future stability of upland blanket peat following historical erosion and recent re-vegetation. Durham University.

Clymo, R.S., 1984. The limits to peat bog growth. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 303, 605–654.

Comas, X., Slater, L., Reeve, A., 2005. Stratigraphic controls on pool formation in a domed bog inferred from ground penetrating radar (GPR). J. Hydrol. 315, 40–51. doi:10.1016/j.jhydrol.2005.04.020

Comas, X., Slater, L., Reeve, a. S., 2011. Pool patterning in a northern peatland: Geophysical evidence for the role of postglacial landforms. J. Hydrol. 399, 173–184. doi:10.1016/j.jhydrol.2010.12.031

Cooper, D.J., Chimner, R.A., Merrit, D.M., 2012. Western Mountain Wetlands, in: Batzer, D.P., Baldwin, A.H. (Eds.), Wetland Habitats of North America: Ecology and Conservation Concerns. University of California Press, Berkeley, pp. 313–328.

Corbett, J.E., Tfaily, M.M., Burdige, D.J., Cooper, W.T., Glaser, P.H., Chanton, J.P., 2012. Partitioning pathways of CO2 production in peatlands with stable carbon isotopes. Biogeochemistry 114, 327–340. doi:10.1007/s10533-012-9813-1

Correll, D., Jordan, T., Weller, D., 2000. Beaver pond biogeochemical effects in the Maryland Coastal Plain. Biogeochemistry 217–239.

Cowell, D.W., 1984. The Canadian beaver, Castor canadensis, as a geomorphic agent in karst terrain. Can. Field-Naturalist 98, 227–230.

Cunliffe, A.M., Baird, A.J., Holden, J., 2013. Hydrological hotspots in blanket peatlands: Spatial variation in peat permeability around a natural soil pipe. Water Resour. Res. 49, 5342–5354. doi:10.1002/wrcr.20435

Dimitrov, D.D., Grant, R.F., Lafleur, P.M., Humphreys, E.R., 2011. Modeling the effects of hydrology on gross primary productivity and net ecosystem productivity at Mer Bleue bog. J. Geophys. Res. 116, G04010. doi:10.1029/2010JG001586

Duval, T., Waddington, J., Branfireun, B., 2012. Hydrological and biogeochemical controls on plant species distribution within calcareous fens. Ecohydrology 89, 73–89. doi:10.1002/eco

Duval, T.P., Waddington, J.M., 2012. Landscape and weather controls on fine-scale calcareous fen hydrodynamics. Hydrol. Res. 43, 780. doi:10.2166/nh.2011.127

Duval, T.P., Waddington, J.M., 2011. Extreme variability of water table dynamics in temperate calcareous fens: Implications for biodiversity. Hydrol. Process. 25, 3790–3802. doi:10.1002/hyp.8109

Elder, J.F., Rybicki, N.B., Carter, V., Weintraub, V., 2000. Sources and yields of dissolved carbon in northern Wisconsin stream catchments with differing amounts of peatland. Wetlands 20, 113–125. doi:10.1672/0277-5212(2000)020[0113:SAYODC]2.0.CO;2

Elliott, S.M., Roe, H.M., Patterson, R.T., 2012. Testate amoebae as indicators of hydroseral change: An 8500 year record from Mer Bleue Bog, eastern Ontario, Canada. Quat. Int. 268, 128–144. doi:10.1016/j.quaint.2011.08.020

ESRI, 2015. ArcGIS Desktop.

Evans, M., Warburton, J., 2005. Sediment budget for an eroding peat-moorland catchment in northern England. Earth Surf. Process. Landforms 30, 557–577. doi:10.1002/esp.1153

Evans, M.G., Burt, T.P., Holden, J., Adamson, J.K., 1999. Runoff generation and water table fluctuations in blanket peat: evidence from UK data spanning the dry summer of 1995. J. Hydrol. 221, 141–160. doi:10.1016/S0022-1694(99)00085-2

Fang, X., Pomeroy, J.W., Westbrook, C.J., Guo, X., Minke, A.G., Brown, T., 2010. Prediction of snowmelt derived streamflow in a wetland dominated prairie basin. Hydrol. Earth Syst. Sci. 991–1006. doi:10.5194/hess-14-991-2010

Ferone, J.M., Devito, K.J., 2004. Shallow groundwater–surface water interactions in pond–peatland complexes along a Boreal Plains topographic gradient. J. Hydrol. 292, 75–95. doi:10.1016/j.jhydrol.2003.12.032

Flynn, N.J., 2006. Spatial associations of beaver ponds and culverts in boreal headwater streams. University of Alberta.

Foster, D.R., Wright, H.E., 1990. Role of ecosystem development and climate change in bog formation in central Sweden. Ecology 71, 450–463.

Fraser, C., Roulet, N., Lafleur, M., 2001. Groundwater flow patterns in a large peatland. J. Hydrol. 246, 142–154.

Freeman, C., Ostle, N., Kang, H., 2001. An enzymic “latch” on a global carbon store. Nature 409, 149–150.

Frolking, S., Roulet, N.T., Moore, T.R., Richard, P.J.H., Lavoie, M., Muller, S.D., 2001. Modeling Northern Peatland Decomposition and Peat Accumulation. Ecosystems 4, 479–498. doi:10.1007/s10021-001-0105-1

Gałka, M., Tobolski, K., Górska, A., Lamentowicz, M., 2017. Resilience of plant and testate amoeba communities after climatic and anthropogenic disturbances in a Baltic bog in

Northern Poland: Implications for ecological restoration. The Holocene 27, 130–141. doi:10.1177/0959683616652704

Glaser, P.H., Bennett, P.C., Siegel, D.I., Romanowicz, E. a., 1996. Palaeo-reversals in groundwater flow and peatland development at Lost River, Minnesota, USA. The Holocene 6, 413–421. doi:10.1177/095968369600600403

Glaser, P.H., Chanton, J.P., Morin, P., Rosenberry, D.O., Siegel, D.I., Ruud, O., Chasar, L.I., Reeve, a. S., 2004. Surface deformations as indicators of deep ebullition fluxes in a large northern peatland. Global Biogeochem. Cycles 18, n/a-n/a. doi:10.1029/2003GB002069

Gleason, R. a, Tangen, B. a, Laubhan, M.K., Kermes, K.E., Euliss, N.H., 2007. Estimating water storage capacity of existing and potentially restorable wetland depressions in a subbasin of the Red River of the North.

Gorham, E., 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. 1, 182–195.

Gorham, E., Lehman, C., Dyke, A., Janssens, J., Dyke, L., 2007. Temporal and spatial aspects of peatland initiation following deglaciation in North America. Quat. Sci. Rev. 26, 300–311. doi:10.1016/j.quascirev.2006.08.008

Granath, G., Strengbom, J., Rydin, H., 2010. Rapid ecosystem shifts in peatlands : linking plant physiology and succession. Ecology 91, 3047–3056.

Granberg, A.G., Sundh, I., Svensson, B.H., Nilsson, M., Ecology, S., Jul, N., 2001. Effects of Temperature, and Nitrogen and Sulfur Deposition, on Methane Emission from a Boreal Mire. Ecology 82, 1982–1998.

Green, K.C., Westbrook, C.J., 2009. Changes in riparian area structure, channel hydraulics, and sediment yield following loss of beaver dams. BC J. Ecosyst. Manag. 10, 68–79.

Grundling, P., Grootjans, a. P., Price, J.S., Ellery, W.N., 2013. Development and persistence of an African mire: How the oldest South African fen has survived in a marginal climate. Catena 110, 176–183. doi:10.1016/j.catena.2013.06.004

Gurnell, A.M., 1998. The hydrogeomorphological effects of beaver dam-building activity. Prog. Phys. Geogr. 22, 167–189. doi:10.1177/030913339802200202

Halley, D., Rosell, F., Saveljev, A., 2012. Population and distribution of Eurasian beaver (Castor fiber). Balt. For. 18, 168–175.

Halsey, L., Vitt, D., Zoltai, S., 1997. Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada. Wetlands 17, 243–262. doi:10.1007/BF03161413

Hay, K.G., 2010. Succession of Beaver Ponds in Colorado 50 Years After Beaver Removal. J. Wildl. Manage. 74, 1732–1736. doi:10.2193/2009-055

Hayashi, M., Quinton, W.L., Pietroniro, A., Gibson, J.J., 2004. Hydrologic functions of wetlands in a discontinuous permafrost basin indicated by isotopic and chemical signatures. J. Hydrol. 296, 81–97. doi:10.1016/j.jhydrol.2004.03.020

Hayashi, M., van der Kamp, G., 2000. Simple equations to represent the volume-area-depth relations of shallow wetlands in small topographic depressions. J. Hydrol. 237, 74–85. doi:10.1016/S0022-1694(00)00300-0

Heikkinen, J.E.P., Elsakov, V., Martikainen, P.J., 2002. Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in NE Europe, Russia. Global Biogeochem. Cycles 16, 62-1-62–15. doi:10.1029/2002GB001930

Heiskanen, J., 1995. Physical properties of two-component growth media based on Sphagnum peat and their implications for plant-available water and aeration. Plant Soil 45–54.

Henn, J.J., Anderson, C.B., Martínez Pastur, G., 2016. Landscape-level impact and habitat factors associated with invasive beaver distribution in Tierra del Fuego. Biol. Invasions 18, 1679–1688. doi:10.1007/s10530-016-1110-9

Herczeg, A.L., Smith, A.K., Dighton, J.C., 2001. A 120 year record of changes in nitrogen and carbon cycling in Lake Alexandrina, South Australia: C : N, delta N-15 and delta C-13 in sediments. Appl. Geochemistry 16, 73–84.

Hill, A.R., 2012. The impact of pipe flow in riparian peat deposits on nitrate transport and removal. Hydrol. Process. 26, 3135–3146. doi:10.1002/hyp.8388

Hill, A.R., Cardaci, M., 2004. Denitrification and Organic Carbon Availability in Riparian Wetland Soils and Subsurface Sediments. Soil Sci. Soc. Am. J. 68, 320. doi:10.2136/sssaj2004.0320

Hill, A.R., Duval, T.P., 2009. Beaver dams along an agricultural stream in southern Ontario, Canada: their impact on riparian zone hydrology and nitrogen chemistry. Hydrol. Process. 23, 1324–1336. doi:10.1002/hyp

Hillman, G.R., 1998. Flood wave attenuation by a wetland following a beaver dam failure on a second order boreal stream. Wetlands 18, 21–34.

Hines, M.E., Duddleston, K.N., Rooney-Varga, J.N., Fields, D., Chanton, J.P., 2008. Uncoupling of acetate degradation from methane formation in Alaskan wetlands: Connections to vegetation distribution. Global Biogeochem. Cycles 22, n/a-n/a. doi:10.1029/2006GB002903

Hobbs, N.B., 1986. Mire morphology and the properties and behaviour of some British and foreign peats. Q. J. Eng. Geol. 19, 7–80.

Hogan, J.M., Kamp, G. Van Der, Barbour, S.L., Schmidt, R., 2006. Field methods for measuring hydraulic properties of peat. Hydrol. Process. 20, 3635–3649. doi:10.1002/hyp.6379

Holden, J., 2006. Peatland hydrology, in: Martini, I.P., Martinez Cortizas, A., Chesworth, W. (Ed.), Peatlands: Evolution and Records of Environmental and Climate Changes. Elsevier B.V., pp. 319–346. doi:10.1016/S0928-2025(06)09014-6

Holden, J., Burt, T.., 2002. Piping and pipeflow in a deep peat catchment. Catena 48, 163–199. doi:10.1016/S0341-8162(01)00189-8

Holden, J., Burt, T., Cox, N., 2001. Macroporosity and infiltration in blanket peat: the implications of tension disc infiltrometer measurements. Hydrol. Process. 303, 289–303.

Holden, J., Burt, T.P., 2003. Hydraulic conductivity in upland blanket peat: measurement and variability. Hydrol. Process. 17, 1227–1237. doi:10.1002/hyp.1182

Holden, J., Evans, M.G., Burt, T.P., Horton, M., 2006. Impact of land drainage on peatland hydrology. J. Environ. Qual. 35, 1764–78. doi:10.2134/jeq2005.0477

Holden, J., Gell, K.F., 2009. Morphological characterization of solute flow in a brown earth grassland soil with cranefly larvae burrows (leatherjackets). Geoderma 152, 181–186. doi:10.1016/j.geoderma.2009.06.006

Holden, J., Wallage, Z.E., Lane, S.N., McDonald, a. T., 2011. Water table dynamics in undisturbed, drained and restored blanket peat. J. Hydrol. 402, 103–114. doi:10.1016/j.jhydrol.2011.03.010

Hood, G.A., Bayley, S.E., 2008. Beaver (Castor canadensis) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada. Biol. Conserv. 141, 556–567. doi:10.1016/j.biocon.2007.12.003

Hood, G. a., Larson, D.G., 2015. Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. Freshw. Biol. 60, 198–208. doi:10.1111/fwb.12487

Hornibrook, E.R.C., Longstaffe, F.J., Fyfe, W.S., 1997. Spatial distribution of microbial methane production pathways in temperate zone wetland soils: Stable carbon and hydrogen isotope evidence. Geochim. Cosmochim. Acta 61, 745–753. doi:10.1016/S0016-7037(96)00368-7

Hornibrook, E.R.C., Longstaffe, F.J., Fyfe, W.S., Bloom, Y., 2000. Carbon-isotope ratios and carbon, nitrogen and sulfur abundances in flora and soil organic matter from a temperate-zone bog and marsh. Geochem. J. 34, 237–245. doi:10.2343/geochemj.34.237

Huang, S., Young, C., Feng, M., Heidemann, K., Cushing, M., Mushet, D.M., Liu, S., 2011. Demonstration of a conceptual model for using LiDAR to improve the estimation of floodwater mitigation potential of Prairie Pothole Region wetlands. J. Hydrol. 405, 417–426. doi:10.1016/j.jhydrol.2011.05.040

Hubbard, D.E., 1982. Surface area-volume relationship of wetland basins in the interior of the Coteau Des Prairies. Proc. South Dakota Acad. Sci. 61, 154–158.

Hutchinson, G.E., 1957. A Treatise on Limnology, Vol. 1. “Geology, Physics and Chemistry.” John Wiley and Sons, New York.

Ingram, H.A.P., 1982. Size and shape in raised mire ecosystems: a geophysical model. Nature 297, 300–303.

Ingram, H. a. P., 1978. Soil Layers in Mires: Function and Terminology. J. Soil Sci. 29, 224–227. doi:10.1111/j.1365-2389.1978.tb02053.x

Innis, H., 1956. The fur trade in Canada: An introduction to Canadian economic history. University of Toronto Press.

Ireland, A.W., Clifford, M.J., Booth, R.K., 2014. Widespread dust deposition on North American peatlands coincident with European land-clearance. Veg. Hist. Archaeobot. 23, 693–700. doi:10.1007/s00334-014-0466-y

Ives, R., 1942. The beaver meadow complex. J. Geomorphol. 5, 191–203.

Janzen, K., Westbrook, C.J., 2011. Hyporheic Flows Along a Channelled Peatland: Influence of Beaver Dams. Can. Water Resour. J. 36, 331–347. doi:10.4296/cwrj3604846

Jarema, S.I., Samson, J., Mcgill, B.J., Humphries, M.M., 2009. Variation in abundance across a species’ range predicts climate change responses in the range interior will exceed those at the edge: a case study with North American beaver. Glob. Chang. Biol. 15, 508–522. doi:10.1111/j.1365-2486.2008.01732.x

Jassey, V.E.J., Reczuga, M.K., Zielin´ska, M., Słowin´ska, S., Robroek, B.J.M., Mariotte, P., Seppey, C.V.W., Lara, E., Barabach, J., Słowin´ski, M., Bragazza, L., Chojnicki, B.H., Lamentowicz, M., Mitchell, E.A.D., Buttler, A., 2017. Tipping point in plant-fungal interactions under severe drought causes abrupt rise in peatland ecosystem respiration. Glob. Chang. Biol. 1–15. doi:10.1111/gcb.13928

Javernick, L., Brasington, J., Caruso, B., 2014. Modeling the topography of shallow braided rivers using Structure-from-Motion photogrammetry. Geomorphology 213, 166–182. doi:10.1016/j.geomorph.2014.01.006

Jenny, H., 1994. Factors of soil formation. A system of quantitative pedology. Dover Publications, INC.

Jin, L., Siegel, D.I., Lautz, L.K., Otz, M.H., 2009. Transient storage and downstream solute transport in nested stream reaches affected by beaver dams. Hydrol. Process. 23, 2438–2449. doi:10.1002/hyp

Joabsson, A., Christensen, T., Wallén, B., 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. Trends Ecol. Evol. 14, 385–388.

Johnson, D., Chance, D., 1974. Presettlement overharvest of upper Columbia River beaver populations. Can. J. Zool. 1828, 3–5.

Johnston, C., 2001. Wetland soil and landscape alteration by beavers, in: Richardson, J., Vepraskas, M. (Eds.), Wetland Soils: Their Genesis, Morphology, Hydrology, Landscapes and Classification. CRC Press, Boca Raton, pp. 391–404.

Johnston, C.A., 2017. Beavers: Boreal Ecosystem Engineers. Springer International Publishing, Cham. doi:10.1007/978-3-319-61533-2

Johnston, C.A., 2014. Beaver pond effects on carbon storage in soils. Geoderma 213, 371–378. doi:10.1016/j.geoderma.2013.08.025

Johnston, C.A., 2012. Beaver Wetlands, in: Batzer, D.P., Baldwin, A.H. (Eds.), Wetland Habitats of North America: Ecology and Conservation Concerns. University of California Press, Berkeley, pp. 161–171.

Johnston, C.A., Naiman, R.J., 1990. The use of a geographic information system to analyze long-term landscape alteration by beaver. Landsc. Ecol. 4, 5–19. doi:10.1007/BF02573947

Johnston, C.A., Naiman, R.J., 1987. Boundary dynamics at the aquatic-terrestrial interface: The influence of beaver and geomorphology. Landsc. Ecol. 1, 47–57. doi:10.1007/BF02275265

Johnston, C., Naiman, R., 1990. Browse selection by beaver: effects on riparian forest composition. Can. J. For. ….

Jones, C., Lawton, J., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos.

Jones, M.C., Peteet, D.M., Sambrotto, R., 2010. Late-glacial and Holocene δ15N and δ13C variation from a Kenai Peninsula, Alaska peatland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 293, 132–143. doi:10.1016/j.palaeo.2010.05.007

Jones, M.C., Yu, Z., 2010. Rapid deglacial and early Holocene expansion of peatlands in Alaska. Proc. Natl. Acad. Sci. 107, 7347–7352. doi:10.1073/pnas.0911387107

Jung, T., Staniforth, J., 2010. Unusual Beaver, Castor canadensis, Dams in Central Yukon. Can. Field-Naturalist 124, 274–275.

Karran, D.J., Westbrook, C.J., Bedard-Haughn, A., 2018. Beaver-mediated water table dynamics in a Rocky Mountain fen. Ecohydrology 11, e1923. doi:10.1002/eco.1923

Karran, D.J., Westbrook, C.J., Wheaton, J.M., Johnston, C.A., Bedard-Haughn, A., 2017. Rapid surface-water volume estimations in beaver ponds. Hydrol. Earth Syst. Sci. 21, 1039–1050. doi:10.5194/hess-21-1039-2017

Kaye, C., 1962. Early Postglacial Beavers in Southeastern New England. Science (80-.). 138, 906–907.

Kettridge, N., Turetsky, M.R., Sherwood, J.H., Thompson, D.K., Miller, C.A., Benscoter, B.W., Flannigan, M.D., Wotton, B.M., Waddington, J.M., 2015. Moderate drop in water table increases peatland vulnerability to post-fire regime shift. Sci. Rep. 5, 8063. doi:10.1038/srep08063

Kotowski, W., Andel, J. Van, Diggelen, R. Van, Hogendorf, J., 2001. Responses of fen plant species to groundwater level and light intensity. Plant Ecol. 155, 147–156. doi:10.1023/A:1013214716842

Kramer, N., Wohl, E.E., Harry, D.L., 2012. Using ground penetrating radar to “unearth” buried beaver dams. Geology 40, 43–46. doi:10.1130/G32682.1

Kroetsch, D.J., Geng, X., Chang, S.X., Saurette, D.D., 2011. Organic Soils of canada: Part 1. Wetland Organic soils. Can. J. Soil Sci. 91, 807–822. doi:10.4141/cjss10043

Kroll, C.N., Croteau, K.E., Vogel, R.M., 2015. Hypothesis tests for hydrologic alteration. J. Hydrol. 530, 117–126. doi:10.1016/j.jhydrol.2015.09.057

Kubiw, H., Hickman, M., Vitt, D.F., 1989. The developmental history of peatlands at Muskiki and Marguerite lakes, Alberta. Can. J. Bot. 67, 3534–3544. doi:10.1139/b89-435

Kuhry, P., 1994. The role of fire in the development of Sphagnum-dominated peatlands in western boreal Canada. J. Ecol. 82, 899–910.

Kuhry, P., Turunen, J., 2006. The Postglacial Development of Boreal and Subarctic Peatlands, in: Boreal and Peatland Ecosysytems. Springer Link, pp. 25–46.

Lane, C.R., D'Amico, E., 2010. Calculating the ecosystem service of water storage in isolated wetlands using LiDAR in north central Florida, USA. Wetlands 30, 967–977. doi:10.1007/s13157-010-0085-z

Lanman, R., Perryman, H., Dolman, B., James, C., 2012. The historical range of beaver in the Sierra Nevada: a review of the evidence. Calif. Fish Game 98, 65–80.

Larsson, A., Segerström, U., Laudon, H., Nilsson, M.B., 2017. Holocene carbon and nitrogen accumulation rates in a boreal oligotrophic fen. The Holocene 27, 811–821. doi:10.1177/0959683616675936

Lautz, L.K., Siegel, D.I., Bauer, R.L., 2006. Impact of debris dams on hyporheic interaction along a semi-arid stream. Hydrol. Process. 20, 183–196. doi:10.1002/hyp.5910

Lavoie, M., Paré, D., Bergeron, Y., 2005a. Impact of global change and forest management on carbon sequestration in northern forested peatlands. Environ. Rev. 13, 199–240. doi:10.1139/A05-014

Lavoie, M., Paré, D., Fenton, N., Groot, A., 2005b. Paludification and management of forested peatlands in Canada: a literature review. Environ. Rev. 50, 21–50. doi:10.1139/A05-006

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280. doi:10.1007/s004420100716

Lehmann, M.F., Bernasconi, S.M., Barbieri, A., McKenzie, J.A., 2002. Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during simulated and in situ early sedimentary diagenesis. Geochim. Cosmochim. Acta 66, 3573–3584. doi:10.1016/S0016-7037(02)00968-7

Lemieux, J.M., Sudicky, E.A., Peltier, W.R., Tarasov, L., 2008. Dynamics of groundwater recharge and seepage over the Canadian landscape during the Wisconsinian glaciation. J. Geophys. Res. Earth Surf. 113, 1–18. doi:10.1029/2007JF000838

Levine, R., Meyer, G.A., 2014. Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA. Geomorphology 205, 51–64. doi:10.1016/j.geomorph.2013.04.035

Levy, Z.F., Siegel, D.I., Dasgupta, S.S., Glaser, P.H., Welker, J.M., 2013. Stable isotopes of water show deep seasonal recharge in northern bogs and fens. Hydrol. Process. n/a-n/a.

doi:10.1002/hyp.9983

Liebner, S., Zeyer, J., Wagner, D., Schubert, C., Pfeiffer, E.M., Knoblauch, C., 2011. Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. J. Ecol. 99, 914–922. doi:10.1111/j.1365-2745.2011.01823.x

Limpens, J., Berendse, F., Blodau, C., 2008. Peatlands and the carbon cycle: from local processes to global implications–a synthesis. Biogeosciences 1475–1491.

Lin, X., Green, S., Tfaily, M.M., Prakash, O., Konstantinidis, K.T., Corbett, J.E., Chanton, J.P., Cooper, W.T., Kostka, J.E., 2012. Microbial community structure and activity linked to contrasting biogeochemical gradients in bog and fen environments of the Glacial Lake Agassiz Peatland. Appl. Environ. Microbiol. 78, 7023–31. doi:10.1128/AEM.01750-12

Loisel, J., Garneau, M., 2010. Late Holocene paleoecohydrology and carbon accumulation estimates from two boreal peat bogs in eastern Canada: Potential and limits of multi-proxy archives. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291, 493–533. doi:10.1016/j.palaeo.2010.03.020

Loisel, J., van Bellen, S., Pelletier, L., Talbot, J., Hugelius, G., Karran, D., Yu, Z., Nichols, J., Holmquist, J., 2017. Insights and issues with estimating northern peatland carbon stocks and fluxes since the Last Glacial Maximum. Earth-Science Rev. 165, 59–80. doi:10.1016/j.earscirev.2016.12.001

Loisel, J., Yu, Z., 2013. Recent acceleration of carbon accumulation in a boreal peatland, south central Alaska. J. Geophys. Res. Biogeosciences 118, 41–53. doi:10.1029/2012JG001978

Loisel, J., Yu, Z., Beilman, D.W., Camill, P., Alm, J., Amesbury, M.J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L.R., Bunbury, J., Chambers, F.M., Charman, D.J., De Vleeschouwer, F., Fia kiewicz-Kozie , B., Finkelstein, S. a., Ga ka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M.C., Klein, E.S., Kokfelt, U., Korhola, a., Kuhry, P., Lamarre, a., Lamentowicz, M., Large, D., Lavoie, M., MacDonald, G., Magnan, G., Makila, M., Mallon, G., Mathijssen, P., Mauquoy, D., McCarroll, J., Moore, T.R., Nichols, J., O'Reilly, B., Oksanen, P., Packalen, M., Peteet, D., Richard, P.J., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, a. B.K., Tarnocai, C., Thom, T., Tuittila, E.-S., Turetsky, M., Valiranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D., Zhao, Y., Zhou, W., 2014. A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. The Holocene 24, 1028–

1042. doi:10.1177/0959683614538073

Long, T., Or, D., 2005. Aquatic habitats and diffusion constraints affecting microbial coexistence in unsaturated porous media. Water Resour. Res. 41, 1–10. doi:10.1029/2004WR003796

Lowry, C.S., 2008. Controls on groundwater flow in a peat dominated wetland/stream complex, Allequash Wetland, Northern Wisconsin. University of Wisconsin, Madison.

Lowry, C.S., Fratta, D., Anderson, M.P., 2009. Ground penetrating radar and spring formation in a groundwater dominated peat wetland. J. Hydrol. 373, 68–79. doi:10.1016/j.jhydrol.2009.04.023

Lowry, C.S., Walker, J.F., Hunt, R.J., Anderson, M.P., 2007. Identifying spatial variability of groundwater discharge in a wetland stream using a distributed temperature sensor. Water Resour. Res. 43, 1–9. doi:10.1029/2007WR006145

Lowry, M.M., 1993. Groundwater elevations and temperature adjacent to a beaver pond in central Oregon. Oregon State University.

Macfarlane, W.W., Wheaton, J.M., Bouwes, N., Jensen, M.L., Gilbert, J.T., Hough-Snee, N., Shivik, J.A., 2017. Modeling the capacity of riverscapes to support beaver dams. Geomorphology 277, 72–99. doi:10.1016/j.geomorph.2015.11.019

Majerova, M., Neilson, B.T., Schmadel, N.M., Wheaton, J.M., Snow, C.J., 2015. Impacts of beaver dams on hydrologic and temperature regimes in a mountain stream. Hydrol. Earth Syst. Sci. 19, 3541–3556. doi:10.5194/hess-19-3541-2015

Malhotra, A., Roulet, N.T., Wilson, P., Giroux-Bougard, X., Harris, L.I., 2016. Ecohydrological feedbacks in peatlands: an empirical test of the relationship among vegetation, microtopography and water table. Ecohydrology 9, 1346–1357. doi:10.1002/eco.1731

Marcisz, K., Colombaroli, D., Jassey, V.E.J., Tinner, W., Kołaczek, P., Gałka, M., Karpińska-Kołaczek, M., Słowiński, M., Lamentowicz, M., 2016. A novel testate amoebae trait-based approach to infer environmental disturbance in Sphagnum peatlands. Sci. Rep. 6, 33907. doi:10.1038/srep33907

Maret, T.J., Parker, M., Fannin, T.E., 1987. The effect of beaver ponds on the nonpoint source water quality of a stream in Southwestern Wyoming. Water Res. 21, 263–268. doi:10.1016/0043-1354(87)90204-1

Marston, R.A., 1994. River entrenchment in small mountain valleys of the Western USA: Influence of beaver, grazing and clear cut logging. Rev. Geogr. Lyon 69, 11–15.

McClain, M.E., Boyer, E.W., Dent, C.L., Gergel, S.E., Grimm, N.B., Groffman, P.M., Hart, S.C., Harvey, J.W., Johnston, C. a., Mayorga, E., McDowell, W.H., Pinay, G., 2003. Biogeochemical Hot Spots and Hot Moments at the Interface of Terrestrial and Aquatic Ecosystems. Ecosystems 6, 301–312. doi:10.1007/s10021-003-0161-9

McDonnell, J.J., Sivapalan, M., Vaché, K., Dunn, S., Grant, G., Haggerty, R., Hinz, C., Hooper, R., Kirchner, J., Roderick, M.L., Selker, J., Weiler, M., 2007. Moving beyond heterogeneity and process complexity: A new vision for watershed hydrology. Water Resour. Res. 43, n/a-n/a. doi:10.1029/2006WR005467

McIntyre, S.H., Duthie, H.C., Warner, B.C., 1991. Postglacial development of a marl and peat complex on the Precambrian Shield of northwestern Ontario. J. Paleolimnol. 6, 141–155. doi:10.1007/BF00153738

Mckee, T.B., Doesken, N.J., Kleist, J., 1993. The relationship of drought frequency and duration to time scales. In: Proceedings of the Ninth Conference on Applied Climatology., in: Eighth Conference on Applied Climatology. pp. 17–22.

Meentemeyer, R.K., Vogler, J.B., Butler, D.R., 1998. The geomorphic influences of burrowing beavers on streambanks, Bolin creek, North Carolina. Zeitschrift Fur Geomorphol. 42, 453–468.

Menberu, M.W., Tahvanainen, T., Marttila, H., Irannezhad, M., Ronkanen, A.-K., Penttinen, J., Kløve, B., 2016. Water-table-dependent hydrological changes following peatland forestry drainage and restoration: Analysis of restoration success. Water Resour. Res. 52, 3742–3760. doi:10.1002/2015WR018578

Menounos, B., Osborn, G., Clague, J.J., Luckman, B.H., 2009. Latest Pleistocene and Holocene glacier fluctuations in western Canada. Quat. Sci. Rev. 28, 2049–2074. doi:10.1016/j.quascirev.2008.10.018

Milbrath, J.T., 2013. Land-cover change within the peatlands along the Rocky Mountain Front, Montana: 1937-2009. University of Montana (Missoula).

Milly, P.C.D., Betancourt, J., Falkenmark, M., Hirsch, R.M., Kundzewicz, Z.W., Lettenmaier, D.P., Stouffer, R.J., 2008. Climate change. Stationarity is dead: whither water management? Science 319, 573–574. doi:10.1126/science.1151915

Minke, A.G., Westbrook, C.J., van der Kamp, G., 2010. Simplified volume-area-depth method for estimating water storage of prairie potholes. Wetlands 30, 541–551. doi:10.1007/s13157-010-

0044-8

Mitchell, C.C., Niering, W.A., 1993. Vegetation Change in a Topogenic Bog Following Beaver Flooding. Bull. Torrey Bot. Club 120, 136–147.

Moore, T., Dalva, M., 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. Eur. J. Soil Sci. 44, 651–664. doi:10.1111/j.1365-2389.1993.tb02330.x

Morris, P.J., Waddington, J.M., 2011. Groundwater residence time distributions in peatlands: Implications for peat decomposition and accumulation. Water Resour. Res. 47, n/a-n/a. doi:10.1029/2010WR009492

Morris, P.J., Waddington, J.M., Benscoter, B.W., Turetsky, M.R., 2011. Conceptual frameworks in peatland ecohydrology: looking beyond the two-layered (acrotelm-catotelm) model. Ecohydrology 4, 1–11. doi:10.1002/eco.191

Morrison, A., Westbrook, C.J., Bedard-Haughn, A., 2015. Distribution of Canadian Rocky Mountain wetlands impacted by beaver. Wetlands. doi:10.1007/s13157-014-0595-1

Naiman, R.J., Pinay, G., Johnston, C.A., Pastor, J., 1994. Beaver influences on the long-term biogeochemical characteristics of boreal forest drainage networks. Ecology 75, 905–921.

Naiman, R., Johnston, C., Kelley, J., 1988. Alteration of North American streams by beaver. Bioscience 38, 753–762.

Naiman, R.J., Melillo, J.M., Hobbie, J.E., 1986. Ecosystem alteration of boreal forest streams by beaver (Castor Canadensis). Ecology 67, 1254–1269.

Newton, R.M., Burns, D. a., Blette, V.L., Driscoll, C.T., 1996. Effect of whole catchment liming on the episodic acidification of two adirondack streams. Biogeochemistry 32, 299–322. doi:10.1007/BF02187143

Nichols, J.E., Walcott, M., Bradley, R., Pilcher, J., Huang, Y., 2009. Quantitative assessment of precipitation seasonality and summer surface wetness using ombrotrophic sediments from an Arctic Norwegian peatland. Quat. Res. 72, 443–451. doi:10.1016/j.yqres.2009.07.007

Nummi, P., Kuuluvainen, T., 2013. Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. Boreal Environ. Res. 18, 13–24.

NWWG (National Wetlands Working Group), 1997. The Canadian Wetland Classification System. Waterloo.

Olea, R.A., 2006. A six-step practical approach to semivariogram modeling. Stoch. Environ. Res.

Risk Assess. 20, 307–318. doi:10.1007/s00477-005-0026-1

Olson, R., Hubert, W., 1994. Beaver: water resources and riparian habitat manager.

Passalacqua, P., Belmont, P., Staley, D.M., Simley, J.D., Arrowsmith, J.R., Bode, C.A., Crosby, C., DeLong, S.B., Glenn, N.F., Kelly, S.A., Lague, D., Sangireddy, H., Schaffrath, K., Tarboton, D.G., Wasklewicz, T., Wheaton, J.M., 2015. Analyzing high resolution topography for advancing the understanding of mass and energy transfer through landscapes: A review. Earth-Science Rev. 148, 174–193. doi:10.1016/j.earscirev.2015.05.012

Patrick, W., Wyatt, R., 1964. Soil nitrogen loss as a result of alternate submergence and drying. Soil Sci. Soc. Am. J. 28, 647–653.

Pauli, D., Peintinger, M., Schmid, B., 2002. Nutrient enrichment in calcareous fens: effects on plant species and community structure. Basic App.Ecol. 3, 255–266.

Payne, R.J., Kishaba, K., Blackford, J.J., Mitchell, E.A.D., 2006. Ecology of testate amoebae (Protista) in south-central Alaska peatlands: building transfer-function models for palaeoenvironmental studies. The Holocene 16, 403–414. doi:10.1191/0959683606hl936rp

Pebesma, E.J., Wesseling, C.G., 1998. Gstat: a program for geostatistical modelling, prediction and simulation. Comput. Geosci. 24, 17–31. doi:10.1016/S0098-3004(97)00082-4

Peros, M., Chan, K., Magnan, G., Ponsford, L., Carroll, J., McCloskey, T., 2016. A 9600-year record of water table depth, vegetation and fire inferred from a raised peat bog, Prince Edward Island, Canadian Maritimes. J. Quat. Sci. 31, 512–525. doi:10.1002/jqs.2875

Persico, L., Meyer, G., 2009. Holocene beaver damming, fluvial geomorphology, and climate in Yellowstone National Park, Wyoming. Quat. Res. 71, 340–353. doi:10.1016/j.yqres.2008.09.007

Peters, D.L., Prowse, T.D., Marsh, P., Lafleur, P.M., Buttle, J.M., 2006. Persistence of Water within Perched Basins of the Peace-Athabasca Delta, Northern Canada. Wetl. Ecol. Manag. 14, 221–243. doi:10.1007/s11273-005-1114-1

Petrone, R.M., Silins, U., Devito, K.J., 2007. Dynamics of evapotranspiration from a riparian pond complex in the Western Boreal Forest, Alberta, Canada. Hydrol. Process. 21, 1391–1401. doi:10.1002/hyp.6298

Pihlatie, M., Syväsalo, E., Simojoki, A., Esala, M., Regina, K., 2004. Contribution of nitrification and denitrification to N2O production in peat, clay and loamy sand soils under different soil moisture conditions. Nutr. Cycl. Agroecosystems 70, 135–141.

doi:10.1023/B:FRES.0000048475.81211.3c

Pollock, M.M., Beechie, T.J., Jordan, C.E., 2007. Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. Earth Surf. Process. Landforms 32, 1174–1185. doi:10.1002/esp.1553

Pollock, M.M., Heim, M., Werner, D., 2003. Hydrologic and geomorphic effects of beaver dams and their influence on fishes. Am. Fish. Soc. Symp. 37, 213–233.

Polvi, L.E., Wohl, E., 2012. The beaver meadow complex revisited - the role of beavers in post-glacial floodplain development. Earth Surf. Process. Landforms 37, 332–346. doi:10.1002/esp.2261

Pomeroy, J.W., Stewart, R.E., Whitfield, P.H., 2015. The 2013 flood event in the South Saskatchewan and Elk River basins: Causes, assessment and damages. Can. Water Resour. J. / Rev. Can. des ressources hydriques 1784, 1–10. doi:10.1080/07011784.2014.999825

Potvin, L.R., Kane, E.S., Chimner, R. a., Kolka, R.K., Lilleskov, E. a., 2014. Effects of water table position and plant functional group on plant community, aboveground production, and peat properties in a peatland mesocosm experiment (PEATcosm). Plant Soil 387, 277–294. doi:10.1007/s11104-014-2301-8

Price, J., Schlotzhauer, S., 1999. Importance of shrinkage and compression in determining water storage changes in peat: the case of a mined peatland. Hydrol. Process. c.

Price, J.S., 2003. Role and character of seasonal peat soil deformation on the hydrology of undisturbed and cutover peatlands. Water Resour. Res. 39, n/a-n/a. doi:10.1029/2002WR001302

Price, J.S., 1996. Hydrology and microclimate of a partly restored cutover bog, Quebec. Hydrol. Process. 10, 1263–1272.

Price, J.S., 1992. Blanket bog in Newfoundland. Part 1. The occurrence and accumulation of fog-water deposits. J. Hydrol. 135, 87–101. doi:10.1016/0022-1694(92)90082-7

Proulx-McInnis, S., St-Hilaire, A., Rousseau, A.N., Jutras, S., Carrer, G., Levrel, G., 2013. Seasonal and monthly hydrological budgets of a fen-dominated forested watershed, James Bay region, Quebec. Hydrol. Process. 27, 1365–1378. doi:10.1002/hyp.9241

Puttock, A., Graham, H.A., Cunliffe, A.M., Elliott, M., Brazier, R.E., 2017. Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. Sci. Total Environ. 576, 430–443.

doi:10.1016/j.scitotenv.2016.10.122
Ray, A.M., Rebertus, A.J., Ray, H.L., 2001. Macrophyte succession in Minnesota beaver ponds. Can. J. Bot. 79, 487–499. doi:10.1139/cjb-79-4-487
Rebertus, A.J., 1986. Bogs as beaver habitat in north-central Minnesota. Am. Midl. Nat. 116, 240–245.
Reddoch, J.M., Reddoch, A.H., 2005. Consequences of beaver, Castor canadensis, flooding on a small shore fen in southwestern Quebec. Can. Field-Naturalist 119, 385–394.
Regina, K., Silvola, J., Martikainen, P.J., 1999. Short-term effects of changing water table on N2O fluxes from peat monoliths from natural and drained boreal peatlands. Glob. Chang. Biol. 5, 183–189. doi:10.1046/j.1365-2486.1999.00217.x
Reimer, P.J., Edouard Bard, B., Alex Bayliss, B., Warren Beck, B.J., Paul Blackwell, B.G., Christopher Bronk Ramsey, B., 2013. Intcal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years Cal Bp. Radiocarbon 55, 1869–1887.
Rezanezhad, F., Price, J.S., Quinton, W.L., Lennartz, B., Milojevic, T., Van Cappellen, P., 2016a. Structure of peat soils and implications for water storage, flow and solute transport: A review update for geochemists. Chem. Geol. 429, 75–84. doi:10.1016/j.chemgeo.2016.03.010
Rezanezhad, F., Price, J.S., Quinton, W.L., Lennartz, B., Milojevic, T., Van Cappellen, P., 2016b. Structure of peat soils and implications for water storage, flow and solute transport: A review update for geochemists. Chem. Geol. 429, 75–84. doi:10.1016/j.chemgeo.2016.03.010
Richardson, J.L., Arndt, J.L., Freeland, J., 1994. Wetland soils of the prairie potholes. Adv. Agron. 52, 121–171. doi:10.1016/S0065-2113(08)60623-9
Rooney-Varga, J.N., Giewat, M.W., Duddleston, K.N., Chanton, J.P., Hines, M.E., 2007. Links between archaeal community structure, vegetation type and methanogenic pathway in Alaskan peatlands. FEMS Microbiol. Ecol. 60, 240–51. doi:10.1111/j.1574-6941.2007.00278.x
Rosell, F., Bozsér, O., Collen, P., Parker, H., 2005. Ecological impact of beaers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mamm. Rev. 35, 248–276. doi:10.1111/j.1365-2907.2005.00067.x
Roulet, N., Crill, P., Comer, N., 1997. CO2 and CH4 flux between a boreal beaver pond and the atmosphere. J. Geophys. Res. 102.
Roulet, N.T., 1991. Surface Level and Water Table Fluctuations in a Subarctic Fen. Arct. Alp.

Res. 23, 303. doi:10.2307/1551608

Roulet, N.T., Ash, R., Moore, T.R., 1992. Low Boreal Wetlands as a Source of Atmospheric Methane. J. Geophys. Res. 97, 3739–3749.

RStudio Team, 2015. Integrated Development for R.

Ruedemann, R., Schoonmaker, W.J., 1938. Beaver-dams as geologic Agents. Science (80-.). 88, 523–525.

Schwind, L.T.F., Arrieira, R.L., Dias, J.D., Simões, N.R., Bonecker, C.C., Lansac-Tôha, F.A., 2016. The structure of planktonic communities of testate amoebae (Arcellinida and uglyphida) in three environments of the Upper Paraná River basin, Brazil. J. Limnol. 75, 78–89. doi:10.4081/jlimnol.2015.1180

Shannon, R., White, J., Lawson, J., Gilmour, B., 1996. Methane efflux from emergent vegetation in peatlands. J. Ecol. 84, 239–246.

Sharma, S., Mora, G., Johnston, J.W., Thompson, T.A., 2005. Stable isotope ratios in swale sequences of Lake Superior as indicators of climate and lake level fluctuations during the Late Holocene. Quat. Sci. Rev. 24, 1941–1951. doi:10.1016/j.quascirev.2004.11.009

Shaw, E.L., 2009. Lateral exchange of water and nitrogen along a beaver-dammed stream draining a rocky mountain valley. University of Saskatchewan.

Shaw, R.D., Prepas, E.E., 1990. Groundwater-lake interactions: II. Nearshore seepage patterns and the contribution of groundwater to lakes in central Alberta. J. Hydrol. 119, 121–136.

Sherwood, J.H., Kettridge, N., Thompson, D.K., Morris, P.J., Silins, U., Waddington, J.M., 2013. Effect of drainage and wildfire on peat hydrophysical properties. Hydrol. Process. 27, 1866–1874. doi:10.1002/hyp.9820

Shook, K.R., Pomeroy, J.W., 2011. Memory effects of depressional storage in Northern Prairie hydrology. Hydrol. Process. 25, 3890–3898. doi:10.1002/hyp.8381

Sjörs, H., 1959. Bogs and fens in the Hudson Bay lowlands. Arctic 12, 3–19.

Smart, R.P., Holden, J., Dinsmore, K.J., Baird, a. J., Billett, M.F., Chapman, P.J., Grayson, R., 2013. The dynamics of natural pipe hydrological behaviour in blanket peat. Hydrol. Process. 27, 1523–1534. doi:10.1002/hyp.9242

Spence, C., Guan, X.J., Phillips, R., 2011. The hydrological functions of a boreal wetland. Wetlands 31, 75–85. doi:10.1007/s13157-010-0123-x

Stimson, A.G., Allott, T.E.H., Boult, S., Evans, M.G., 2017. Fluvial organic carbon composition and concentration variability within a peatland catchment—Implications for carbon cycling and water treatment. Hydrol. Process. 31, 4183–4194. doi:10.1002/hyp.11352

Strack, M., Waddington, J.M., Bourbonniere, R.A., Buckton, E.L., Shaw, K., Whittington, P., Price, J.S., 2008. Effect of water table drawdown on peatland dissolved organic carbon export and dynamics. Hydrol. Process. 22, 3373–3385. doi:10.1002/hyp.6931

Strahler, A.N., 1952. Hypsometric (area-altitude) analysis of erosional topography. Geol. Soc. Am. Bull. 63, 1117. doi:10.1130/0016-7606(1952)63[1117:HAAOET]2.0.CO;2

Sulman, B.N., Desai, A.R., Saliendra, N.Z., Lafleur, P.M., Flanagan, L.B., Sonnentag, O., Mackay, D.S., Barr, A.G., van der Kamp, G., 2010. CO 2 fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table. Geophys. Res. Lett. 37, n/a-n/a. doi:10.1029/2010GL044018

Sundh, I., Nilsson, M., Granberg, G., Svensson, B., 1994. Depth distribution of microbial production and oxidation of methane in northern boreal fens. Microb. Ecol. 253–265.

Suzuki, N., McComb, W., 1998. Habitat classification models for beaver (Castor canadensis) in the streams of the central Oregon Coast Range. Northwest Sci. 72, 102–110.

Tallis, J.H., 1998. Growth and degradation of British and Irish blanket mires. Environ. Rev. 122, 81–122.

Tarnocai, C., 2009. The impact of climate change on Canadian peatlands. Can. Water Resour. J. 34, 453–466. doi:10.4296/cwrj3404453

Thormann, M.N., Bayley, S.E., 1997. Response of aboveground net primary plant production to nitrogen and phosphorus fertilization in peatlands in sourthern boreal Alberta, Canada. Wetlands 17, 502–512. doi:10.1007/BF03161516

Toop, D.C., de la Cruz, N.N., 2002. Hydrogeology of the Canmore corridor and northwestern Kananaskis Country, Alberta. Edmonton, Alberta.

Trigg, M.A., Cook, P.G., Brunner, P., 2014. Groundwater fluxes in a shallow seasonal wetland pond: The effect of bathymetric uncertainty on predicted water and solute balances. J. Hydrol. 517, 901–912. doi:10.1016/j.jhydrol.2014.06.020

Tuittila, E.-S., Juutinen, S., Frolking, S., Valiranta, M., Laine, a. M., Miettinen, a., Sevakivi, M.-L., Quillet, a., Merila, P., 2012. Wetland chronosequence as a model of peatland development: Vegetation succession, peat and carbon accumulation. The Holocene 23, 25–35. doi:10.1177/0959683612450197

Turetsky, M.R., St. Louis, V., 2006. Disturbance in Boreal Peatlands, in: Wieder, K., Vitt, D.H. (Eds.), Boreal Peatland Ecosystems. pp. 359–379. doi:10.1007/978-3-540-31913-9

Turunen, J., Roulet, N.T., Moore, T.R., Richard, P.J.H., 2004. Nitrogen deposition and increased carbon accumulation in ombrotrophic peatlands in eastern Canada. Global Biogeochem. Cycles 18, 1–12. doi:10.1029/2003GB002154

Updegraff, K., Pastor, J., Bridgham, S., Johnston, C., 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecol. Appl. 5, 151–163.

Van Bellen, S., Mauquoy, D., Payne, R.J., Roland, T.P., Daley, T.J., Hughes, P.D.M., Loader, N.J., Street-Perrott, F.A., Rice, E.M., Pancotto, V.A., 2014. Testate amoebae as a proxy for reconstructing Holocene water table dynamics in southern Patagonian peat bogs. J. Quat. Sci. 29, 463–474. doi:10.1002/jqs.2719

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J. Clim. 23, 1696–1718. doi:10.1175/2009JCLI2909.1

Waddington, J.M., Kellner, E., Strack, M., Price, J.S., 2010. Differential peat deformation, compressibility, and water storage between peatland microforms: Implications for ecosystem function and development. Water Resour. Res. 46, n/a-n/a. doi:10.1029/2009WR008802

Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K., Moore, P. a., 2015. Hydrological feedbacks in northern peatlands. Ecohydrology 8, 113–127. doi:10.1002/eco.1493

Waddington, J.M., Quinton, W.L., Price, J.S., Lafleur, P.M., 2009. Advances in Canadian peatland hydrology. Can. Water Resour. J. 34, 139–148.

Walbridge, M., 1994. Plant community composition and surface water chemistry of fen peatlands in West Virginia's Appalachian Plateau. Water. Air. Soil Pollut. 247–269.

Wang, M., Moore, T.R., 2014. Carbon, nitrogen, phosphorus, and potassium stoichiometry in an ombrotrophic peatland reflects plant functional type. Ecosystems 17, 673–684. doi:10.1007/s10021-014-9752-x

Wang, X., Helgason, B., Westbrook, C.J., Bedard-Haughn, A., 2016a. Effect of mineral sediments on carbon mineralization, organic matter composition and microbial community dynamics in a mountain peatland. Soil Biol. Biochem. 103, 16–27. doi:10.1016/j.soilbio.2016.07.025

Wang, X., Siciliano, S., Helgason, B., Bedard-Haughn, A., 2017. Responses of a mountain peatland to increasing temperature: A microcosm study of greenhouse gas emissions and microbial community dynamics. Soil Biol. Biochem. 110, 22–33. doi:10.1016/j.soilbio.2017.02.013

Wang, X., Westbrook, C.J., Bedard-Haughn, A., 2016b. Effect of mineral horizons on spatial distribution of soil properties and N cycling in a mountain peatland. Geoderma 273, 73–82. doi:10.1016/j.geoderma.2016.03.012

Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J.I., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk, H., Bardgett, R.D., 2015. Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. Ecology 96, 113–123. doi:10.1890/14-0292.1

Watters, J.R., Stanley, E.H., 2007. Stream channels in peatlands: The role of biological processes in controlling channel form. Geomorphology 89, 97–110. doi:10.1016/j.geomorph.2006.07.015

Webster, K.L., McLaughlin, J.W., Kim, Y., Packalen, M.S., Li, C.S., 2013. Modelling carbon dynamics and response to environmental change along a boreal fen nutrient gradient. Ecol. Modell. 248, 148–164. doi:10.1016/j.ecolmodel.2012.10.004

Wegener, P., Covino, T., Wohl, E., 2017. Beaver-mediated lateral hydrologic connectivity, fluvial carbon and nutrient flux, and aquatic ecosystem metabolism. Water Resour. Res. 53, 4606–4623. doi:10.1002/2016WR019790

Weiss, R., Alm, J., Laiho, R., Laine, J., 1998. Modeling moisture retention in peat soils. Soil Sci. Soc. Am. J. 62, 305–313. doi:10.2136/sssaj1998.03615995006200020002x

Westbrook, C.J., Bedard-Haughn, A., 2016. Sibbald Research Wetland: Mountain peatland form and ecohydrologic function as influenced by beaver. For. Chron. 92, 37–38.

Westbrook, C.J., Cooper, D.J., Anderson, C.B., 2017. Alteration of hydrogeomorphic processes by invasive beavers in southern South America. Sci. Total Environ. 574, 183–190. doi:10.1016/j.scitotenv.2016.09.045

Westbrook, C.J., Cooper, D.J., Baker, B.W., 2011. Beaver assisted river valley formation. River Res. Apllications 256, 247–256. doi:10.1002/rra

Westbrook, C.J., Cooper, D.J., Baker, B.W., 2006. Beaver dams and overbank floods influence groundwater-surface water interactions of a Rocky Mountain riparian area. Water Resour. Res. 42, n/a-n/a. doi:10.1029/2005WR004560

Westbrook, C.J., Cooper, D.J., Butler, D.R., 2013. Beaver hydrology and geomorphology, in:

Shroder, J., Butler, D., Hupp, C. (Eds.), Treatise on Geomorphology. Academic Press, San Diego, pp. 293–306.

Weyhenmeyer, C.E., 1999. Methane emissions from beaver ponds: Rates, patterns, and transport mechanisms. Global Biogeochem. Cycles 13, 1079–1090.

Whitehouse, H., Bayley, S., 2005. Vegetation patterns and biodiversity of peatland plant communities surrounding mid-boreal wetland ponds in Alberta, Canada. Can. J. Bot. 637, 621–637. doi:10.1139/B05-034

Whitfield, C.J., Baulch, H.M., Chun, K.P., Westbrook, C.J., 2014. Beaver-mediated methane emission: The effects of population growth in Eurasia and the Americas. Ambio 44, 7–15. doi:10.1007/s13280-014-0575-y

Whitfield, S., Reed, M., Thomson, K., Christie, M., Stringer, L.C., Quinn, C.H., Anderson, R., Moxey, A., Hubacek, K., 2011. Managing peatland ecosystem services: Current UK policy and future challenges in a changing world. Scottish Geogr. J. 127, 209–230. doi:10.1080/14702541.2011.616864

Whiticar, M.J., 1999. Carbon and hydrogen isotope systematics of bacterial formation and oxidation of methane. Chem. Geol. 161, 291–314. doi:10.1016/S0009-2541(99)00092-3

Whittington, G., Edwards, K.J., Zanchetta, G., Keen, D.H., Bunting, M.J., Fallick, A.E., Bryant, C.L., 2015. Lateglacial and early Holocene climates of the Atlantic margins of Europe: Stable isotope, mollusc and pollen records from Orkney, Scotland. Quat. Sci. Rev. 122, 112–130. doi:10.1016/j.quascirev.2015.05.026

Whittington, P., Strack, M., Haarlem, R. Van, 2007. The influence of peat volume change and vegetation on the hydrology of a kettle-hole wetland in Southern Ontario, Canada. Mires Peat c, 1–14.

Whittington, P.N., Price, J.S., 2006. The effects of water table draw-down (as a surrogate for climate change) on the hydrology of a fen peatland , Canada. Hydrol. Process. 3600, 3589–3600. doi:10.1002/hyp

Wiens, L.H., 2001. A Surface Area-Volume Relationship for Prairie Wetlands in the Upper Assiniboine River Basin, Saskatchewan. Can. Water Resour. J. 26, 503–513. doi:10.4296/cwrj2604503

Wik, M., Varner, R.K., Anthony, K.W., MacIntyre, S., Bastviken, D., 2016. Climate-sensitive northern lakes and ponds are critical components of methane release. Nat. Geosci. 9, 99–106.

doi:10.1038/ngeo2578

Wohl, E., Dwire, K., Sutfin, N., Polvi, L., Bazan, R., 2012. Mechanisms of carbon storage in mountainous headwater rivers. Nat. Commun. 3, 1263. doi:10.1038/ncomms2274

Wójcicki, K., 2012. Stratigraphy of organic-rich deposits in floodplain environments: examples from the Upper Odra River Basin. Quaest. Geogr. 31. doi:10.2478/v10117-012-0024-6

Wolf, E.C., Cooper, D.J., Hobbs, N.T., 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. Ecol. Appl. 17, 1572–87.

Woo, M., Waddington, J.M., 1990. Effects of beaver dams on subarctic wetland hydrology. Arctic 43, 223–230.

Xu, C.-Y., Singh, V.P., 2004. Review on regional water resources assessment models under stationary and changing climate. Water Resour. Manag. 18, 591–612. doi:10.1007/s11269-004-9130-0

Yu, Z., 2006. Holocene carbon accumulation of fen peatlands in boreal western Canada: A complex ecosystem response to climate variation and disturbance. Ecosystems 9, 1278–1288. doi:10.1007/s10021-006-0174-2

Yu, Z., Beilman, D.W., Jones, M.C., 2009. Sensitivity of northern peatland carbon dynamics to Holocene climate change, in: Baird, A.J., Belyea, L.R., Comas, X., Reeve, A.S., Slater, L.. (Eds.), Carbon Cycling in Northern Peatlands. American Geophysical Union, Washington D.C., pp. 55–69. doi:10.1029/2008GM000822

Yu, Z., Loisel, J., Brosseau, D.P., Beilman, D.W., Hunt, S.J., 2010. Global peatland dynamics since the Last Glacial Maximum. Geophys. Res. Lett. 37, n/a-n/a. doi:10.1029/2010GL043584

Yu, Z., Loisel, J., Turetsky, M.R., Cai, S., Zhao, Y., Frolking, S., MacDonald, G.M., Bubier, J.L., 2013. Evidence for elevated emissions from high-latitude wetlands contributing to high atmospheric CH4 concentration in the early Holocene. Global Biogeochem. Cycles 27, 131–140. doi:10.1002/gbc.20025

Zehe, E., Ehret, U., Pfister, L., Blume, T., Schröder, B., Westhoff, M., Jackisch, C., Schymanski, S.J., Weiler, M., Schulz, K., Allroggen, N., Tronicke, J., Dietrich, P., Scherer, U., Eccard, J., Wulfmeyer, V., Kleidon, a., 2014. HESS Opinions: Functional units: a novel framework to explore the link between spatial organization and hydrological functioning of intermediate scale catchments. Hydrol. Earth Syst. Sci. Discuss. 11, 3249–3313. doi:10.5194/hessd-11-

3249-2014

Zoltai, S., Johnson, J.D., 1985. Development of a treed bog island in a minerotrophic fen. Can. J. Bot. 63, 1076–1085.