

# Hydrological feedbacks in northern peatlands

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## ABSTRACT

Northern peatlands provide important global and regional ecosystem services (carbon storage, water storage, and biodiversity). However, these ecosystems face increases in the severity, areal extent and frequency of climate-mediated (e.g. wildfire and drought) and land-use change (e.g. drainage, flooding and mining) disturbances that are placing the future security of these critical ecosystem services in doubt. Here, we provide the first detailed synthesis of autogenic hydrological feedbacks that operate within northern peatlands to regulate their response to changes in seasonal water deficit and varying disturbances. We review, synthesize and critique the current process-based understanding and qualitatively assess the relative strengths of these feedbacks for different peatland types within different climate regions. We suggest that understanding the role of hydrological feedbacks in regulating changes in precipitation and temperature are essential for understanding the resistance, resilience and vulnerability of northern peatlands to a changing climate. Finally, we propose that these hydrological feedbacks also represent the foundation of developing an ecohydrological understanding of coupled hydrological, biogeochemical and ecological feedbacks. Copyright © 2014 John Wiley & Sons, Ltd.

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## INTRODUCTION

Northern peatlands (i.e. those north of 45° N) and their carbon-rich soils (Gorham, 1991; Smith *et al.*, 2004) exhibit a number of important feedbacks with the global climate system (Frolking and Roulet, 2007; Bridgman *et al.*, 2008). Both positive and negative feedbacks compete for dominance of the peatland carbon budget over a range of spatial and temporal scales, and often in complex manners (Davidson and Janssens, 2006; Belyea, 2009). As such, the magnitude and direction of the response of peatland carbon stocks, water storage and biodiversity to climatic and land-use changes are difficult to assess with confidence (cf. Moore *et al.*, 1998). For example, increased emissions of the greenhouse gases carbon dioxide (CO<sub>2</sub>) and methane (CH<sub>4</sub>) are projected because of enhanced decomposition resulting from altered soil moisture and thermal regimes (Davidson and Janssens, 2006; Roulet *et al.*, 2007; Bridgman *et al.*, 2008). However, such emissions may be offset by increased carbon sequestration due to changes in peatland vegetation (Strack and Waddington, 2007; Loisel and Yu, 2013). The resultant change in peatland-atmosphere

exchanges of CO<sub>2</sub> and CH<sub>4</sub> seems likely to provide a direct feedback to the global climate system (Frolking and Roulet, 2007). Although at an early stage, ongoing efforts to incorporate a satisfactory representation of northern peatlands within global climate models will allow the strengths and directions of peatland-climate feedbacks to be estimated with more confidence (e.g. Frolking *et al.*, 2009).

Feedbacks between peatland carbon emissions and climate and land-use changes are distinct from numerous autogenic (within-peatland) feedbacks (Belyea, 2009; Dise, 2009) that regulate the response of peatlands to external forcings. Studies of peatland hydrology have described a group of these autogenic feedbacks that may amplify or dampen external interactions between the peatland and atmosphere. This is because peatland carbon and water budgets are closely linked, with hydrological metrics such as water table depth (WTD) often being powerful predictors of the ecological and biogeochemical processes that regulate fluxes of carbon to, from and within peatlands (Yu, 2006; Beer and Blodau, 2007; Wu *et al.*, 2011). We argue that in order to determine the sensitivity of peatlands to external pressures, there is a need for a greater understanding of both the breadth and interconnected nature of such autogenic feedbacks within the confines of peatland hydrology and also transcending the disciplines of

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hydrology, ecology and biogeochemistry. As a necessary first step towards the development of an integrated trans-disciplinary process understanding of peatland ecosystems, here, we provide a synthesis of the hydrological feedbacks that operate in peatland ecosystems. The aim of this synthesis is to not only summarize and critique these feedbacks but to also assess qualitatively how their strengths (e.g. strong and weak) vary according to peatland type and climatic region. We discuss how these hydrological processes fit with current ecological and biogeochemical theories and invite the peatland research community to undertake a similar review of ecological and biogeochemical feedbacks.

#### A SYNTHESIS OF HYDROLOGICAL FEEDBACKS

Many aspects of peatland ecohydrology exhibit complexity and contain strong memory effects, suggesting that peatlands are examples of complex adaptive systems (Belyea and Baird, 2006). However, we have deliberately focussed on hydrological feedbacks that are directly or indirectly linked to WTD. We have chosen this approach mainly because WTD is commonly used to predict a number of important ecohydrological variables in peatland hydrology, ecology and biogeochemistry including run-off, saturation, redox potential, soil structure, CH<sub>4</sub> emissions, carbon quality and organic matter decomposition. We also incorporate a discussion of some feedbacks using the 'hot-spot and cold-spot' conceptual model of peatland ecohydrology recently proposed by Morris *et al.* (2011a). The hydrological feedbacks (identified by Roman letters in text, tables and figures for simplicity) that we identify here include the following: (A) *WTD—afforestation and/or shrubification feedback*; (B) *WTD—moss surface resistance and albedo feedback*; (C) *WTD—transmissivity feedback*; (D) *WTD—peat deformation feedback*; (E) *WTD—specific yield feedback*; (F) *WTD—peat decomposition feedback*; and (G) *WTD—moss productivity feedback*. We do not assert that this synthesis represents an exhaustive and complete collection of all autogenic hydrological feedbacks in northern peatlands. However, we consider here feedbacks that (1) we believe have the potential to be important for the response of peatlands to future climate change, (2) we believe are important for controlling vulnerability of seasonal disturbances such as wildfire, (3) demonstrate high potential for interaction with broader ecological and biogeochemical peatland processes, (4) are well documented by observational studies and (5) provide a strong theoretical basis for an improved representation of northern peatlands in the next generation of land surface models (cf. Frothingham *et al.*, 2009).

##### (A) *WTD—afforestation and/or shrubification feedback*

A number of studies have observed rapid shrubification of tundra (Tape *et al.*, 2006; Myers-Smith *et al.*, 2011; Ropars and Boudreau, 2012) and subarctic peatlands (Berg *et al.*,

2009) in response to climatic warming. Laboratory experiments have linked warming and drying to increased shrub cover in peat monoliths (Weltzin *et al.*, 2003). Moreover, afforestation of peatlands has also been observed where water tables have been lowered for experimental or industrial purposes (e.g. Dang and Lieffers, 1989; Pellerin and Lavoie, 2003; Linderholm and Leine, 2004) or have been coupled with a dry climatic period during the first part of the 20th century (Pellerin and Lavoie, 2000, 2003). In contrast, a colder and wetter climate may raise the water table. This may cause a prolonged inundation of the rooting zone, which causes stunted growth or mortality of many tree species due to root oxygen stress (Boggie, 1972; Mitsch and Gosselink, 1993; Roy *et al.*, 2000). A warmer climate can also have this same effect through the thaw of permafrost peatlands (Camill, 1999; Camill *et al.*, 2001). The positive relationship between below-ground and above-ground vascular plant biomass with average WTD has been quantified in several studies and seems to hold for both shrubs and trees (Lieffers and Rothwell, 1987; Murphy *et al.*, 2009a, 2009b). Over longer timescales, the growth dynamics and establishment phases of several pine species have been attributed to the groundwater level (Boggie, 1972; Edvardsson *et al.*, 2012).

*A<sub>1</sub>. Transpiration and interception.* The incursion of trees and/or shrubs onto previously non-forested peatlands has the potential to cause a positive drying feedback, whereby increased root uptake for transpiration demand causes a lowering of the water table, in turn promoting further afforestation and/or shrubification as root oxygenation and root zone thickness increase (Lieffers and MacDonald, 1990; Woods *et al.*, 1991; Landhäusser *et al.*, 2003; Murphy *et al.*, 2009a Figure 1). Although stand age, stand vigour, climatic factors and hydrology all modify the rates of canopy conductance (Lundblad and Lindroth, 2002; Ewers *et al.*, 2005; Angstrom *et al.*, 2012), stand density and leaf area index (LAI) provide the primary indicator of the bulk rates of transpiration from peatland ecosystems under given micrometeorological conditions (Humphreys *et al.*, 2006). This positive feedback is amplified further by the increased levels of interception with an increased canopy and/or a shrub cover density (Farrick and Price, 2009; Baisley, 2012; Figure 1). Water intercepted by the canopy is lost directly via evaporation, reducing the net input of water to the peatland. In the year following a clear-cut treatment, Dubé *et al.* (1995) observed a decrease in WTD across several different peatland sites, where the change in water level was largely associated with decreased interception. Moreover, in a similar logging experiment, Pothier *et al.* (2003) observed a return to pre-disturbance water table levels after several years. Interception can be a greater factor in explaining water loss although there is a

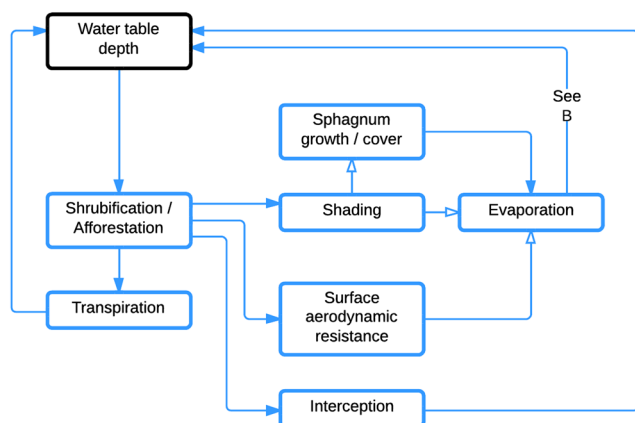


Figure 1. The water table depth—afforestation and/or shrubification feedback (feedback A). Solid and outline arrows represent positive and negative relationships, respectively. See feedback B for a full description of this feedback.

compensatory effect from surface evaporation to changing vascular leaf area (Campbell and Williamson, 1997), particularly for sites with very shallow water tables. It is important to note, however, that the effect of trees as inferred from clear-cut experiments is both stepwise and instantaneous. Under more natural conditions, higher percent tree cover in many northern peatlands is associated with lower shrub cover, and vice versa (Liu *et al.*, 2003), so changes in interception losses may be less pronounced. Furthermore, Strilesky and Humphreys (2012) show that the treed portion of a bog had lower total evapotranspiration (ET) compared with the non-treed portion of a bog due to lower stomatal conductance of black spruce despite there being a higher LAI in the treed portion of the bog.

Though transpiration has been shown to be a major driver of changes in soil moisture, low moisture availability due to frozen soil after snowmelt can itself influence transpiration rates. As the thawing front descends from the peat surface, fine roots must be thawed before they can take up water, meaning that actual transpiration rises gradually to equal potential (Goodine *et al.*, 2008). Given the shallow water tables typical of most peatlands, root density is greatest near the surface, with 90% of fine root biomass occurring within 20 cm of the peat surface (Steele *et al.*, 1997). Stomatal conductance in spruce doubles as soil temperature increase from 0 to 15 °C under constant atmospheric conditions (Delucia, 1986). Consequently, the observed recent increases in shrub density in northern peatlands (e.g. Berg *et al.*, 2009) likely results in earlier snowmelt (Pomeroy *et al.*, 2003), which leads to a positive feedback of an earlier start of transpiration and ultimately increased seasonal ET. As such, the WTD-transpiration positive feedback interacts with the ice-transpiration negative feedback as the lower soil moisture resulting from increased transpiration leads to faster springtime thaw rates due to lower soil ice content. However, this lower soil

moisture also enhances the maximum depth of frost in peatlands with high transpiration, as the maximum depth of frost and freezing rates are greater in drier peat compared with wetter peat (Nagare *et al.*, 2011).

*A<sub>2</sub>. Shading and evaporation.* Increasing density and LAI of shrubs and/or tree stands not only impacts directly on transpiration rates but also results in shading of the peat surface and thereby reduces the available energy for evaporation. Moss evaporation provides an important (Kim and Verma, 1996; Heijmans *et al.*, 2004), if not dominant, component of the ET flux (Lafleur and Schreder, 1994) from *Sphagnum*-dominated peatlands, particularly early and late in the growing season when vascular plants are senesced or have low LAI (Admiral and Lafleur, 2007). The reduction of surface evaporation with increasing shrub/tree cover therefore counteracts increases in transpiration and interception (Kettridge *et al.*, 2013). The reduction in radiation associated with a discontinuous tree canopy is dependent on the density and spatial organization of tree stems (Kettridge *et al.*, 2013) and shows strong small-scale spatial variations across a peatland. The reduction in solar radiation associated with a vascular vegetation cover is widely characterised by Beer's law (Kettridge and Baird, 2010), indicating an exponential decline in radiation received with increasing LAI.

An increase in the tree and/or shrub cover due to drying not only reduces the available energy for ET (Figure 1), but shading and resultant light competition can also modify vegetation composition within the subcanopy. Shade-tolerant species are likely to prosper according to species-specific photosynthetic light responses between bryophytes (Marschall and Proctor, 2004; Hájek *et al.*, 2009). Current understanding of the rate and magnitude of the ecological response to an alteration in photosynthetically active radiation is limited, and it is difficult to isolate experimentally the independent effect of light from that of soil moisture (see feedback G). For example, feather moss has been shown generally to out-compete *Sphagnum* under low light conditions when canopy closure exceeds 80% (Bisbee *et al.*, 2001). However, feather mosses dry out more readily in open habitats because of their more erect and uneven growing structure, which reduces boundary layer thickness (Skre *et al.*, 1983; Rice *et al.*, 2001). Because surface resistance to evaporation is significantly higher in feather moss than *Sphagnum* (Brown *et al.*, 2010; Kettridge *et al.*, 2013), such a transition under low light conditions would reduce peatland evaporation and provide a potential negative feedback response to drying (Figure 1).

*A<sub>3</sub>. Aerodynamics.* Variations in the density and spatial arrangement of trees also impact the aerodynamic properties of the subsurface, modifying the aerodynamic resistance to evaporation. The development of a sparse tree canopy above a

previously treeless peatland substantially increases the aerodynamic roughness of the surface, reducing the aerodynamic resistance and increasing evaporation (Figure 2). For example, the surface roughness of a treeless poor fen in Michigan, USA, and a treed fen in central Alberta, Canada, were equal to 0.05 (Moore *et al.*, 2013) and 0.22 m (Thompson, 2012), respectively. However, a further increase in tree density produces a smoother aerodynamic surface as the tree canopy fills in (thereby reducing surface roughness) and raises the zero-plane displacement height [equal to zero within a treeless peatland (Molder and Kellner, 2002)], increasing the resistance from the canopy sublayer to the evaporation surface (Niu and Yang, 2004). As a result, the aerodynamic effect of the continued afforestation of a treed peatland will provide a negative feedback to drying (Figure 1).

#### (B) WTD—moss surface resistance and albedo feedback

The WTD-transpiration feedback (feedback A<sub>1</sub>) may be counteracted in part by a negative feedback between WTD and surface evaporation from the live moss layer as mediated by changes in surface resistance and/or surface albedo (Figure 2). Observational evidence is neither abundant nor unambiguous, but laboratory manipulations (e.g. Hayward and Clymo, 1982; Price *et al.*, 2009) and theoretical studies (e.g. Thompson and Waddington, 2008) suggest that surface resistance to evaporation from a moss surface increases as WTD increases. Williams and Flanagan (1996) show that moss resistance to evaporation increases once surface moisture content is below a critical threshold, although strong evidence on differences between moss species is lacking (Bond-Lamberty *et al.*, 2011). The result is a negative feedback to evaporation during drought conditions (Figure 2). When peatland water tables become deeper than a threshold value, the ability of the moss to conduct water upwards via capillarity will become greatly constrained, reducing the rate of supply of water from the saturated zone and slowing further evaporative losses. A

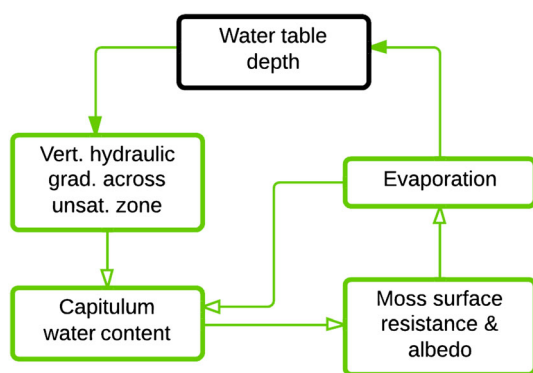


Figure 2. The water table depth—moss surface resistance and albedo feedback (feedback B). Solid and outline arrows represent positive and negative relationships, respectively.

number of studies (e.g. Price, 1991; Kim and Verma, 1996; Kellner, 2001) have indicated that this threshold WTD is approximately 40 to 50 cm. Lafleur *et al.* (2005) similarly show a threshold-type response of ET to WTD but suggested that decreasing moss evaporation is initially offset by increased transpiration until the water table drops below the vascular rooting depth. This feedback is further enhanced through changes in moss surface albedo as drying *Sphagnum* moss has been shown to increase albedo by becoming lighter in colour (cf. Nungesser, 2003) and decreasing surface evaporation (Figure 2). Although field evidence is limited, Kettridge and Baird (2008) found a moderate increase in *Sphagnum magellanicum* albedo with a small increase in WTD. However, the strength of this moss albedo feedback likely depends on the species identity where light coloured species are predicted to exhibit a greater increase in albedo compared with darker species with a drop in water table (Nungesser, 2003).

Although WTD has been widely applied to explain variations in the rate of evaporation from peatlands, the near-surface matric potential is the principal internal regulator of evaporation (Hayward and Clymo, 1982) and is often only weakly related to WTD under drought conditions (Price, 1997; Kettridge and Waddington, 2013). If the supply of water to the peat surface is unable to meet evaporative demand, the near-surface peat will dry (at the small scale, moss apices), reducing peat matric potential and so reducing evaporation, forming this potentially strong negative feedback (Dilks and Proctor, 1979; McCarter and Price, 2012; Kettridge and Waddington, 2013).

The supply of water to the peat surface is regulated by unsaturated hydraulic conductivity ( $K_{\text{unsat}}$ ) in the vadose zone, which is in turn controlled principally by the degree of saturation and the pore structure of the peat; pore structure is in turn closely linked to degree of humification (peat decomposition, see feedback F). Loose, poorly decomposed peat has an open pore structure and so a high saturated hydraulic conductivity ( $K_{\text{sat}}$ ) (Boelter, 1965; Sherwood *et al.*, 2013). However, as poorly decomposed peat dries, its volumetric water content (WC)—and so too its unsaturated hydraulic conductivity—declines rapidly even for modest reductions in matric potential, as water is evacuated from large pore spaces (Price *et al.*, 2008) (Figure 3). By comparison, more decomposed peat retains more water (by volume) at lower matric potential, which acts to increase  $K_{\text{unsat}}$  relative to fresh peat at the same matric potential. However, this effect conflicts with the fact that older, more decomposed peat also has a lower  $K_{\text{sat}}$  than fresh, loose peat. We are aware of no current agreement as to the overall effects of humification (degree of decomposition) upon peat  $K_{\text{unsat}}$ , and resolving the two competing effects requires a case-by-case consideration of  $K_{\text{sat}}$  and the parameters that describe water retention [e.g. the  $\alpha$ ,  $m$  and  $n$  parameters from van Genuchten's (1980)



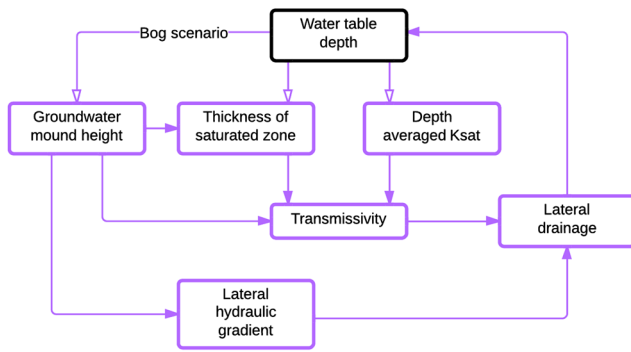


Figure 3. The water table depth—transmissivity feedback (feedback C). Solid and outline arrows represent positive and negative relationships, respectively. This diagram is presented for a raised bog peatland.

model]. Whether peat is old and well-decomposed or fresh and loosely structured, the negative feedback between evaporative losses, matric potential,  $K_{unsat}$  and upward supply of water to the surface holds, as in mineral soils. However, whether peat humification weakens or strengthens this feedback is currently unclear, and this question presents a valuable research goal for peat hydrologists.

At small scales, near-surface frozen peat reduces the  $K_{unsat}$  and capillary rise in the peat. Although  $K_{unsat}$  data for frozen peat are not available, observations in frozen medium-textured mineral soils showed that vertical  $K_{unsat}$  declined by three orders of magnitude compared with unfrozen soils (Lundin, 1990). Following snowmelt in non-permafrost systems, where a frozen unsaturated peat layer can be underlain by unfrozen saturated peat and overlain by a thin thawed layer at the surface, frozen unsaturated peat can impede vertical capillary rise and lead to a decrease in surface moisture content. For example, in a continental boreal climate where spring evaporative demand is high, surface peat moisture observed during this period can be drier than during summer water table minima (Thompson and Waddington, 2013). In permafrost regions, palsas form as the result of permanent ice lenses up to 1 m thick forming near the peat surface; matric potentials near the surface of palsas can fall below -15 Mbar (Ryden, 1980). In palsas, a positive feedback exists where the low surface soil moisture causes low thermal diffusivity and so contributes to ice lens stability (Seppälä, 2011) also leading to the loss of *Sphagnum* cover (Ryden, 1980). The lower surface moisture of bogs makes palsas more common in bogs compared with fens (Seppälä, 2011).

(C) WTD—transmissivity feedback

Ingram (1982, 1983) demonstrated how a theoretical raised bog with uniform  $K_{sat}$  would exhibit a negative feedback between WTD and lateral drainage, which would act to maintain a high groundwater mound even during dry summer months. Falling water tables lead to the following: (1) a reduced hydraulic gradient between the bog dome and

its margins and (2) a lower transmissivity due to a reduced thickness of flow. Contrary to Ingram’s assumption, however, peat hydrophysical properties such as  $K_{sat}$ , porosity and water-retention parameters are rarely constant with depth. A commonly observed reduction in depth-integrated  $K_{sat}$  with increasing WTD (e.g. Clymo, 1978; Fraser *et al.*, 2001) would further reduce transmissivity, thereby forming a third mechanism through which an increasing WTD leads to reduced lateral drainage (Figure 3). This group of negative feedbacks would dampen water table drawdown under a warmer and drier climate but is only likely to be important in peatlands where lateral groundwater outflow is a non-negligible term in the annual water budget, such as maritime raised bogs (cf. Belyea, 2009; Frohling *et al.*, 2009) and some fens.

Performing the same function as low conductivity peat in the transmissivity feedback is frozen peat. Freezing of saturated peat reduces  $K_{sat}$  sufficiently that it acts as an impermeable layer to lateral and vertical flow (Hogan *et al.*, 2006), reducing infiltration (Roulet and Woo, 1986), groundwater upwelling (Price, 1983) and transmissivity. In the case of permafrost where ice persists in deeper and denser peat layers, ice decreases  $K_{sat}$  in an already low conductivity horizon. Additionally, the perennially frozen peat reduces decomposition rates in deeper peat layers by up to two orders of magnitude (Panikov and Dedysh, 2000). In discontinuous permafrost plateaus, frozen saturated peat is of sufficiently low conductivity that precipitation flows off the plateaus to the surrounding non-permafrost bogs and fens (Quinton *et al.*, 2009). As a result, the plateaus feature deep water tables that allow for a dense tree cover (Chasmer *et al.*, 2011; see feedback A<sub>1</sub>).

(D) WTD—peat deformation feedback

In some peatlands, the peat surface has been observed to rise and fall synchronously with seasonal water table fluctuations, thereby dampening changes in WTD relative to the peat surface (Ingram, 1983; Price, 2003). This surface adjustment through peat deformation can help to maintain high WC in moss capitula (see feedback G) during summer months and forms a negative feedback to an increasing WTD (Figure 4).

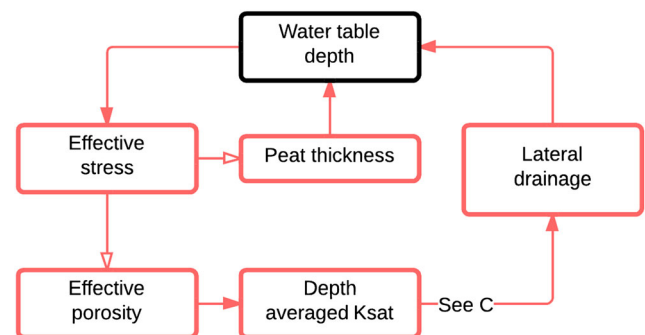


Figure 4. The water table depth—peat deformation feedback (feedback D). Solid and outline arrows represent positive and negative relationships, respectively. See feedback C for a full description of this feedback.

The magnitude of surface adjustment, both in absolute terms and as a proportion of a water table fluctuation, differs between peatlands and appears to be controlled by the physical properties of the peat (Price, 2003; Waddington *et al.*, 2010). Surface adjustment and peat deformation in dense, highly compressed peat that contains roots of trees and woody shrubs is a highly subdued reflection of water table movements; whereas in loose, uncompressed peat or floating sedge mats, the magnitude and timing of surface adjustments may mirror those of the water table closely (Waddington *et al.*, 2010).

As well as causing changes to the surface datum, peat deformation due to the temporary compression or relaxation of weak layers is highly influential on pore size distribution and peat hydrophysical properties such as  $K_{sat}$ , effective porosity and moisture-retention parameters (Whittington and Price, 2006). As WTD increases, effective stress increases and the resulting peat compression causes pore spaces to close, thereby reducing permeability and increasing moisture retention, whereas the buoyant expansion of near-surface layers has the opposite effect (Figure 4). Water losses that cause the surface to fall therefore promote greater water retention, dampening further losses because peat compression leads to a decrease in  $K_{sat}$  and lateral drainage. Similarly, any addition of water to the peat column that causes the surface datum to rise is likely to be accompanied by an expansion of pore spaces and an associated reduction in moisture-retention capability, leading to increased potential for drainage and ET. Again, this negative feedback is likely to be most important in peatlands that experience the greatest range of surface-datum fluctuations (Table I).

(E) WTD—specific yield feedback

Specific yield determines the rate of water table change per unit volume addition (removal) of water to (from) the saturated zone. Similar to  $K_{sat}$ , specific yield demonstrates a strong association with pore size distribution (Boelter, 1965), and there is strong observational evidence that specific yield declines sharply with depth in the upper few dm of a peat profile (e.g. Vorob'ev, 1963; Chason and Siegel, 1986; Price, 1992). This occurs because the degree of humification tends to increase with depth in a peat profile. With decomposition, large fibres are broken down and consolidation occurs as the peat matrix is no longer able to support the given level of stress without deformation. Therefore, with greater levels of humification, peat loses large pore spaces and experiences an increase in the relative proportion of small pore spaces. This provides a feedback between water table change and specific yield, the direction of which is determined by the direction of change of the water table (Figure 5). If we consider a

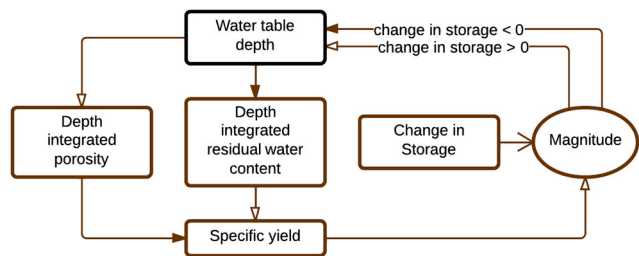


Figure 5. The water table depth—specific yield feedback (feedback E). Solid and outline arrows represent positive and negative relationships, respectively.

Table I. Suggested strengths and signs of hydrological feedbacks in different northern peatlands.

	Maritime climate peatlands <sup>a</sup>		Continental climate peatlands	
	Bog/poor fen	Rich fen	Bog/poor fen	Rich fen
(A) WTD—afforestation and/or shrubification feedback	**	*	+++	+
A <sub>1</sub> . Transpiration and interception	++	+	+++	+
A <sub>2</sub> . Shading and evaporation	--	0	+++	+
A <sub>3</sub> . Aerodynamics	++	0	+++	+
(B) WTD—moss surface resistance and albedo feedback	-	0	---	0
(C) WTD—transmissivity feedback	--	---	0	-
(D) WTD—peat deformation feedback	--	---	0	-
(E) WTD—specific yield feedback (falling WT; see text)	++	+	+++	+
(F) WTD—peat decomposition feedback	---	--	--	--
F <sub>1</sub> . Water residence time—porewater chemistry	---	--	--	--
F <sub>2</sub> . Water residence time—entrapped gas	--	--	--	--
(G) WTD—moss productivity feedback	---	-	*	0
G <sub>1</sub> . Moss species moisture retention	---	0	---	0
G <sub>2</sub> . Decomposition—peat moisture retention	--	---	0	-

WTD, water table depth.

A negative feedback acts to moderate water table depth, whereas a positive feedback enhances water table depth. The symbols +, ++, +++, -, --, ---, \* and 0 indicate weakly positive, moderately positive, strongly positive, weakly negative, moderately negative, strongly negative, variable response and negligible response, respectively. See text for a description of the characteristics of the four northern peatland categories and for an explanation on how some of these feedbacks are influenced by the presence of ice.

<sup>a</sup> excludes blanket bogs.

hypothetical peat profile in which specific yield declines monotonically with depth, and to which water is being added to the saturated zone at a constant volumetric rate, the rising water table will experience ever-increasing specific yield, thereby slowing the rate of water table rise. However, if water is removed from the soil column, then water would be extracted from progressively smaller pores. If a constant volumetric rate of water loss could be maintained, then the increase in WTD would accelerate. In isolation, this feedback has the potential not only to buffer peatlands (negative feedback) against inundation (rising water table) but also to cause runaway drying (positive feedback for falling water table). Consequently, either together or in combination, the previous points imply that WTD is negatively correlated with specific yield (Figure 5). How this ends up feeding back on WTD depends on the sign of subsequent changes in storage. As specific yield increases, the magnitude of WT response to a given change in storage will decrease, and vice versa (represented by *magnitude and change in storage boxes* in Figure 5). In reality, however—and in common with all the other feedbacks we discuss—this feedback would likely never act in isolation. In particular, interaction with feedbacks B (WTD—moss surface resistance and albedo) and D (WTD—peat deformation) would likely make a constant volumetric rate of groundwater loss all but impossible to sustain (perhaps aside from artificial drainage), which would counteract runaway drying (Waddington *et al.*, 2010; Figure 5).

#### (F) WTD—peat decomposition feedback

A decline in water table position beyond the thickness of the capillary fringe will increase oxygen availability in peat and enhance peat decomposition rates (Figure 6). Peat decomposition is central to the ecohydrology of these systems and their apparent ability to self-organize.

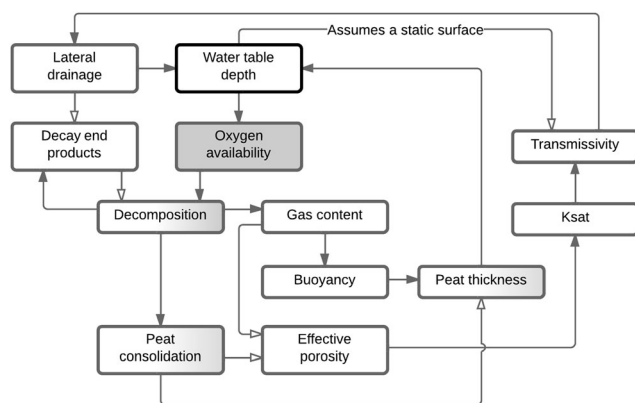


Figure 6. The water table depth—peat decomposition feedback (feedback F). Solid and outline arrows represent positive and negative relationships, respectively. Grey shading implies a process occurring in the unsaturated zone and a white-to-grey gradient implies both the saturated and unsaturated zone.

Enhanced near-surface decomposition has far-reaching consequences for both the physical hydrology and hydro-chemistry of peatlands.

*F<sub>1</sub>. Water residence time—porewater chemistry.* Decomposition leads to a weakening of the internal structure of peat soils and so the progressive closure of pore spaces in older, more decomposed peat. The result is that both saturated and unsaturated fluxes of water are presented with narrower, more tortuous pathways for flow. This is manifested as changes in important hydraulic properties of peat that govern moisture retention and drainage, such as hydraulic conductivity, porosity and specific yield (Rycroft *et al.*, 1975; Ivanov, 1981; Grover and Baldock, 2013). As such, more highly decomposed peat leads to slower lateral drainage and is able to retain greater volumetric WCs when subjected to a given suction (e.g. due to evaporative demand) than fresher, less decomposed peat. Importantly, this relationship between decomposition and peat hydraulic properties leads to a potentially strong negative feedback to decomposition. As near-surface peat begins to dry out, perhaps due to low summer rainfall or rapid lateral drainage rates, it begins to decompose more rapidly. This enhanced decomposition weakens pore structures, which eventually begin to collapse, in turn reducing further drainage and impacting evaporative losses. Due to this heightened retention of both saturated and unsaturated water, further decomposition is slowed. Modelling studies by Morris *et al.* (2011b) and Swindles *et al.* (2012) have demonstrated that feedbacks of this kind may play a key role in enabling peatlands to maintain high water tables and high near-surface WCs, thereby resisting the drying effects of variations in external climate (see also Frohling *et al.*, 2010). This ability to undergo rapid (yearly to decadal—Swindles *et al.*, 2012) changes in soil hydraulic properties is unique to peat soils and is entirely unaccounted for in linked land surface models. Although the available observational evidence for the links between peat humification and hydraulic properties is convincing, it does not yet allow a satisfactory mechanistic representation of these hydrophysical-biogeochemical links in peatland development models because of a lack of process-level understanding (although simple relationships may be derived theoretically: see Frohling *et al.*, 2010 and Morris *et al.*, 2011b).

A number of inorganic chemicals are formed as by-products of peat decomposition, including phenols and methane, which dissolve in porewater. Recent experimental work (Beer and Blodau, 2007; Beer *et al.*, 2008) has demonstrated that the build-up up of these decay end-products (DEP) in peat porewater has the potential to slow or even halt decomposition, a mechanism that has been termed a thermodynamic limit to decomposition. High DEP concentrations lead to a reduction in Gibbs free

energy, thereby denying terminal electron acceptors to decomposers and forming a negative feedback between decomposition and porewater chemistry. This mechanism is poorly understood at present, and there are recent conflicting results regarding the effect of DEP (Tfaily *et al.*, 2013). Nevertheless, the existing research suggests the potential for the interaction of this negative feedback with other aspects of peatland ecohydrology, particularly porewater residence time. For instance, slow turnover of peatland porewater (represented by lateral drainage in Figure 6) can lead to high DEP concentrations, leading to soil conditions unfavourable to decomposition. Morris and Waddington (2011) used a modified Ingram (1982, 1983) model to demonstrate that high rainfall rates may help to flush near-surface layers and maintain high decomposition rates at shallow depths, whereas the deepest peat layers are more likely to become chemically disconnected from rainfall and so resistant to decomposition. At the same time, Morris and Waddington (2011) showed that the flushing of peat pores by fresh water (from either precipitation or shallow groundwater flow) is strongly influenced by peat transmissivity. We postulate that the thermodynamic limit to decomposition is directly involved in two hydrologically mediated negative feedbacks: (1) between depth-integrated decomposition and porewater DEP concentration and (2) between decomposition, peat permeability, drainage and porewater DEP concentration (Figure 6). We suggest that in some peatlands, peat porewater residence time may be more important than WTD in controlling peat decomposition because of the apparent ability of high porewater DEP concentrations to inhibit decomposer respiration.

*F<sub>2</sub>. Water residence time—entrapped gas.* Entrapped gas (particularly methane) is another by-product of peat decomposition that can impact peatland biogeochemistry and hydrology (Strack *et al.*, 2005; Coulthard *et al.*, 2009). Trapped gas bubbles can cause a reduction in peat saturated hydraulic conductivity (Beckwith and Baird, 2001; Kettridge *et al.*, 2013) and can also influence peat buoyancy and deformation (Strack *et al.*, 2006; Karofeld and Tönisson, 2012) (Figure 6). Similar to the DEP discussed earlier, hydrological feedbacks driven by trapped gas represent a strong link to peatland biogeochemistry because the transition of dissolved gas such as methane between gaseous (free) and aqueous (dissolved) phases is governed in part by Henry's law (Slabaugh and Parsons, 1976). Strack *et al.* (2005) present a detailed review of peat bubble biogeochemistry; briefly, gas solubility decreases with increasing peat temperature, causing exsolution of dissolved gas and forming bubbles. Moreover, reductions in pressure (e.g. decreasing atmospheric pressure or a greater WTD) will potentially cause a net transfer of gas from the aqueous phase to the gaseous phase (Baird and

Gaffney, 1995; Strack *et al.*, 2006) and bubble expansion according to the ideal gas law (Kellner *et al.*, 2004).

Following bubble production, zones of entrapped gas develop as the bubbles do not immediately move upward through the peat (Coulthard *et al.*, 2009) because of the presence of a confining layer such as woody peat strata (Glaser *et al.*, 2004), sedge horizons or peat with small pore diameters (Kellner *et al.*, 2004). The bubbles themselves may then block even smaller bubbles (Romanowicz *et al.*, 1995; Kellner *et al.*, 2004). This entrapped gas affects peatland hydrology by reducing saturated hydraulic conductivity and permeability (Beckwith and Baird, 2001). A reduction in permeability causes a concomitant decrease in lateral drainage and promotes a higher water table mound, resulting in a net negative feedback (Figure 6). In these 'hotspots', the continued production of gas together with the lower permeability creates overpressuring in the peat that changes hydraulic gradients locally, although the impacts on large-scale peatland hydrology are uncertain.

A small increase in gas content can greatly increase the upward buoyant force of the peat: Strack *et al.* (2004) suggest that gas contents of just 5% may reduce the density of peat to below that of water, enabling surficial peat to float on the water table. Peat buoyancy plays an important role in ecosystem structure and function as the peat surface moves up and down with water table fluctuations (Fechner-Levy and Hemond, 1996; Strack and Waddington, 2008). Peat surface movement thereby limits the impact of water storage changes resulting in a negative feedback as outlined in the WTD—peat deformation feedback (feedback D).

#### (G) WTD—moss productivity feedback

There are important feedbacks manifested by changes in WTD that affect moss productivity and by extension peat thickness and peatland succession (cf. fen–bog transitions in Granath *et al.*, 2010). The strongest predictor for moss production is water availability, and moss production shows a strong non-linear relationship with tissue gravimetric WC (e.g. Schipperges and Rydin, 1998; Tuittila *et al.*, 2004). For *Sphagnum*, optimum capitulum WC varies but seems to concentrate around a WC between 700% and 1300%, depending on species and measurement conditions (Hájek, 2014). With increasing WC, declines in CO<sub>2</sub> diffusion reduce photosynthesis; if WC drops further, water loss from hyaline and chlorophyllous cells inhibits photosynthesis and can even cause cellular damage to chlorophyll pigments (Gerdol *et al.*, 1996). WC is linked to WTD, but this relationship depends on species morphology (e.g. hyaline cell configuration and branch structure along the stem, which largely determine capillary water transport capability) and *Sphagnum* canopy structure (e.g. shoot density; Rydin and Jeglum, 2013). Furthermore, the relationship between WC and WTD is not linear (Rydin,



1985; Belyea and Clymo, 2001): Thompson and Waddington (2008) advocated the use of matric potential measurements as the best method of linking the hydrological and ecological functioning of *Sphagnum* (i.e. growth) in peatlands and forms the basis for the *WTD—moss productivity feedback* (feedback G, Figure 7).

In case of an increasing WTD (Figure 7), matric potential at the surface declines, and hollow species that retain water less readily (e.g. loosely structured mats) are likely to face desiccation and a severe reduction in growth (G<sub>1</sub>. Moss species moisture retention, Figure 7, Table I). However, this potential loss of *Sphagna* is counteracted by increased moisture retention due to an increase in bulk density, which is an effect of the greater decomposition (G<sub>2</sub>. Decomposition—peat moisture retention, Figure 7, Table I) that is likely to occur throughout the unsaturated zone in case of a sustained water table drawdown (see feedback F; Silvola *et al.*, 1996; Belyea and Clymo, 2001). In addition, dense hummock species can remain hydrated and maintain photosynthesis with increasing WTD. They are also able to increase the proportion of hyaline cell area, further enhancing their water holding capacity compared with hollow/lawn species that appear to lack the ability of such morphological adjustments (Bu *et al.*, 2013). Thus, if hollow species cannot achieve sufficient growth to stay competitive, their coverage will decrease in favour of hummock species, and a greater coverage of hummock species will increase overall moisture retention at the moss surface (Figure 7). It is also possible that the *Sphagnum* mosses, to some extent, can respond to a greater WTD by increasing shoot density, at the cost of length growth, to augment capillary transport. The cumulative effect of increased moisture retention results in sustained water availability for *Sphagnum* capitula, which therefore can maintain production and the accumulation of peat. The more recalcitrant litter produced by hummock species will further accelerate the peat accumulation (Johnson and Damman, 1993; Belyea, 1996). Moreover, lateral shifts in microtopography (hummock–hollow) may provide the

peatland with resilience to changes in hydrology (Belyea and Clymo, 2001) and suggest important mechanisms involved in the fen–bog transition (e.g. Granath *et al.*, 2010).

The matric potential approach has proven useful for describing and gaining a better process-based understanding of the hydrological feedbacks related to *Sphagnum* production (cf. Thompson and Waddington, 2008; McCarter and Price, 2012). However, with the aim of developing an integrated trans-disciplinary (i.e. ecohydrological) understanding of peatland ecosystems, any process-based hydrological approach also needs to be linked to the many aspects of *Sphagnum* ecology such as species competition and facilitation, nutrient availability and plant traits that collectively regulate these hydrological processes. This is likely especially important for feedbacks G and A, though we believe all hydrological feedbacks presented in this synthesis would benefit from such integration. For example, there are strong links between the hydrology of peatlands and several functional traits in *Sphagnum*. In fact, *Sphagnum* acts as an ecosystem engineer in boreal peatlands, rapidly forming an environment (hydrological, biogeochemical) where its own success is facilitated (van Breemen, 1995). Hence, the peat properties and the plant composition dynamics are largely governed by the features of *Sphagnum*. Information on how plant traits vary within and among *Sphagnum* species, and other abundant bryophytes on peatlands, remains limited, but some recent studies have been undertaken (Rice *et al.*, 2008; Turetsky *et al.*, 2008; Granath *et al.*, 2010; McCarter and Price, 2012; Laing *et al.*, 2014). Consequently, we argue that the identification of plant traits, their variation and mechanisms behind the observed variation, can provide a natural link between process-based hydrological models, ecosystem/biogeochemical models (Dimitrov *et al.*, 2011; Wu and Blodau, 2013) and vegetation models (e.g. Benscoter and Vitt, 2008) and should be the focus of future research.

HYDROLOGICAL FEEDBACK STRENGTHS

Our synthesis has highlighted that hydrological feedbacks in peatland ecosystems have the potential for strong autogenic moderation of WTD responses to external drying and wetting forcings. More specifically, negative feedbacks (which act to moderate water table changes) far outnumber the positive feedbacks (which act to amplify water table changes). However, the relative strengths of these feedbacks and, indeed in some cases, the signs (positive vs negative) can vary depending on the peatland type and/or climate. As a first attempt to assess the strength of these feedbacks in northern peatlands, we considered four categories that cover the majority of northern peatlands: (1) maritime bogs or poor fens; (2) maritime rich fens; (3) continental bogs or poor fens; and (4) continental rich fens. Maritime peatlands are characterized by annual precipitation (P) exceeding potential

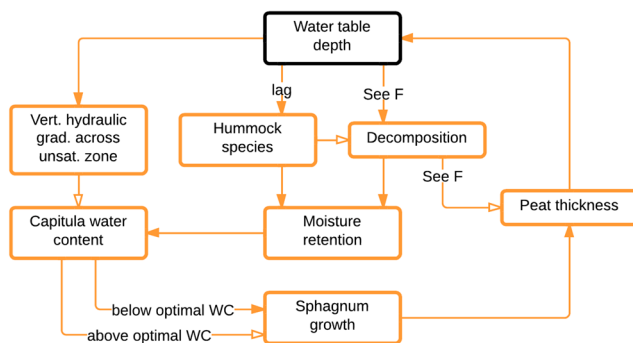


Figure 7. The water table depth—moss productivity feedback (feedback G). Solid and outline arrows represent positive and negative relationships, respectively. See feedback F for a full description of this feedback.

ET, a low variation in annual temperature over the year, and high humidity. Maritime peatlands are also generally characterized by a loose, low-density and, in some cases, floating peat matrix with small variations in water table position during the year. In contrast, continental peatlands generally have a higher peat bulk density (Zoltai *et al.*, 2000) and have a denser shrub and/or tree cover than maritime peatlands, which is particularly pronounced in North America (Rydin and Jeglum, 2013). Continental peatlands have a higher variation in inter-annual temperature and water table position, bringing about the possibility of seasonal to multi-year water deficits. In such continental peatlands, wildfire may be a common part of the peatland's natural cycle. In this assessment, we also assumed that bogs and poor fens have a greater WTD and have higher tree and/or shrub cover than rich fens. However, given that there is large heterogeneity both within and among peatlands in a particular category (Rydin and Jeglum, 2013), we would expect the response in sub-habitats to potentially differ from the overall category pattern. For example, our assessment does not account for blanket bogs in maritime climate; blanket bogs generally feature denser peat and large pipe and macropore networks compared with other maritime peatlands. Moreover, our assessment does not include continuous permafrost or thermokarst peatlands. Nevertheless, with caveats and assumptions in mind, we view our hydrological feedback assessment (Table I) cautiously as a starting point from which to categorise the world's peatlands broadly, so that they might be characterized in large-scale land surface models. We used a combination of literature data, personal observations and predictions deduced from theory and models to summarize the sign and sensitivity of the feedbacks (Table I).

#### *Negative feedbacks*

Negative feedbacks exhibiting a response ranging from negligible to strongly negative include the WTD—moss surface resistance and albedo feedback (feedback B), the WTD—transmissivity feedback (feedback C), the WTD—peat deformation feedback (feedback D) and the WTD—decomposition feedback (feedback F). The WTD—decomposition feedback is important for all peatland types and is also likely very important for long-term carbon accumulation. As such, this feedback has been incorporated into the latest generation of peatland development models (e.g. Baird *et al.*, 2012; Morris *et al.*, 2012). The sensitivity of the WTD—moss surface resistance and albedo feedback is strongly negative in continental bogs and poor fens where WTD and vapour pressure deficits can both be large. The response of this feedback in rich fens in both maritime and continental climates is likely negligible because of limited water table drawdown. Similarly, the species substitution feedback to maintain high water retention ( $G_1$ , WTD—moss productivity feedback) is negligible in rich fens that normally

have a sparse *Sphagnum* cover. However, *Sphagnum* spread and takeover of rich fens (rich fen—poor fen/bog transition) after a water table drawdown is an important species substitution feedback to maintain the peatland habitat and increase peat accumulation (Rydin and Jeglum, 2013). Finally, feedback  $G_2$  (Decomposition—peat moisture-retention feedback) likely operates strongly in more maritime peatlands, whereas it is likely to have less importance in continental peatlands because of their constant high WTD and generally higher decomposition rates.

#### *Positive feedbacks*

The WTD—specific yield feedback (feedback E) during a period of falling water table is weakly positive in rich fens and moderately to strongly positive in bogs and poor fens in maritime and continental climates, respectively. The WTD—afforestation and/or shrubification feedback (feedback A) is also positive with the feedback strengths (e.g. weakly positive in rich fens) as feedback E and demonstrates that without strong negative feedbacks operating in those peatlands, the two feedbacks A and E working together has the potential to result in extensive water table decline during a period of soil water deficit. However, feedback  $A_2$  is likely moderately negative in maritime bog/poor fen peatlands.

## CONCLUSIONS AND FUTURE DIRECTIONS

This synthesis has provided the first detailed discussion of internal (within-peatland) hydrological feedbacks that operate, on varying time scales, within northern peatlands to regulate their response to changes in seasonal water deficit and varying disturbances (land-use change, wildfire, drought etc.). We summarize these feedbacks and their interactions in a conceptual model illustrated in Figure 8. Although the majority of feedbacks that we have considered in this synthesis are hydrological, many present obvious routes for interaction with other aspects of peatland science, such as plant ecology, soil biogeochemistry and micro-meteorology, and so interactions with (even) wider feedback loops. As such, we encourage colleagues in complementary areas of peatland science to pursue similar exercises so as to develop similarly detailed syntheses of their own subjects that are able to mesh with our conceptual model of feedback interactions (Figure 8), with the eventual goal of developing an integrated trans-disciplinary process understanding of peatland ecosystems. We suggest that structured, formal 'brainstorming' research exercises such as ours across other peatland sub-disciplines will lead to the formulation of a detailed, integrated conceptual model of peatland response to climate-mediated and human disturbances. This is particularly important because the uncertainty as to the likely effects of these

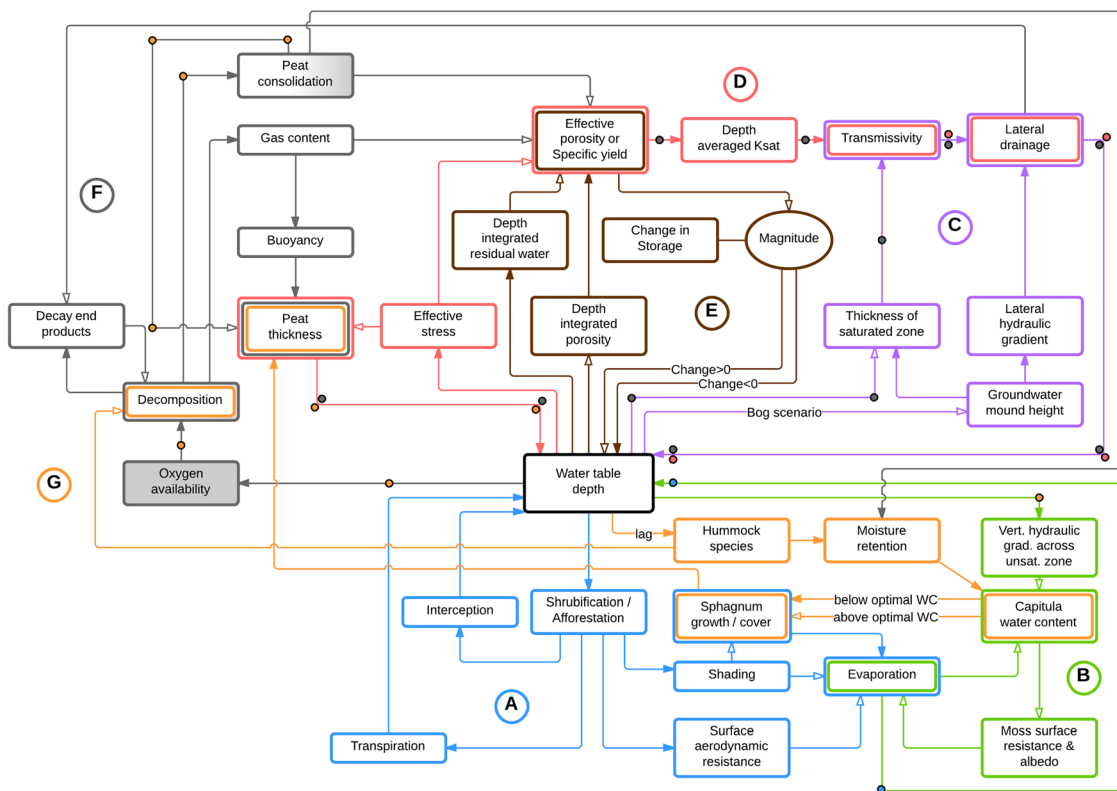


Figure 8. Overview of hydrological feedbacks in northern peatlands. Solid and outline arrows represent positive and negative relationships, respectively. Grey shading implies a process occurring in the unsaturated zone and a white-to-grey gradient implies both the saturated and unsaturated zone. Colours denote feedbacks A–G (see text and Figures 1–7 for details).

disturbances on peatland structure and function can be attributed in part to the rate, duration and in some cases even the direction of response of important peatland state variables (particularly WTD and carbon accumulation rates) to any given disturbance, because of the high prevalence of the feedbacks that tend to dominate complex systems. We suggest that the study of the kinds of complex interactions in our integrated ‘ecohydrological’ conceptual model lends itself readily to a numerical modelling approach, such as the utilization of global/regional climate models with an improved representation of peatlands. However, current land surface schemes feature a highly simplified representation of peatland carbon and water balances compared with our synthesis and are therefore seem prone to misrepresent potentially important feedbacks between peatlands and climate. Even comparatively detailed models designed to understand peatland development (e.g. Ise *et al.*, 2008; Frohling *et al.*, 2010; Morris *et al.*, 2011b) neglect the majority of the hydrological complexity presented in this synthesis and summarized in our conceptual model. Consequently we suggest that a pressing objective for future work is to establish what constitutes a minimalist representation of peatland response to climatic and/or land-use change influences (i.e. a model that can provide a satisfactory representation of internal

processes without missing important behaviours yet without wasting valuable computational resources on superfluous processes; cf. Grimm *et al.*, 2005). This task appears to be highly challenging because of the numerous interacting processes involved in peatland ecohydrology and the feedbacks that they participate in. Moreover, defining what processes are unnecessary is also complicated given that the relative strengths of the feedbacks vary across peatland types, among functions and time scales (Table I). In order to answer this question, there would appear to be great value in the construction and analysis of an offline (i.e. not linked to an ocean-atmosphere model in the first instance) numerical model that simulates in detail the processes we have described here and their manifold interactions. Such a model should be constructed so as to allow the incorporation of the linkages between hydrological, ecological and biogeochemical processes in peatlands. The analysis of such a model would go a long way towards determining a truly essential and fundamental set of peatland processes and feedbacks and would demonstrate the necessity (or lack thereof) for the improvement of land surface models accordingly. As such, we remain optimistic that a minimal subset can be established through experimental and modelling work for incorporation in both the next generation of land surface schemes and peatland hydrological impact models (e.g. Guertin *et al.*, 1987).

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