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Pore-scale controls on hydrological and geochemical processes in peat: Implications on interacting processes

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ABSTRACT

Peatlands are wetlands that provide important ecosystem services including carbon sequestration and water storage that respond to hydrological, biological, and biogeochemical processes. These processes are strongly influenced by the complex pore structure of peat soils. We explore the literature on peat pore structure and the implications for hydrological, biogeochemical, and microbial processes in peat, highlighting the gaps in our current knowledge and a path to move forward. Peat is an elastic and multi-porous structured organic soil. Surficial (near-surface) peats are typically dominated by large interconnected macropores that rapidly transmit water and solutes when saturated, but these large pores drain rapidly with a reduction in pore-water pressure, and disproportionally decrease the bulk effective hydraulic conductivity, thus water fluxes that drive ecohydrological functions. The more advanced state of decomposition of older (deeper) peat, with a greater abundance of small pores, restricts the loss of moisture at similar soil water pressures and is associated with higher unsaturated hydraulic conductivities. As evaporation and precipitation occur, peat soils shrink and swell, respectively, changing the hydrological connectivity that maintain physiological processes at the peat surface. Due to the disproportionate change in pore structure and associated hydraulic properties with state of decomposition, transport processes are limited at depth, creating a zone of enhanced transport in the less decomposed peat near the surface. At the micro-scale, rapid equilibration of solutes and water occurs between the mobile and immobile pores due to diffusion, resulting in pore regions with similar chemical concentrations that are not affected by advective fluxes. These immobile regions may be the primary sites for microbial biogeochemical processes in peat. Mass transfer limitations may therefore largely regulate belowground microbial turnover and, hence, biogeochemical cycling. For peat, the development of a comprehensive theory that links the hydrological, biological, and biogeochemical processes will require a concerted interdisciplinary effort. To that end, we have highlighted four primary areas to focus our collective research: 1) understanding the combined and interrelated effects of parent material, decomposition, and nutrient status on peat pore connectivity, macropore development and collapse, and solute transport, 2) determining the influence of changing pore structure due to freeze-thaw or dewatering on the hydrology and biogeochemistry, 3) better elucidating the non-equilibrium transport processes in peat, and 4) exploring the implications of peat's pore structure on microbiological and biogeochemical processes.

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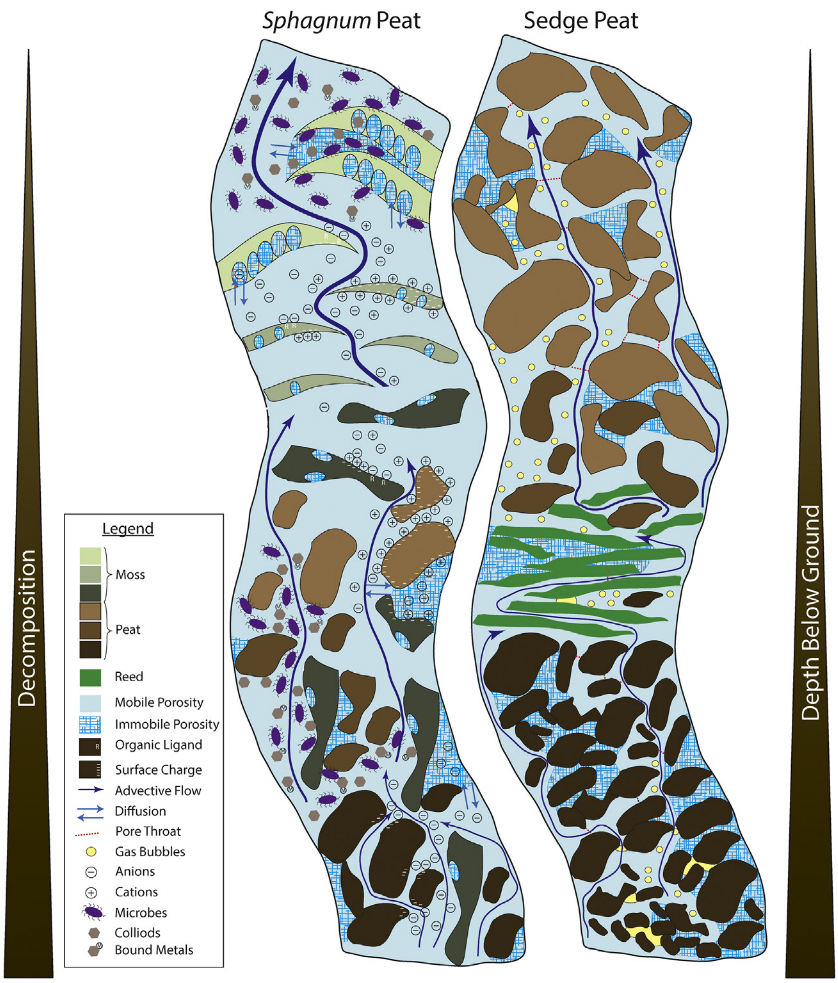

Fig. 1. A conceptual diagram of the various hydro-biogeochemical processes in peat with increasing degree of decomposition from top to bottom between *Sphagnum* (bog) and sedge (fen) peat. The flow lines represent the flow accumulation into larger pores in less decomposed peat through increasing width. Size sieving and anion exclusion are illustrated by the absence of anions and colloids/microbes in relatively large pore spaces due to small pore throats. Note, the relatively greater proportion of dissolved cations in the more decomposed peat than less decomposed peat due to increases in specific surface area. All processes are active in both peat types but are separated here for clarity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1. Introduction

Peatlands are a valuable but environmentally vulnerable resource, as they represent a globally-significant carbon and energy reservoir (Gorham, 2008) and play major roles in the hydrological and biogeochemical cycles of many landscapes (Emili and Price, 2013; Glaser et al., 1981; Szkokan-Emilson et al., 2013). Compared to most mineral soils, the organic soils that dominate peatlands are a structured and highly complex porous medium, with unique physical, chemical, thermal, and hydraulic properties (Fig. 1) (Andreasson et al., 1988; Boelter, 1969; Gogo et al., 2010; McCarter et al., 2017b; McCarter and Price, 2014; McCarter et al., 2018; Nichols and Boelter, 1984; Oke, 1987; Rezanezhad et al., 2016; Schwärzel et al., 2002). These properties are partly derived from their botanical composition, such as *Sphagnum* moss (a non-vascular plant), or graminoids and other vascular plants, and the degree of decomposition and compaction (Fig. 2) (Boelter, 1965; Boelter, 1969; Nichols and Boelter, 1984; Verry and Boelter, 1977). Peats are often characterized by a complex pore structure, comprising open, dead-end, and partially/fully closed pores (Fig. 2) (Rezanezhad et al., 2012; Weber et al., 2017a; Weber et al., 2017b). This pore structure influences the flow and transport of water and solutes through advection in open, connected pores (mobile porosity) and molecular diffusion into closed and dead-end pores (immobile porosity) (McCarter et al., 2019; Rezanezhad et al., 2012). Herein, the term mobile porosity represents pores that can actively participate in advective flow and transport, while the immobile porosity refers to the pores that are connected to the mobile porosity but do not contribute to advective flow and transport. Much of our understanding of the physical structure of peat comes from *Sphagnum* peat (Holden, 2009a; McCarter and Price, 2014; Taylor and Price, 2015), particularly solute transport processes (Hoag and Price, 1997; Ours et al., 1997; Rezanezhad et al., 2012; Rezanezhad et al., 2016), while the pore structure of sedge or woody peats (from fen or swamps) remains less clear (Liu and Lennartz, 2019). Furthermore, within peatlands average pore diameters diminish with an increasing degree of decomposition, which commonly occurs with increasing depth below the surface (Gharedaghloo et al., 2018; McCarter and Price, 2014; Rezanezhad et al., 2009). The influence of the pore size distribution and connectivity on many interrelated processes that govern peatlands remains unclear.

Historically, peat has been identified by its parent material (*e.g.*, *Sphagnum* moss, wood, and sedge/graminoid) or by its wetland classification (*e.g.*, bog, fen, or swamp) but these descriptors alone do not give reliable information on the hydrological or biogeochemical properties of peat without another hydrophysical measurement such as bulk density (*i.e.*, the undisturbed dry mass of peat per sample volume), drainable porosity, saturated hydraulic conductivity (K_{sat}), *etc.*, (Liu and Lennartz, 2019). Each of these physical measurements are governed by the specific pore network within peat. Generally, there is a decrease in average pore size and pore connectivity with increasing depth/degree of decomposition that controls the movement of water and solutes in peatlands (Baird and Gaffney, 2000; Beckwith et al., 2003a; Gharedaghloo et al., 2018; Hoag and Price, 1995; McCarter and Price, 2017a; McCarter and Price, 2017b). However, the conditions in some peatlands results in an inversion of this profile, where the upper most peat is the most degraded (as indicated by higher bulk densities) and deeper peats are less degraded (Kleimeier et al., 2017; Liu et al., 2016; Liu and Lennartz, 2015). In either case, the specific structure of

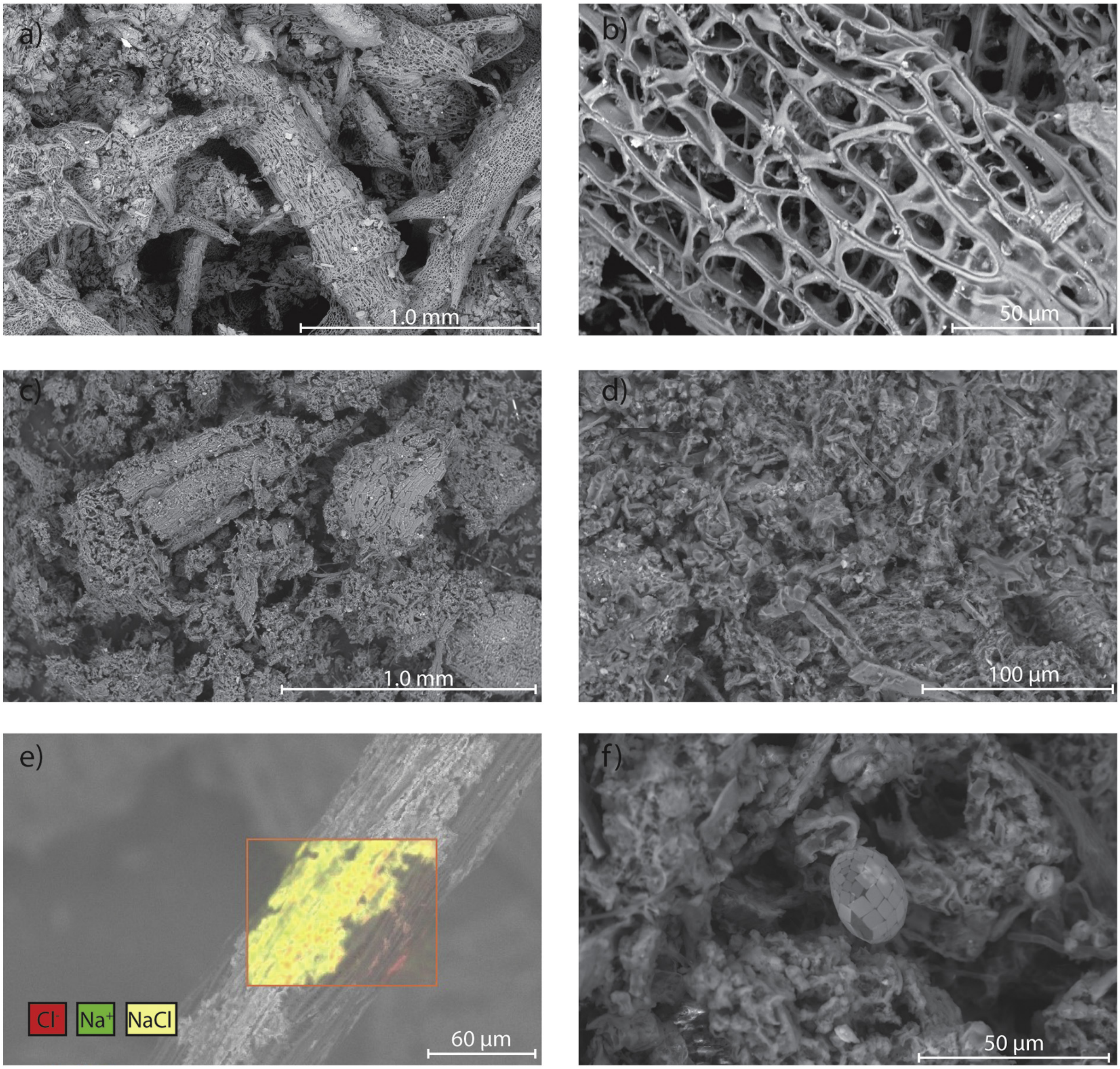

Fig. 2. Scanning Electron Microscope (SEM) images of peat under varying decomposition states and illustrating geochemical and biological processes. a) Undecomposed *Sphagnum* peat showing the complex leaf and branch pore structure, and resultant large pores. b) Desiccated hyaline cells of undecomposed *Sphagnum*, highlighting the network of enclosed pores. c) Decomposed *Sphagnum* peat (~30 cm bgs) highlighting the collapse of the large pores and degradation of the *Sphagnum* plant material. d) A magnification of the decomposed *Sphagnum* peat, further highlighting the reduction in large pores. e) Adsorbed Cl^-, Na^+, and precipitated NaCl on peat. Conditions in the SEM preclude any liquid water in the sample. The individual red and green spots suggesting adsorption of the individual ions. The NaCl likely combines both adsorbed Na^+ and precipitated NaCl during imaging. f) A testate amoeba within peat highlighting size exclusion from the smaller pores. Note, samples were completely desiccated during the imaging process. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the peat pore network induces variations in the diffusion of solutes (McCarter et al., 2019; Rezanezhad et al., 2017), colloids (Andreasson et al., 1988; Kalmykova et al., 2010), and (or locomotion of) microbes (Ginn et al., 2002) into the immobile pores spaces or excluded from a portion of the mobile porosity may influence the biological and biogeochemical processes. Although these processes are broadly understood in peat soils and peatlands, there remain many gaps in our knowledge, specifically on: 1) the nature of hydrological pore connectivity due to diffusional and hydraulic tortuosity, 2) micro-scale anisotropy, 3) the magnitude and role of soil colloids on solute transport, 4) the implications of pore-scale processes on peat biogeochemistry, and 5) the effect of freeze-thaw cycles on peat pore structure and implications for hydrology. This review will focus on first illuminating the hydrological and (bio)geochemical processes in peat soils, second highlighting the feedbacks between these processes and lastly identifying the current gaps in knowledge, while providing a path to advance our understanding of peat pore processes.

2. Pore structure of peats

2.1. Conceptualization of pores and porosity in peat

The decomposition of organic matter and subsequent compression of pores in peatlands changes the physical characteristics of pores, which affects flow through pore networks (Malmer et al., 2003; Quinton et al., 2009; Rezanezhad et al., 2010; Rezanezhad et al., 2009). Plant litter is buried as newer peat accumulates above it, and roots, rhizomes, and microbes die in situ. Below the water table, anoxic conditions limit the decomposition rate, resulting in a strong gradient of organic matter age and degree of decomposition with depth (Boelter,

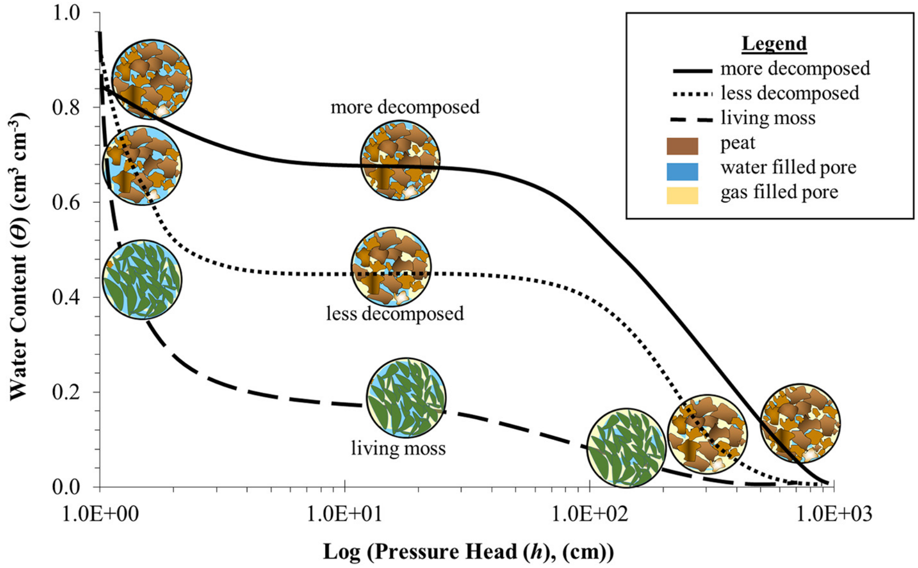

Fig. 3. Idealized soil water retention curves under varying degrees of decomposition. The increasing proportion of yellow space as pressure increases indicating a greater proportion of air-filled pores. The axis values represent an approximate value rather than specific values and do not represent the inherent variability observed in peat. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1969; Holmquist et al., 2016; Kechavarzi et al., 2010; Liu and Lennartz, 2019; Moore et al., 2005; Nichols and Boelter, 1984; Tfaily et al., 2014; Turetsky et al., 2004). In general, the degree of complexity of pore networks increases with depth below the ground surface (Quinton et al., 2009; Rezanezhad et al., 2010; Rezanezhad et al., 2009). However, the porosity of a given peat depth will depend on its' parent material, geochemical conditions and hydroclimatic conditions when buried (Ise et al., 2008; Xia et al., 2019). Depending on these conditions, regions of high (or low) porosity at depth are possible in peatlands (Xia et al., 2019), which can have important implications for water flow and solute transport (Liu and Lennartz, 2015; McCarter and Price, 2017a). Thus, it is important to note that although in many peatland depth and degree of decomposition are positively related, this trend is not universal.

The distribution of pores between the immobile and mobile porosities is critical to understanding water and solute flow in peat. (Hoag and Price, 1997; Kleimeier et al., 2017; Rezanezhad et al., 2012; Weber et al., 2017b). The mobile porosity contributes to advective water flow and solute transport, while the pores belonging to immobile porosity do not participate in advective water flow, but experience the diffusion of solutes to and from them (McCarter et al., 2019). As decomposition increases, the proportion of immobile pores typically increases, along with a decrease in the average pore diameter, thought to be partially caused by a general flattening of the large pores (Fig. 2) (Hoag and Price, 1997; Kleimeier et al., 2017; Quinton et al., 2008). In peat, the mobile porosity has been assumed to be between 15 – 60 % of the total pore volume (Hoag and Price, 1997; Kleimeier et al., 2017; Liu et al., 2017; Rezanezhad et al., 2012). However, Carey et al. (2007) found that less than 0.1 % of the pore volume, chiefly macropores, was contributing to active water flow in saturated surficial *Sphagnum* mosses on hillslopes in the Wolf Creek Research Basin, Yukon Territory, based on tension infiltrometer and CT image analysis. This extremely low mobile porosity suggests that large-scale factors, such as landscape slope, and micro-scale factors such as macropore density and diameter affect the porosity available for water and solute flow in some situations. Notwithstanding the results of Carey et al. (2007), the proportion of immobile pores typically increases with degree of decomposition (Hoag and Price, 1997; Kleimeier et al., 2017; Liu et al., 2017; Liu et al., 2016; McCarter et al., 2019; Rezanezhad et al., 2012), which can potentially have significant implications for mass transport (Hoag and Price, 1997; Liu et al., 2017; Liu et al., 2016; Rezanezhad et al., 2016) and biogeochemical processes (*e.g.*, adsorption or methanogenesis) (McCarter et al., 2017a; Rezanezhad et al., 2017).

The pore size distribution or pore throat size distribution of *Sphagnum* peat has been characterized as a log-normal and bi- and trimodal, where pore sizes in poorly decomposed near-surface peats are dominated by macropores (> 3 mm) (Hayward and Clymo, 1982; Holden, 2009a; Holden et al., 2012; McCarter and Price, 2014; Rezanezhad et al., 2017; Rezanezhad et al., 2012; Wallage and Holden, 2011; Weber et al., 2017a). Hayward and Clymo (1982) proposed that *Sphagnum* derived peat had two distinct pore modes that were separated around -100 mbar of matric pressure, which corresponds with the upper range of pressures at which hyaline cells begin to drain and the mosses desiccate. Hyaline cells are large hyalocytes that provide significant physiological water storage (Hayward and Clymo, 1982; Lewis, 1988), which allow *Sphagnum* species to avoid desiccation under increased hydrological stress (Hayward and Clymo, 1982; McCarter and Price, 2014). Hyaline cells are storage cells that provide water to the capitulum during periods of moisture stress and are most abundant in the living portion of *Sphagnum* moss (Bengtsson et al., 2016; Hayward and Clymo, 1982). The capitula (plural of capitulum) is the floret at the top of the living moss and surface of the peat, typically described as an apical tuft of expanding leaves and branches where most of the photosynthesis occurs (Bengtsson et al., 2016; Hayward and Clymo, 1982; Silvola and Aaltonen, 1984). The range of hyaline cell drainage, thus desiccation avoidance, was extended to -600 mbar of pressure (Lewis, 1988) and numerical simulations with a -400 mbar pressure limit on the capitula tend to agree with our conceptual understanding that once hyaline cells drain, evaporation is greatly reduced (Gauthier et al., 2018; McCarter and Price, 2014). Rezanezhad et al. (2012) extended the hyaline cell concept to include three pore classes, where open and connected pores account for approximately 35% of the total porosity, closed or partially closed pores ~20%, and dead-end or isolated pores the remaining 45% of the total porosity in the degraded poor fen peat they studied. Indeed, this conceptual understanding of the pores within peat agrees with the limits of hyaline cell drainage (Lewis, 1988), where the closed or partially closed pores defined by Rezanezhad et al. (2012) typically drained at pressures between -100 to -1000 mb of pressure (Fig. 3). However, this representation (Hayward and Clymo, 1982; Rezanezhad et al., 2012) of the pore distribution in peat is simplistic and ignores the hydraulic properties of each pore region (Weber et al., 2017a).

2.1.1. Macropores in peat

Recently, Weber et al. (2017a) observed three distinct ranges of pore-sizes in *Sphagnum*-derived bog peat, consisting of inter-plant pore spaces (effective diameter > 300 μm, macropores), intra-plant pore spaces (effective diameter = 300 – 30 μm), and inner-plant pore spaces (effective diameter = 30 – 10 μm). By comparison, Holden (2009a) among others (Baird, 1997; Holden, 2009a; Holden, 2009b; Holden et al., 2012; Wallage and Holden, 2011), defined macropores to be any pore with an effective diameter > 250 μm (which is the definition adopted hereafter as it is the more common definition of macropore throughout the literature). Regardless of the exact definition of macropores used, these large and continuous pores typically dominate the water and solute flow in many different types of peat (Baird and Gaffney, 2000; Holden, 2009a; Holden, 2009b; Kleimeier et al., 2017; McCarter and Price, 2017b; McCarter et al., 2019; Mooney et al., 1999; Rezanezhad et al., 2016). In *Sphagnum* derived peats, macropore abundance rapidly decreases with degree of decomposition and compression (thus, typically depth below the ground surface) coupled with an increased abundance of smaller pores (Holden, 2009a; Holden et al., 2012; McCarter and Price, 2014; Wallage and Holden, 2011), higher advective (mass flow) and diffusional tortuosity (Gharedaghloo et al., 2018; Rezanezhad et al., 2010) and lower pore coordination number (number of pores connected to one pore) (Gharedaghloo et al., 2018). Conversely, fen peat (*e.g.*, vascular plant dominated peat, typically sedges) has a greater abundance of smaller pores at the surface, due to increased aeration and mineralization processes, and an increase in the abundance of immobile pores at depth (Kleimeier et al., 2017; Liu et al., 2016; Rezanezhad et al., 2016); yet, macropores still provide an important flow path for both water and solutes in fen peat, as they do in *Sphagnum* peat (Baird, 1997; Baird and Gaffney, 2000). In most peat types, the abundance of these large diameter pores coupled with smaller pore throats (Gharedaghloo et al., 2018) can significantly delay the re-wetting of peat due to hysteresis (Hayward and Clymo, 1982; Hayward and Clymo, 1983; McCarter and Price, 2014; McCarter and Price, 2015; Taylor and Price, 2015). However, the influence of macropores at depth had not been extensively characterized, nor their influence on solute and water flow.

2.2. Influence of plant parent material and plants on peat pore structure

2.2.1. Sphagnum peat

In *Sphagnum* dominated peats, the pore networks tend to have a greater proportion of macropores at the surface, due to the structure of a *Sphagnum* plant/community and abundance of vascular plant roots (Fig. 2) (Holden, 2009a; Holden et al., 2012; Weber et al., 2017a). Macropore abundance typically decreases with depth as the degree of decomposition increases and woody inclusions are less prevalent. Living *Sphagnum* moss and lightly decomposed *Sphagnum* peat has an immobile porosity attributed to the presence of hyaline cells, while the immobile porosity in peat under a greater degree of decomposition is attributed to the collapse and isolation of pores (Hoag and Price, 1997; Rezanezhad et al., 2012). The decay-resistant properties of *Sphagnum* moss (Hájek et al., 2011; Painter, 1991) lead to slower decomposition and greater peat depths than in other peatlands (Bengtsson et al., 2016; Hájek et al., 2011; Johnson and Damman, 1991). The slower decomposition rates of *Sphagnum* moss lead to the preservation of hyaline cells deeper within the peat profile, extending their relative influence into deeper peats (Fig. 2). Different species of *Sphagnum* moss have different size hyaline cell openings ranging from ~4 – 17 μm (Lewis, 1988) that control the pressure at which they drain, and the differential cell openings may influence the diffusion rate from the mobile porosity, yet no evidence for differential diffusion rates based on species has been presented within the literature. Furthermore, Hayward and Clymo (1982) suggest that *Sphagnum* species have different size and shape hyaline cells, further altering the availability and volume of water and solutes stored within them. Unlike mineral soils, where the soil type is generally a good descriptor of the pore structure, communities of a given species of *Sphagnum* moss can alter its pore structure to suit its specific physiological growth and community needs (Goetz and Price, 2015; McCarter and Price, 2014; McNeil and Waddington, 2003; Thompson and Waddington, 2008; Turetsky et al., 2008), resulting in many different pore distributions for the broad classification of *Sphagnum* peat. However, to-date there remains a dearth of knowledge on the influence that species and decomposition have on hydraulic and pore properties (Goetz and Price, 2015; Liu and Lennartz, 2019; McCarter and Price, 2014) and only broad descriptors of bog and fen peat have been reliably associated with pedo-transfer functions following bulk density gradients and broad classifications of parent material (*i.e.*, *Sphagnum*, woody, sedge, *etc*,.) in a recent meta-analysis (Liu and Lennartz, 2019).

2.2.2. Sedge and graminoid peat

Sedge-derived peat is typically more susceptible to decay than *Sphagnum* derived peat (Hájek et al., 2011), resulting in more highly decomposed peat closer to the surface (Boelter, 1969; Liu and Lennartz, 2015). This increases proportion of smaller pores, hence tortuosity, resulting in a different pore network than in *Sphagnum* peat at a similar depth (Liu et al., 2017; Liu et al., 2016). Contrary to *Sphagnum* derived peats, where there is an exponential decrease in large water conducting pores with depth below the surface (Gauthier et al., 2018; Rezanezhad et al., 2009; Weber et al., 2017a; Weber et al., 2017b), sedge peat consists of a more uniform pore size distribution and a less extreme exponential decrease in large water conducting pores (Kleimeier et al., 2017; Liu et al., 2017; Liu et al., 2016). There is some evidence that decomposed or disturbed sedge peat contains a large proportion of immobile pores, potentially from the enhanced decomposition of the surficial peat (Liu et al., 2016). Additionally, the physical structure of sedges, and by extension reeds (Baird and Gaffney, 2000), creates the unique opportunity for bedding planes, depending on the orientation of the litter (Fig. 1). For instance, if the majority of reed litter is orientated parallel to the bedding plain, the pore network can be dominated by large continuous horizontal macropores with minimal vertical pore connectivity (Baird and Gaffney, 2000); this can result in a lower vertical hydraulic conductivity than horizontal (Beckwith et al., 2003a). These bedding planes result in a micro-scale anisotropy that may not exist in other peats (Gharedaghloo et al., 2018).

2.2.3. Woody peat

Woody peat typically makes up a smaller proportion of the peat profile than other peat types, yet can have a disproportionate effect on the connectivity of the pore network (Dommain et al., 2010; Holden, 2005; Päivänen, 1973). Relative to other peat types, woody peat remains relatively understudied, particularly the pore scale. Similar to reed bedding planes, the orientation of woody peat can greatly enhance the hydrological connectivity by creating connected macropores that allows the rapid movement of water and solutes, typically in the horizontal plane (Boelter, 1965; Boelter, 1969; Dommain et al., 2010; Holden, 2005; Holden, 2009a; Holden et al., 2001; Ong and Yogeswaran, 1992). Alternatively, when no preferential flow macropores are present, the pore network within woody peat remains relatively disconnected, as illustrated by the two to three order of magnitude decrease in K_{sat} between the woody intrusion and surrounding peat (Dommain et al., 2010; Ong and Yogeswaran, 1992). Distinct rooting zones within the peat can create a confining layer, or capillary barrier if unsaturated, limiting the upward migration of water and solutes (Balliston and Price, 2020); however, the ecohydrological implications of these rooting zones remain unknown. Päivänen (1973) observed a more rapid initial decrease but shallower tail of soil water retention as matric suction increased in woody peat, compared to that in sedge or *Sphagnum* peat, suggesting that the pore domain was dominated by macropores and small pores with relatively few intermediate pore sizes. It is likely that the macropores were due to preferential flow along and between the wood inclusions, rather than within the wood itself. Indeed, most studies attribute the preferential flow in woody peat to this phenomenon (Dommain et al., 2010; Holden, 2005; Ong and Yogeswaran, 1992; Päivänen, 1973). Although in northern peatlands woody peat and wood inclusions may play an important role in preferential flow (Boelter, 1965; Holden, 2005; Holden, 2009a; Verry et al., 2011), in tropical peatlands, woody peat can have a greater influence due to the prevalence of peat swamp forests contributing the most of organic matter to the peat profile (Chimner and Ewel, 2005; Dommain et al., 2010; Könönen et al., 2015; Wösten et al., 2008).

3. Pore-scale controls on water flow

3.1. Hydraulic conductivity and pore connectivity

The permeability of a porous medium is a physical property of the matrix that increases with increasing pore diameter and orientation along the predominant flow path, which accounts for the effect of pore shape on flow (Bear, 1972; Freeze and Cherry, 1979). The permeability, in conjunction with fluid properties, governs the hydraulic conductivity (K_{sat}), where a proportional increase in permeability will increase the K_{sat} in a water saturated medium (Bear, 1972; Freeze and Cherry, 1979). In peat, the reduction in K_{sat} with depth reported in the literature is far out of proportion to the relatively small reductions in pore diameters over the same depth. Quinton et al. (2000) reported a four-order reduction of K_{sat} from 1000 m d^{-1} within the 0-0.1 m peat layer, to 0.5 m d^{-1} at 0.35 m depth; other studies have also reported this extreme, or larger, systematic decrease (Baird, 1997; Beckwith et al., 2003a; Boelter, 1965; Boelter, 1969; Branham and Strack, 2014; Gnatowski et al., 2010; Hoag and Price, 1995; McCarter and Price, 2014; McCarter and Price, 2017a; Price and Maloney, 1994; Quinton et al., 2009; Quinton et al., 2008; Wallage and Holden, 2011). Over this same depth range, Quinton et al. (2000) reported that the mean pore diameters decreased from 1.58 to 0.39 mm, while the total porosity over this depth range decreased by only 10%, and the mobile porosity decreased from 0.8 to 0.5 over the same depth range. To further investigate the relation between K_{sat} and pore geometry, Quinton et al. (2008) derived K_{sat} from the conductance of individual pores whose diameters were measured from thin sections. This analysis followed Schlueter et al. (1997) who used the hydraulic radius and the Hagen–Poiseuille formula to calculate the hydraulic conductance of individual pores. This approach produced a good match between the measured values of K_{sat} (prior to resin impregnation) and computed values based on image analysis on the same peat samples, where pore shape had a disproportionate control on the permeability of peat relative to pore size. In another approach, Gharedaghloo et al., 2018 used 3D pore network modelling of flow and transport processes in peat, which takes pore connectivity, pore radii variation, and pore tortuosity into account, and calculated the K_{sat} of peat and its variations with depth. They observed that the reduction of peat K_{sat} with its depth is a cumulative effect of reduction in pore radii and increased pore tortuosity with depth. These analyses suggest that peat K_{sat} is essentially controlled by effective pore diameter and pore tortuosity, which respectively decreases and increases with depth due to decomposition and increasing compaction by overlying peat. Thus, the total volume of pore-spaces available for conduction of water greatly diminishes as decomposition increases, and coupled with the large reduction in permeability, the pore water velocity decreases under standard pressures. As the hydraulic flow path length increases, K_{sat} decreases, resulting in a strong control on the flow of water in peatlands (Carey et al., 2007; McCarter and Price, 2017a; Quinton et al., 2000; Quinton et al., 2005).

3.2. Anisotropy of peat and pore connectivity

Historically, the anisotropy of peat was assumed to be derived from the physical structure of the pores as they decompose and collapse from approximately round to elliptical (Boelter, 1965; Boelter, 1969). It was suggested that large surficial pores undergo decomposition and collapse, whereas the horizontal connectivity is maintained at the expense of the vertical connectivity (Beckwith et al., 2003a; Beckwith et al., 2003b), generating an exponential decrease in peat vertical transmissivity (*i.e.*, the ability of the aquifer profile to transmit water vertically) and severe anisotropy (Beckwith et al., 2003a; Deiss et al., 2004). However, recent 3D CT scans and pore-scale hydrological modelling have revealed that the pore network within peat is not inherently anisotropic (Gharedaghloo et al., 2018). Thus, anisotropy occurs due to the measurement of K_{sat} at larger scales, while the measured vertical K_{sat} is more severely influenced by the lower conductivity of deeper peat compared to the upscaled horizontal K_{sat}. This suggests that the apparent anisotropy of peat is, at least in part, due to methodological issues and that anisotropy in peatlands is in part due to meso-scale heterogeneities (> 1 cm), rather than micro-scale ones (pores) (Dommain et al., 2010; Gnatowski et al., 2010; Ong and Yogeswaran, 1992). In deeper, more decomposed peats, woody inclusions result in abnormally high horizontal K_{sat} that can create anisotropy at the micro-scale due to bedding planes and preferential flow (Ong and Yogeswaran, 1992; Päivänen, 1973). These processes potentially create a dual-permeability medium (Liu et al., 2016) in which most of the water and solutes flow occur along these preferential flow paths, while the matrix flow behaves similar to the immobile porosity due to its far lower permeability; these pore-scale properties have not been accurately measured in peatlands.

4. Pore-scale controls on gas and vapour transport

4.1. Gas and vapour in peat

Gas is present in peatlands above and below the water table. Biogenic gases, notably methane, are common in shallow peat especially later in summer when dissolved methane concentrations increase, soil temperatures rise and water tables decrease, causing gas to come out of solution (Strack et al., 2005). Following a rainfall or storm, or after snowmelt, increases in water table is associated with water imbibition into the partially saturated peat soil, during which aqueous phase might bypass the air phase. This bypassing effect can trap the air phase in pore space below the rising water table. Gas contents of up to 19% of peat volume have been reported (Tokida et al., 2005). The presence of biogenic gas affects peat buoyancy, hence surface level adjustment of the peatland (Kellner et al., 2005), decreases the permeability (Beckwith and Baird, 2001; Kettridge et al., 2013) and can alter hydrological flow paths (Strack et al., 2005). Methane over-pressuring (Kellner et al., 2005) results in episodic gas ebullition (Bon et al., 2014; Strack et al., 2005), which substantially contributes to the methane flux to the atmosphere in boreal (Strack et al., 2005) and tropical peatlands (Wright et al., 2018).

Biogenic compounds are released from solution forming biogenic gasses when their concentration in the aqueous phase exceeds their solubility limit. This might happen by reduction in their solubility (*e.g.* due to temperature change, decreased pore pressure after water table decline or reduced atmospheric pressure) (Kellner et al., 2006; Tokida et al., 2005) or because of continuing anaerobic microbial activity. Since the surface area to volume ratio decreases as gas bubble size increases, thermodynamically released bubbles tend to merge and form larger bubbles over time. This process in porous media is called coalescence, and its occurrence depends on several factors including size of bubbles and the wettability of the porous medium (Constantinides and Payatakes, 1991). The larger the gas bubble, the more the buoyancy force driving the bubble upward toward the water table, leading to ebullition. This likely is a contributing process to peat buoyancy.

4.2. Gas and vapour transport

The pore structures of peat soils play an important role specifically in the ebullition and the migration gas through the peat soils. The continuous upward movement of the gas phase might happen if the driving forces of the gas bubble (*e.g.* buoyancy force) overcome the capillary force (gas entry pressure) of peat pore throats along the pathway of the gas bubble. Indeed, pore-scale morphological characteristics of peat including the aspect ratio (ratio of pore body size to pore throat size) will be a controlling factor in preventing/promoting upward gas migration. The decrease in pore throat size with depth (Gharedaghloo et al. (2018) suggests that it might be more difficult for a given gas bubble to overcome pore throat's entry pressure in deeper peat compared to shallower peat. This agrees with the fact that a threshold gas volume is required for ebullition to take place (Baird et al., 2004). The threshold volume is the state of gas bubble volume when the forces driving it upward (proportional to the volume of the bubble and increasing with bubble size) overcome the capillarity in all the pore throats along bubble's flowpath. If the gas bubble volume is below the threshold, the buoyancy force is not strong enough to push the bubble through the pore throat. Considering that lower peat porosity is associated with smaller pore throat radii, the gas bubble size and the threshold gas volume required to overcome the capillarity of pore throats will increase with decreasing porosity. It explains the larger gas bubbles sizes observed in lower porosity peat soil in Ramirez et al. (2015). In addition to the peat depth or porosity, its origin might also play an important role in transport of individual gas bubbles. Ramirez et al. (2016) has shown that the dimension of gas bubbles and their release pattern in the ebullition process depends varies between two *Sphagnum* moss species. Their results suggest that peat pore structure differences due to botanical origin control the micro-scale processes governing upward gas bubble migration.

Pore-scale morphological characteristics also control the trapping of air in the pore space. Aspect ratio could be directly proportional with the trapped saturation of non-wetting phase (Chatzis et al., 1983; Tanino and Blunt, 2012), here air. Although aspect ratio hasn't been documented for peat soils, it will likely vary within and between peat botanical composition and peatland type depending on the depth and degree of peat decomposition. The average number of pore throats that a pore body is connected to (coordination number) is negatively correlated with the saturation of trapped non-wetting phase (Ruspini et al., 2017; Tanino and Blunt, 2012). Gharedaghloo et al. (2018) has shown that coordination number decreases with depth for peat soil, suggesting that possibility of air trapping is greater in deeper peat compared to the shallower ones. Furthermore, as pore throat size decreases, the pore water velocity increases, decreasing the trapped gas saturation (Fry et al., 1997). This suggests that higher vertical water velocity might lead to entrained trapped gas in peat soils.

5. Pore-scale controls on solute transport

5.1. Advective transport of solutes processes in peat

The size, shape, and connectivity of the pore network governs the delivery of solutes for biogeochemical reactions (Bear, 1972). In peat column studies, the immobile pores create elongated tailing effects and rapid breakthrough, where the magnitude of these effects depends on the diffusion into the immobile pores (Hoag and Price, 1997; Kleimeier et al., 2017; McCarter et al., 2019; McCarter et al., 2018; Rezanezhad et al., 2017; Rezanezhad et al., 2012; Rezanezhad et al., 2016). Yet, the degree of decomposition and parent material will govern the bulk transport of solutes (Gharedaghloo, 2018; Hoag and Price, 1997; Kleimeier et al., 2017; Liu et al., 2017; Liu et al., 2016; McCarter et al., 2019; McCarter et al., 2018; Ours et al., 1997; Rezanezhad et al., 2012; Simhayov et al., 2018). Near-surface macropores in all peat types can result in the rapid transport of solutes, well beyond what would be estimated under steady-state conditions (Baird and Gaffney, 2000). The majority of solute transport observations have focused on that in the upper ~1 m of the peat profile, since low vertical solute velocities at the field scale limit its presence at depth. Solute transport in deeper peats has not been well-documented. Practical constraints with sampling at depth may also have restricted the availability of data there. This remains a critical gap in our knowledge on solute transport processes in peat.

In *Sphagnum* peat, the rapid increase in degree of decomposition results in distinct solute transport properties with depth (Hoag and Price, 1997; McCarter et al., 2019; Ours et al., 1997). The abundance of well-connected large pores in surficial undecomposed *Sphagnum* peat results in rapid solute transport with minimal hydrodynamic dispersion (Hoag and Price, 1997; McCarter et al., 2019; McCarter et al., 2018). This surficial *Sphagnum* peat has very low dispersivity (0.1 to 0.4 cm, a physical property describing the lateral or vertical spread of a solute away from the centre of mass and primary advective transport direction) that result in the observed minimal hydrodynamic dispersion based on breakthrough experiments (Hoag and Price, 1997; McCarter et al., 2019; McCarter et al., 2018) and pore network modelling (Gharedaghloo et al., 2018). As *Sphagnum* derived peat decomposes, the decrease in well-connected large pores results in significant changes to the dispersivity, typically increasing to between 0.2 cm to 0.6 cm in the upper ~60 cm (Hoag and Price, 1997; McCarter et al., 2019). At the field scale, the differences in dispersivity and transmissivity due to rapid changes in pore structure results in most of the solute being transported within the upper few centimetres of the saturated zone and minimal transport within and to the deeper peats (Balliston et al., 2018; Hoag and Price, 1995; McCarter et al., 2017a; McCarter and Price, 2017b).

Conversely, non-*Sphagnum* fen peat has a more uniform pore structure with depth, resulting in less variation of solute transport (Kleimeier et al., 2017; Liu et al., 2017). Yet, anisotropy present in some fen peats can induce differences between vertical and horizontal solute transport, preferentially mobilizing stored solutes in the horizontal flow direction (Wang et al., 2020). The larger abundance of smaller pores in fen peat results in much higher dispersivities (0.8 – 2.6 cm) (Kleimeier et al., 2017; Liu et al., 2017; Rezanezhad et al., 2012) than *Sphagnum* derived peat within the upper 60 cm. Within these more uniform peats, field-scale solute transport is less confined to the upper layers and more vertical transport can occur (Baird and Gaffney, 2000; Ronkanen and Kløve, 2007), increasing the transverse and longitudinal hydrodynamic dispersion. Relative to *Sphagnum* derived peat, there is much less known about solute transport processes in fen peats but recent research (Kleimeier et al., 2017; Liu et al., 2017; Wang et al., 2020) has begun to unravel these important processes.

5.2. Diffusive transport of solutes in peat

The transfer of solutes into the immobile pores is governed by the effective diffusion coefficient, typically presented as a first order mass transfer process (Wierenga and Van Genuchten, 1989). The specific solute, and its free water diffusion coefficient, and the pore throat diameter govern the transfer of solutes into the immobile porosity (the effective diffusion rate) (Wierenga and Van Genuchten, 1989). As the diameter of pore throat connecting active porosity to dead end pores decreases, the mass transfer coefficient should decrease. Recently, McCarter et al. (2019) observed no decrease in mobile-immobile mass transfer coefficient between the mobile and immobile pores with an increasing degree of decomposition, using both chloride and deuterated water tracers; but, these results are preliminary and on a relatively small sample size ($n = 3$ at 2 degrees of decomposition) and only one peat type (*Sphagnum* bog). Notwithstanding this conjecture, there is some evidence (Kleimeier et al., 2017; McCarter et al., 2019; McCarter et al., 2018; Simhayov et al., 2018) that the mobile-immobile mass transfer coefficient can be sufficiently high in peat that physical equilibrium between mobile and immobile porosity establishes as solute moves through the soil (*i.e.* Fickian transport) and a single porosity solute transport model may be the simplest satisfactory model to represent the transport of rapidly diffusing solutes in peat (Simhayov et al., 2018). On the other hand, diffusion into closed cells and partially closed pores (*e.g.* belonging to the roots of vascular plants) can be extremely slow such that it can decrease the total porosity available for solute transport (Gharedaghloo, 2018). Recent research illustrates that the dead-end or immobile pores may result in an extended tailing effect and more rapid breakthrough (the time at which half the maximum solute concentration is detected in the outflow) of anion tracers in *Sphagnum* dominated peats, and some fen peats (Kleimeier et al., 2017; Liu et al., 2017; Liu et al., 2016; McCarter et al., 2018; Rezanezhad et al., 2017; Rezanezhad et al., 2012; Rezanezhad et al., 2016). However, the majority of these extended tails were observed with anion tracers that may be subject to anion sorption (Caron et al., 2015) that may produce similar breakthrough curves as diffusion into the immobile porosity (McCarter et al., 2018) or be subject to anion exclusion in the pore throats, enhancing the transport velocity of anion tracers (McCarter et al., 2019). In either case, the exact mechanisms governing solute mass transfer from the mobile to immobile porosity remains a critical gap in the literature that will require a concerted effort between hydrologist, soil physicists, and biogeochemists to elucidate.

5.3. Colloidal Transport Processes

The movement of highly reactive solutes, such as trace metals, are typically dependent on soil colloid, as well as dissolved organic matter, assisted transport in soils (Amrhein et al., 1993; Gai et al., 2016; Kalmykova et al., 2010). The transport of soil colloids, whether mineral or organic, is dependent on the pore water velocity, stagnant zones, shape of colloid and grains, geometry of pore throats, and local physicochemical conditions (Andreasson et al., 1988; Johnson et al., 2007a; Johnson et al., 2007b; Tong and Johnson, 2006). Additionally, in many mineral soils, colloid sieving can occur where the relative abundance of smaller pores decreases the total number of mobile colloids due to wedging or sorption (Fig. 1). However, the pore structure in peat soils is different than in mineral soils, chiefly due to a high proportion of large-diameter pores and the abundance of well-connected and low tortuosity pore networks in surficial peat (Gharedaghloo et al., 2018; Rezanezhad et al., 2010; Rezanezhad et al., 2009). In contrast, deeper peats typically have more abundant smaller pores with lower pore connectivity and higher tortuosity (Gharedaghloo et al., 2018; Rezanezhad et al., 2010; Rezanezhad et al., 2009). These structural differences could result in dichotomous colloid transport, where colloids are rapidly transported in the upper, undecomposed peat, yet retained in deeper, more decomposed peats (Andreasson et al., 1988). Furthermore, the immobile porosity increases the proportion of stagnant zones, potentially increasing colloidal retention in deeper peats. Yet, the typical chemical conditions within peat and high negative surface charge even at low pH (Andreasson et al., 1988; Vasiliadis et al., 2007) suggest that regardless of the peat pore structure there would be lower colloidal transport rates due to high physicochemical retention (Andreasson et al., 1988). In rich fen or swamp peat, the higher pH and ionic strength of the pore water would likely result in higher colloidal transport. Regardless, these are only theories based on extrapolation from a small body of colloidal research in peat (Andreasson et al., 1988; Forsberg and Aldén, 1988; Kalmykova et al., 2010) and this area remains a significant gap in our knowledge, especially due to the potential for mercury and other trace metal transport (Kalmykova et al., 2010) and the potential for insoluble particle assisted transport, such as pollen (Clymo and Mackay, 1987; Urban et al., 1990)

6. Pore-scale controls on peat biogeochemistry

6.1. Peat biogeochemistry and pore structure

The pore structure exerts a major control on the biogeochemistry of peat soils because it is closely linked to the soil moisture regime, the distribution of microbial habitats, and the transport rates and pathways of water, solutes and gaseous constituents. Microorganisms preferentially inhabit the immobile porosity and, therefore, depend on the supply of substrates from, and the removal of metabolic end-products to, the mobile porosity though diffusion, in order to sustain their biochemical activity (Nunes et al., 2015). Under waterlogged conditions, mass transfer limitations between different pore size classes, as well as on solute and gas transport along the interconnected pores, may therefore largely (down)regulate belowground microbial turnover and, hence, biogeochemical cycling (Schmidt et al., 2007)

The critical roles of soil moisture and water saturation are clearly evident during seasonal water table declines in peatlands, when peak emissions of CO_2 and large changes in pore water composition are observed. The latter include the lowering of pH and increases in sulphate (SO_4^{2-}) and decreases in dissolved organic carbon (DOC) concentrations (Clark et al., 2006). Similarly, aeration accompanying the managed dewatering of peatlands for agricultural and forestry usage greatly accelerates the aerobic decomposition of soil organic matter, causing increased emissions of CO_2 (and N_2O) to the atmosphere (Leifeld and Menichetti, 2018). The enhanced decomposition, however, is mostly restricted to the uppermost soil layers where interconnected macropores allow for the ingression of oxygen (O_2) and increased CO_2 emissions are primarily due to the oxidation of the young, more labile litter fraction. In turn, this explains the relative enrichment of decay-resistant, or recalcitrant, organic compounds in the uppermost layers of drained peatlands, compared to the deeper, undisturbed peat layers where O_2 is unable to penetrate (Bader et al., 2018). It should also be noted that in cold and cold temperate peatlands, late summer water table lowering also exposes the soil to higher temperatures, further stimulating microbial activity and accelerating organic carbon turnover.

6.2. Peat decomposition and preservation

Despite the large amounts of carbon stored in peat soils, it is important to recognize that typically less than 20% of plant produced organic carbon in peatlands is ultimately preserved, because most plant litter is mineralized in the upper 10-15 cm thick aerobic layer above the water table (Clymo, 1984). Here, we focus on the on the slow chemical decomposition of organic litter in the deeper peat layers, which is usually attributed to anoxic conditions and the lack of terminal electron acceptors below, and in part above, the water table that prevent the oxidation of organic substrates. Nonetheless, additional factors also contribute to the accumulation of peat. These include slow transport rates that enable the build-up of gaseous and aqueous decomposition end-products (Blodau et al., 2011; Bonaiuti et al., 2017), for example, methane (CH_4) and dissolved inorganic carbon (DIC), nutrient limitation and inhibition of microbial activity (Freeman et al., 2004; Hartman and Richardson, 2013), and preferential preservation of poorly degradable chemical compounds in the litter and soil organic matter (Leifeld and Menichetti, 2018; Sjögersten et al., 2016). However, the relative importance of these different factors, their mutual interactions, and their relationships to the pore structure of peat, remain to be fully unravelled. Continued efforts to develop a comprehensive mechanistic understanding of organic matter preservation in peat therefore remain essential to evaluate and predict how ongoing and future climate and land-use changes will affect carbon storage in peatlands.

In many soils important mechanisms leading to the long-term preservation of soil organic matter are the occlusion in aggregates (Pronk et al., 2012), adsorption at mineral surfaces (Six et al., 2002) and the formation of mineral-organic matter complexes, in particular with ferric (oxyhydr)oxides (Jung et al., 2012). These mechanisms may render organic compounds that would normally serve as energy substrates inaccessible to microorganisms. In peat, these mechanisms are generally of lesser importance because of the absence or low abundance of minerals. Therefore, more so than for mineral soils, it is often assumed that the high preservation potential of organic material in peatlands reflects the inherent low degradability of much of the peat litter under water-saturated, anoxic conditions (Scanlon and Moore, 2000). Such a view is consistent with molecular and compositional data that show a progressive loss of relatively labile compounds, such as polysaccharides, and a relative increase in more recalcitrant compounds, such as polyphenols, with depth in undisturbed peat soils (Sjögersten et al., 2016). An additional, and relatively simple, indicator of the degradability of a complex mixture of organic compounds is the observed temperature dependence of mineralization, usually expressed as a Q_{10} value (Hogg et al., 1992). This is based on the fact that the less labile fraction of soil organic matter includes more condensed compounds of lower energy contents, which should have higher activation energies towards oxidation to CO_2. According to the Arrhenius Equation, this equates to a stronger temperature dependence. Studies have indeed shown a general increasing Q_{10} trend with depth in undisturbed peat (Scanlon and Moore, 2000).

6.3. Thermodynamic limitation

Soil microbial communities decompose organic matter because it provides them with the chemical energy needed to grow more biomass and maintain cellular integrity. This means that a given organic compound should only be decomposed when it results in an energy gain for the microbes or, using the terminology of chemical thermodynamics, it yields a negative Gibbs energy of reaction (ΔG_r). The value of ΔG_r, in turn, depends on the intrinsic Gibbs energy of formation of the organic compound (reactant) relative to those of the products, as well as the concentrations of reactant and products. Because of the preferential utilization of the more reactive, and more energy-rich, energy substrates, the available energy content of organic compounds (their so-called standard Gibbs energy of formation, $-\Delta G_f^0$) usually decreases with depth in a peat soil (Worrall et al., 2018). Possibly even more important, the accumulation of reactants in the soil solution surrounding the microbes decreases the magnitude of $-\Delta G_r$, thereby making the decomposition increasingly less energetically favourable, eventually causing it to cease. When this happens, even fairly labile organic compounds will no longer be decomposed.

An elegant experimental demonstration of the above was provided in the experiments conducted by Blodau et al. (2011) in which they incubated fully water-saturated columns filled with variable mixtures of sand and peat for extended periods of time (> 1 year). For all the mixtures, the pore water CH_4 and DIC concentrations reached the same levels at depths below 30-40 cm, indicating that the extent of decomposition was regulated by the build-up of the reactants of methanogenesis. Thermodynamic calculations further implied that acetate, rather than hydrogen, was the substrate generating CH_4 under the experimental conditions, and that for methanogenesis to be a viable pathway, a minimum of about 25 kJ of energy needed to be generated per mole CH_4 (the so-called biological energy quantum). In peat soils, the depth where methanogenesis becomes inhibited strongly depends on the ability of the reaction products, CH_4 and DIC, to be removed through the pore network. The degradability of soil organic matter is thus a relative concept that depends not just on the intrinsic (molecular) properties of the compounds, but also on energetic constraints imposed by the geochemical environment (LaRowe and Van Cappellen, 2011), priming effects (Hamer and Marschner, 2002), inhibition of enzymatic activity by, for example, low-molecular phenolics (Freeman et al., 2004), nutrient requirements of the soil microbial populations (Hartman and Richardson, 2013), and temporal variations in water saturation and redox conditions (Nunes et al., 2015; Rezanezhad et al., 2014).

6.4. Geochemical processes

Peat is known as an extremely good material to remove cations from pore water (Crist et al., 1996; Ho and McKay, 1999; Ho et al., 2002; Khan et al., 2019; Kyzoil, 2002; Palmer et al., 2015; Shotyk et al., 2017), while the removal of anions is less efficient (Clymo, 1963; McCarter et al., 2019; McCarter et al., 2018; Richter and Dainty, 1989). Anion sorption is thought to occur primarily with amino acids (Richter and Dainty, 1989). Although relatively minor, these anion exchange processes have been shown to influence anion transport in both *Sphagnum* and sedge peats at varying degrees of decomposition (McCarter et al., 2019; McCarter et al., 2018). In contrast, cation exchange processes in peat is complicated by botanical origin (Crist et al., 1996) and the presence of other cations in the pore water (*i.e.*, competitive adsorption) (Crist et al., 1996; Ho and McKay, 1999; Kalmykova et al., 2010; Khan et al., 2019; Kyzoil, 2002; McCarter et al., 2018). In the leaves of *Sphagnum*, ions are transferred across cell membranes allowing for apparent adsorption in batch experiments but is absorption into the inter-cellular and Donnan space (Clymo, 1963; Richter and Dainty, 1989). This allows for cations to affix throughout the leaf cell walls, not just the surface (Clymo, 1963). Conversely, on the branches and stems of *Sphagnum*, direct ion exchange is the dominant cation removal mechanism and limited if any absorption occurs (Clymo, 1963). Similar to *Sphagnum* stems, in sedge peat direct ion exchange is the dominant process governing cation removal from pore waters (Crist et al., 1996; Kyzoil, 2002; Pennington and Watmough, 2015). As peat decomposes, the exact mechanism of cation removal from pore waters is less certain but direct ion exchange is the most likely due to loss of intact *Sphagnum* cells (Fig. 2). Generally, an increase in cation adsorption with increased degree of decomposition has been observed based on batch experiments, attributed to an increase in specific surface area and bulk density, which is proportional to the total adsorbed mass (Gharedaghloo, 2018), and a decrease in surface charge (Andreasson et al., 1988; Vasiliadis et al., 2007). Regardless of peat origin or degree of decomposition, cation exchange with the peat surface releases bound H^+, or organic acids, into the pore water (Clymo, 1963; McCarter et al., 2018; Richter and Dainty, 1989). These changes in pH arising from geochemical exchanges, further modify the reactivity of the peat surface and dissolved and bound solutes and colloids (Andreasson et al., 1988; Kalmykova et al., 2010) that can feedback into the flocculation of colloids, changing the peat permeability (Baird and Gaffney, 2000; Forsberg and Aldén, 1988; Hoag and Price, 1995; Ours et al., 1997). However, there remains little detailed information on structural and chemical implications of the peat surface (Andreasson et al., 1988) on solute adsorption in peat and remains a critical gap in our knowledge.

7. Peat Pore Structure Feedbacks

7.1. Pore water chemistry

Changes in the ionic strength of the pore water in peat has led to both the increase and decrease of K_{sat} (Comas and Slater, 2004; Hoag and Price, 1997; Kettridge and Binley, 2010; Ours et al., 1997), and likely solute advection. In more well-decomposed blanket bog peat (Hoag and Price, 1997), flocculation due to increases in solution ionic strength was thought to be the primary cause of the observed decrease in K_{sat}, where organic matter would have detached from the peat surface, forming colloids that clogged the smaller pore throats, resulting in less pore connectivity (Forsberg and Aldén, 1988; Hoag and Price, 1997). Conversely, in less decomposed peat there has been an observed increase in K_{sat}, which was primarily thought to be caused by protein coiling and flocculation, and subsequent flushing out of large pores, thus increasing average pore diameter (Forsberg and Aldén, 1988; Kettridge and Binley, 2010; Ours et al., 1997). Changes in electrical conductivity (a proxy for ionic strength) from 0.01 to 0.1 S m^{-1} have been observed to drive these increases in K_{sat} (Comas and Slater, 2004; Ours et al., 1997). If protein coiling was the primary cause, the change in K_{sat} should be reversible (Kettridge and Binley, 2010), while if flocculation and clogging occur, the change is irreversible. However, neither of these hypotheses have been specifically tested, particularly with regards to solute transport, and likely depend on the peat parent material and level of decomposition. McCarter et al. (2018) observed an increase in K_{sat} when sodium chloride was present, relative to deionized water, but no systematic investigation was completed on the changes in K_{sat} under varying/sequential solute loads and resultant changes to solute transport. In any case, the reduction or increase in K_{sat} will alter the solute velocity within peat, which, in turn, can affect K_{sat} due to changes in the ionic strength as the solute is flushed into or out of the pores at different rates.

7.2. Biogenic gas

Biogenic gas, such as carbon dioxide or methane, is readily produced in peatlands (Bottrell et al., 2007; Shotyk, 1988). However, like changes in ionic strength that alter the pore connectivity, biogenic gas bubbles can become entrained in peat that can change peat's hydrophysical properties (Beckwith and Baird, 2001). For instance, Kettridge and Binley (2008) examined the potential of using X-ray computed tomography (CT) to analyse individual biogenic gas bubbles entrapped within *Sphagnum* peat and observed that the vertical variations in *Sphagnum* pore structure produced zones of preferential gas entrapment. In contrast, Comas et al. (2014) observed that the presence of woody peat has much higher gas content than the surrounding peat and that the pore matrix was the primary control on entrapped gas. Furthermore, Rosenberry et al. (2006) highlighted the importance of peatland morphology and hydrology on the diffusive and ebullitive fluxes and storage of biogenic gas. Abrupt change in the volume of gases may alter hydraulic gradients (Kellner et al., 2005), thus movement of water and solutes in peat. Due to capillarity forces, the biogenic gas bubbles tend occupy larger pores in the pore network, where the decreased frequency of macropores in deeper peat would increase the likelihood of biogenic gas bubbles becoming entrained and lowering the permeability but this process would be less pronounced in shallow peat due to the abundance of large diameter pores (Beckwith and Baird, 2001). Thus, the clogging of flow paths by gas bubbles in deeper peat can cause more severe reduction of permeability compared to that in shallower peat. In any case, when gas bubbles are present, solving for two-phase flow could be used to determine the appropriate macroscopic peat properties. However, there remains minimal research coupling the biogenic gas production to changes in hydraulic properties in peat.

7.3. Ecohydrological feedbacks

Unlike many mineral soils, peat soils shrink and swell depending on the soil water pressure (hence soil water content), typically called "mire breathing" (Golubev and Whittington, 2018; Price, 2003; Schwärzel et al., 2006). Over the course of a growing season, shrinkage due to evaporation and swelling due to precipitation is mostly reversible (Kennedy and Price, 2005; Kennedy and Price, 2004; Schwärzel et al., 2006), yet when oxidation occurs, shrinkage and consolidation are irreversible due to mass loss and changes to the physical structure of the peat matrix (Huat et al., 2011; O'Kelly and Pichan, 2013; Tfaily et al., 2014). These processes can have profound effects on the pore structure of peat soils. A reduction in pressure causes pores to drain, with a concomitant decrease in peat volume (Schwärzel et al., 2006). The net result is that the degree of saturation can be maintained, thus maintaining hydrological connectivity with deeper water stores (Gauthier et al., 2018; Golubev and Whittington, 2018; McCarter and Price, 2014; Schwärzel et al., 2006). However, when peat soils undergo disturbance, such as draining for horticultural peat production or agriculture, oxidation of the organic material creates irreversible pore structure changes (Huat et al., 2011; O'Kelly and Pichan, 2013; Tfaily et al., 2014). As oxidation proceeds, macropores collapse and create a greater proportion of smaller pores with less inter-pore connectivity (McCarter and Price, 2015; Price, 2003; Taylor and Price, 2015). Unlike mire breathing, where increases in soil moisture restores connectivity to the larger pores (Golubev and Whittington, 2018), the degraded peat soils retain a large proportion of smaller pores (McCarter and Price, 2015; Taylor and Price, 2015). This creates a substrate that has much higher soil water retention and associated K_{sat} at a given negative pore water pressure (Baird and Gaffney, 2000; LaRose et al., 1997; McCarter and Price, 2015; Price, 1997; Schwärzel et al., 2002; Schwärzel et al., 2006; Taylor and Price, 2015). This significantly alters the hydrology of the peatland; even post-restoration (LaRose et al., 1997; McCarter and Price, 2013; Price and Schlotzhauer, 1999; Schlotzhauer and Price, 1999; Shantz and Price, 2006; Van Seters and Price, 2001).

In *Sphagnum* peat, the between plant pore spaces dominate water flow under saturated and unsaturated conditions (Weber et al., 2017a); however, the evaporative demand at the surface of *Sphagnum* mosses and peat can result in soil water pressures far lower than observed a few centimetres below, resulting in inner-plant pore spaces or non-capillary water dominating the flow of water under unsaturated conditions (Golubev and Whittington, 2018; McCarter and Price, 2014; Weber et al., 2017a). Decreases in soil water pressure, either from evaporative losses or decreases in water table, rapidly decreases the soil water content within the upper few centimetres of saturated *Sphagnum* peat due to the abundance of macropores (Gauthier et al., 2018; Golubev and Whittington, 2018; McCarter and Price, 2014). This rapid decrease in soil water content exponentially decreases the unsaturated hydraulic conductivity (K_{unsat}) (Fig. 4) (Liu and Lennartz, 2019; McCarter et al., 2017b; McCarter and Price, 2014; Weber et al., 2017a; Weber et al., 2017b), which creates a negative feedback to the flow of water, decreasing the ability of the *Sphagnum* moss to meet evaporative demand (McCarter and Price, 2014). Once drained, the water contents in the

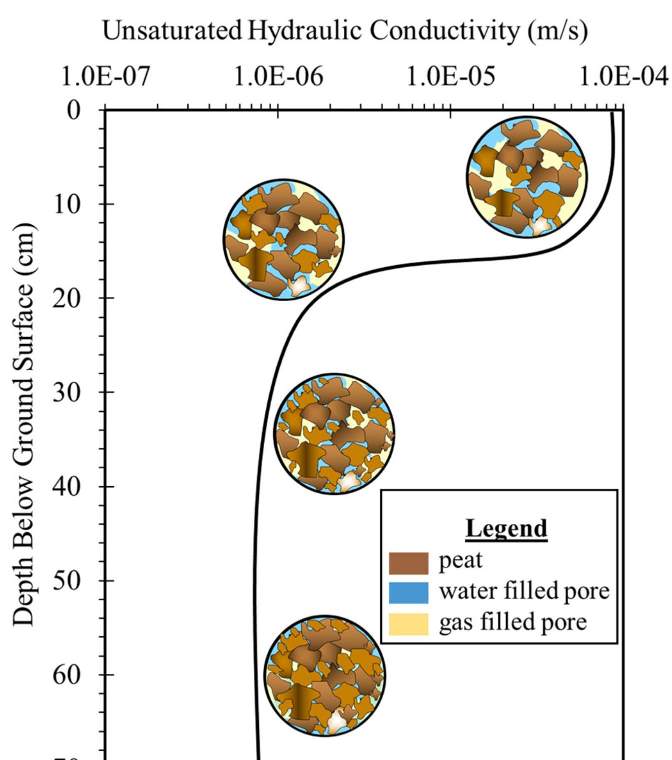

Fig. 4. Idealized unsaturated hydraulic conductivity curve with depth at -40 cm of pressure, with increasing degree of decomposition with greater depth below ground surface. The decreasing proportion of yellow space as depth increases indicating a smaller proportion of air-filled pores at greater depth. The axis values represent an approximate value rather than specific values and do not represent the inherent variability observed in peat. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

upper peat layers becomes remarkably constant due to the aforementioned feedbacks (Ketcheson and Price, 2014; McCarter and Price, 2015; Price and Whittington, 2010). As the ability to meet an evaporative demand declines due to the rapid decrease of the unsaturated K_{unsat}, the *Sphagnum* moss is thought to avoid drought conditions through maintaining soil water pressure above approximately -100 mb (the threshold for hyaline cell desiccation) (Gauthier et al., 2018; Golubev and Whittington, 2018; Hayward and Clymo, 1982; McCarter and Price, 2014); yet, this process has not been directly measured. When coupled with changes to the wetting tendency of peat due to pore-scale variation, significant wetting hysteresis might be observed (Gharedaghloo and Price, 2017; Gharedaghloo and Price, 2019; Hayward and Clymo, 1982; Michel et al., 2001; Schwärzel et al., 2006). The observed hysteresis of the water content in peat can delay the return of moisture to the biologically active region of peatlands, such as *Sphagnum* moss capitula, and further exacerbate periods of hydrological stress (Hayward and Clymo, 1982). The interconnected relationship between pore structure and hydraulic properties, coupled with the immobile porosity of the hyaline cells, creates conditions to maintain water available for physiological processes until a threshold pressure is exceeded. These processes limit the evaporation from *Sphagnum* surfaces, greatly decreasing the total water loss during periods of hydrological stress (Price, 1991). Conversely, in fen peat or degraded bog peat, the abundance of smaller pores within these peats results in a shallow slope of the soil water retention curve, which maintains wetter conditions at the surface (Fig. 3) and allows these peats to better meet evaporative demand than *Sphagnum* mosses (Price, 1996). However, there are still relatively few hydrophysical studies on fen peat relative to *Sphagnum* peat and warrants further research (Liu and Lennartz, 2019).

7.4. Biogeochemical feedbacks

The physical and chemical processes that govern the transport of dissolved solutes and colloids also govern microbial transport with added biological processes, such as active adhesion/detachment and chemotaxis (the movement of a motile organism in a direction corresponding to a chemical gradient) (Ginn et al., 2002). In peat, the large pores in the upper peat layers promote higher flow velocities that may be inhospitable to microbial community development due to low residence time between the microbes and solid phase (Ginn et al., 2002). The diffusion of microbes into the immobile porosity is governed by liquid diffusion, cell concentration gradient (similar to chemical gradients), and the nutrient/ionic gradients (Ginn et al., 2002). Within less-decomposed upper peat, ideal conditions for microbial community development may occur in the immobile porosity where advective processes are absent. However, the ability for a microbial community to inhabit the immobile porosity would depend on a sufficiently high diffusion rate between the mobile and immobile porosities. In less-decomposed peat the potential diffusion rate can be sufficiently high (McCarter et al., 2019) and the immobile pores may be the primary region of biogeochemical activity (Rezanezhad et al., 2017). As the proportion of partially closed pores increase with degree of decomposition, the diffusion rate of solutes into this immobile porosity may decrease, resulting in less biogeochemical activity. Thus, in these more decomposed peats, the mobile porosity is potentially the primary zone of biogeochemical activity, partly due to longer residence times. These diffusion processes, along with differences in organic matter quality, abundance of decomposition products, lower temperatures, decreased oxygen, more recalcitrant carbon, and nutrient availability *etc.,* (Bonaiuti et al., 2017; Keller et al., 2006), potentially partly explain the decrease in biogeochemical processes observed at depth (Bonaiuti et al., 2017; Preston et al., 2012; Sundh et al., 1994).

In contrast to the saturated condition discussed above, under unsaturated conditions the large interconnected mobile pores readily drain, while water in the immobile porosity, whether hyaline cells or isolated pores, remains saturated at common field pressures (Golubev and Whittington, 2018; McCarter and Price, 2014; Weber et al., 2017a; Weber et al., 2017b). The saturated immobile porosity in unsaturated peat may continue to be a biogeochemical hotspot if the oxygen diffusion rate is sufficient to meet demand, or may become anoxic and have a relatively lower biogeochemical reaction rate (Bonaiuti et al., 2017; Nunes et al., 2015). However, given observed reduced sulphur oxidation during low water table periods and increased microbial sulphate reduction during high water table periods (Branfireun et al., 1999; Coleman Wasik et al., 2015; Mitchell et al., 2008), it is likely that sufficient oxygen diffusion occurs. Conversely, both Knorr et al. (2008) and Deppe et al. (2010) noted enhanced methane emissions from the unsaturated zone when the majority of pores remain saturated. This suggests sufficiently anoxic conditions can occur in part of the unsaturated soil profile, depending on the specific pore structure of peat. In either case, these hotspots have been attributed to increased carbon (both carbon dioxide and methane) emissions in peatland (Deppe et al., 2010; Knorr et al., 2008; Morris et al., 2011); thus, the immobile porosity in the vadose zone may be an important contributor to carbon dynamics in peatlands. However, the observed dichotomous biogeochemistry of the unsaturated zone in peatlands suggests a complicated relationship between nutrient and decomposition product transport, microbial habitat, and the pore structure of any given peat (Fig. 1). Although these stagnant zones may be the primary region for microbial processes in peat under saturated or unsaturated conditions, limited physical data of this has been presented in the literature and requires further research to elucidate the exact nature of these complex relationships.

7.5. Feedbacks of freeze-thaw processes

Peatlands in temperate, boreal, and subarctic regions are subject to freezing conditions during the autumn, winter, and spring. In the spring, thawing ground ice can release a significant amount of water to maintain important peatland ecohydrological functions, such as transpiration, but reduces the overall evapotranspiration rate due to competition for energy between thaw and evapotranspiration (Van Huizen et al., 2020). During shoulder seasons, freeze-thaw cycles are increasing in frequency and intensity on an intra-annual basis due to high-latitude warming trends that decrease the duration and depth of snow cover, as well as other anthropogenic stresses (Tarnocai, 2006). While frozen under saturated conditions, peat is relatively impermeable, promoting restricted infiltration, near-surface saturation, and surface ponding (Price, 1987; Woo and Winter, 1993). However, if the freezing front is above the water table, the frozen peat remains relatively porous (Price and Fitzgibbon, 1987). Freeze-thaw cycles are thought to drastically affect the physical and hydraulic properties, greenhouse gas emissions, geochemical processes and composition of microbial communities in soils (Hayashi, 2013), but the implication of freeze-thaw cycles on peat properties have not been well described.

Freeze-thaw processes in peat are hysteretic and highly dependent on pore size, geometry and initial moisture content prior to ground cooling (Nagare et al., 2012; Smerdon and Mendoza, 2010). During soil freezing, the soil water potential drops in a manner analogous to soil drying and ice preferentially develops first in macropores (Kralj and Pande, 1996), while smaller pores can maintain liquid water to several degrees below 0 °C (Hayashi, 2013; Smerdon and Mendoza, 2010). As peat freezes, variable matric, vapour, and thermal gradients in both space and time induce fluxes of water and energy toward the downward propagating freezing front (Mohammed et al., 2014; Nagare et al., 2012); however, a detailed understanding of the relationship between liquid moisture content and temperature as peat soils freeze is still unknown. Moisture migration through peat is further enhanced by the deforming properties of peat materials (Gamayunov et al., 1990), which can be sufficient to raise the water table in a soil column over the winter period or cause the water table to fall when water rises to the freezing front. This has been demonstrated in laboratory and numerical modelling studies (Nagare et al., 2012), and observed in the field in discontinuous permafrost terrains (Quinton and Baltzer, 2013). This is an important mechanism in governing subsurface and solute runoff during snowmelt, as the close proximity of the frost table to the ground surface during the spring freshet can prevent infiltration and induce rapid runoff through the near surface peat (Quinton et al., 2008), or over the surface for peatlands frozen in the saturated condition (Price and Fitzgibbon, 1987).

Frozen peat is an effective medium to transfer heat between permafrost and the atmosphere, due to its relatively high thermal conductivity (~2 W m^{-1} K^{-1}) (Oke, 1987). The freezing and thawing of peat in the active layer (*i.e.*, soil overlying permafrost that freezes and thaws annually) or other seasonally frozen ground exerts a significant control on the thermal state of the underlying substrate and is highly dependent on soil moisture prior to freeze-up (Hayashi, 2013). Due to the high total porosity of peat, changes in the physical state of pore water (*i.e.,* liquid or frozen) can have large implications on the bulk thermal conductivity of the soil, and subsequently on energy transfer throughout the peat soil system. The latent heat associated with freezing and thawing of peatlands can produce "zero-curtain" periods (*i.e.* isothermal period where ground temperatures remain near 0°C as latent heat is dissipated) lasting several weeks or more (Kokelj et al., 2017), that affect the duration of conductive ground cooling (Connon et al., 2018; Kokelj et al., 2010; Romanovsky and Osterkamp, 1995). Hysteretic freezing and thawing of active layer peat (Smerdon and Mendoza, 2010) governs the length of time that the underlying permafrost is coupled to the atmosphere and able to efficiently exchange energy. During the freeze-back period, horizontal flow of water and energy can persist, at least temporarily, between the downward propagating freezing front and underlying soils (Romanovsky and Osterkamp, 2000). As climate warming continues, the duration of the freeze-back period will increase, and in some cases may last throughout the winter (Connon et al., 2018).

Little is known about over-winter hydrological and thermal processes in peatlands, as they are usually ignored or assumed dormant (Walvoord and Kurylyk, 2016; Woo, 2012). Over winter, Price and Fitzgibbon (1987) observed bog peatlands were groundwater recharge zones, while fens discharged groundwater. Recent findings suggest that over-winter mass (water) and energy transport may be an important mechanism for recharging groundwater and increasing baseflow (St. Jacques and Sauchyn, 2009; Walvoord and Striegl, 2007), and providing a sustained energy input through advective heat flux in permafrost regions (Connon et al., 2018; Sjöberg et al., 2016). Seasonal pore dilation, resulting in increased saturated hydraulic conductivity have been observed in peatlands due to freezing pore water; however, these effects were not permanent (Kennedy and Price, 2005). Some hydrological models are being adapted to include routines that can better represent phase transformation from porewater to ice, such as SUTRA (Kurylyk et al., 2016; McKenzie et al., 2007b), Raven (Devoie et al., 2019), the Pan-Arctic Water Balance Model (Rawlins et al., 2003), as these have models have not performed well without this consideration (McKenzie et al., 2007a). Other models, such as the Cold Regions Hydrological Model (Pomeroy et al., 2007), have been specifically developed to incorporate cold region processes, and have been subsequently adapted to include algorithms to represent freeze-thaw in peatlands (Hayashi et al., 2007; Knox et al., 2012; Quinton and Baltzer, 2013; Van Huizen et al., 2020). In peatlands, the presence of perennially thawed layers (*e.g.* taliks) between overlying seasonally frozen soil and permafrost is becoming increasingly prevalent (Connon et al., 2018; Jafarov et al., 2018; Walvoord et al., 2019); however, these features are not always included in hydrological models due to difficulties in estimating spatial distribution (Krogh et al., 2017). Thus, these special properties of peat pore structure and thermal dynamics can affect the energy and mass (water) transfers and thermal properties that provide essential hydrological, ecological and biogeochemical functions in relation to freeze-thaw depth and mechanisms involved in the winter processes in peatlands. Additional studies are required, however, to predictively relate the mechanisms responsible for the effect of enhanced freeze-thaw cycles on pore-scale transport processes (Kadlec et al., 1988; McKenzie et al., 2007a) and, particularly, biogeochemical reactions in peat soils. There is a particularly pressing need to better understand biogeochemical reactions and transport at the pore scale during freeze/thaw cycles in peatlands, especially in thawed layers confined between the downward propagating freezing front and underlying permafrost. With increasing wintertime temperatures and increasing freeze-thaw events in these regions, the effect of freeze-thaw processes will become more important in our understanding of water and solute movement in peat and peatlands.

8. The known unknowns (research gaps)

This review has highlighted the relatively unexplored role the pore structure of peat has on the hydrological and biogeochemical processes governing peat and peatlands (Fig. 1). There is a pressing need to further unravel the role that peat pore structure has on the processes and feedbacks that govern peat and peatlands, particularly as these ecosystems are under increasing development and climate change threats. To that end, we have identified the key gaps in our current understanding that warrant further exploration and research:

1. Given the large diversity of peat pore structures, there needs to be a concerted effort to understand the combined and interrelated effects botanical origin of peat, decomposition, and nutrient status have on peat pore connectivity, diffusional and advective tortuosity, macropore development and collapse, active to inactive pore connectivity, and nutrient availability. A firmer understanding of these processes will allow for more realistic predications of peatland functionality under a changing climate and increased resource development pressures.
2. With increasing variation in temperature and winter-time days above zero, the influence of changing pore structure on the hydrology and biogeochemistry of peat remains a critical gap in our knowledge. Without such knowledge it is impossible to properly asses changes in nutrient and water movement during the spring freshet and under a changing climate.
3. Solute transport in peatlands is still conceptualized relatively simplistically as a dual porosity process and typically ignores the potential for peat to be a dual permeability medium, where two distinct pore networks contribute to advective flow but at different rates and quantities. However, recent studies have highlighted the potential for solute transport in peatlands to rely on these dual permeability processes, at least partially. There needs to be a focus on these hydrogeochemical processes in peatlands to better understand these processes, especially as trace metal transport in peatlands is becoming a concern with increasing industrial development in peatland dominated regions.
4. The unique pore structure of peat creates a complicated relationship with microbiological and biogeochemical processes. Without understanding the role of the immobile porosity and pore space on microbiological processes and how diffusion rate limitations may or may not influence these processes, it is difficult to properly predict how these systems will change under increased external pressures. Furthermore, the peat surface chemistry and variations within the different pore spaces will affect the microbiological processes and the transport and transformations of nutrients and contaminants in peatlands.

The research gaps listed above represent the known unknowns. As we continue to investigate the complex interactions and feedbacks between peat properties and peatland hydrology, biogeochemistry and ecology, some of these will become better-known. However, there undoubtedly remain unknown unknowns that new research may identify (Price, 2017), leading to new challenges and opportunities.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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