Peatland-fire interactions: A review of wildland fire feedbacks and interactions in Canadian boreal peatlands

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Review

Peatland-fire interactions: A review of wildland fire feedbacks and interactions in Canadian boreal peatlands

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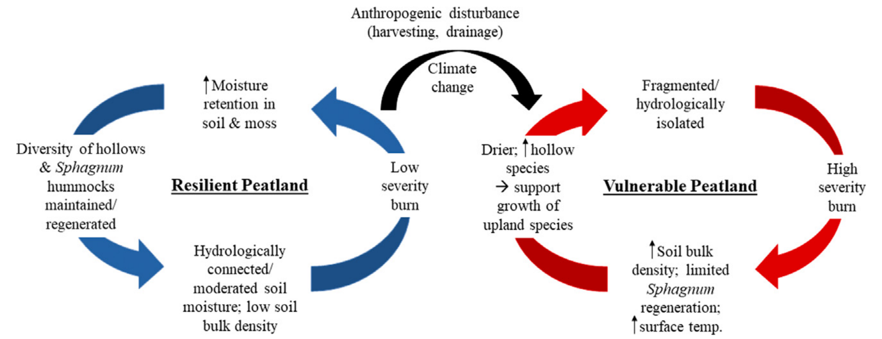
HIGHLIGHTS

- Hydrologically connected, unaltered peatlands more resilient to wildland fire
- Negative feedbacks offset fire and climate change C loss in resilient peatland
- Warming, fragmentation, wildland fire drive positive C feedback cycle
- Positive feedbacks will eventually surpass negative; shift from C sink to source

GRAPHICAL ABSTRACT



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ABSTRACT

Boreal peatlands store a disproportionately large quantity of soil carbon (C) and play a critical role within the global C-climate system; however, with climatic warming, these C stores are at risk. Increased wildfire frequency and severity are expected to increase C loss from boreal peatlands, contributing to a shift from C sink to source. Here, we provide a comprehensive review of pre- and post-fire hydrological and ecological interactions that affect the likelihood of peatland burning, address the connections between peatland fires and the C-climate cycle, and provide a conceptual model of peatland processes as they relate to wildland fire, hydro-climate, and ecosystem change. Despite negative ecohydrological feedback mechanisms that may compensate for increased C loss initially, the cumulative effects of climatic warming, anthropogenic peatland fragmentation, and subsequent peatland drying will increase C loss to the atmosphere, driving a positive C feedback cycle. However, the extent to which negative and positive feedbacks will compensate for one another and the timelines for each remains unclear. We suggest that a multi-disciplinary approach of combining process knowledge with remotely sensed data and ecohydrological and wildland fire models is essential for better understanding the role of boreal peatlands and wildland fire in the global climate system.

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1. Introduction

Boreal and subarctic peatlands contain an estimated one-third of global soil carbon (C) stores, despite occupying only ~2–3% of the world's land cover (Gorham, 1991). Their C stores are comparable to the amount of C in the atmosphere and exceed those in terrestrial vegetation (IPCC, 2013). Within Canada, boreal peatlands store over half the country's soil C, despite occupying only 12% of the land area (Tarnocai, 2006); however, recent modelling by Nichols and Peteet (2019) suggests that C stores may, in fact, be nearly twice that. North American boreal peatlands can be found in regions near climatic moisture deficits, where potential evapotranspiration exceeds precipitation (Petrone et al., 2006). These ecosystems may be especially vulnerable to climatic shifts due to water loss to the atmosphere associated with warming (Brown et al., 2010). Peatlands are considered a potentially critical tipping point of the global climate system (Lenton et al., 2008), and hydrological changes to peatlands could result in greater C losses due to microbial decomposition and wildland fire, offsetting peatlands as a long-term store of C (Wieder et al., 2009; Yu, 2012). It has been widely acknowledged that wildland fire regimes in the boreal are changing over time, increasing in extent, severity, and duration (e.g., Flannigan et al., 2009; Kohlenberg et al., 2018; Hanes et al., 2019), the results of which are likely to enhance C loss, impact air quality, and alter site hydrology and ecology. Though wildland fires are a natural part of ecosystem succession and regeneration, changes in fire regime could shift peatlands from a C sink to an expanding source through time (Turetsky et al., 2004, 2011; Wieder et al., 2009). Understanding processes associated with peatland wildland fire is essential for determining C emissions and boreal peatlands' influence in the global C-climate cycle.

To understand peatland C losses during combustion and implications to climate, hydrology, and human health, we use burn severity as an indicator of the change in vegetation and soil as a result of wildland fire (Whitman et al., 2019). The following review examines the relationship between wildland fire/burn severity (defined here as above- and below-ground fuel consumption; Keeley, 2009), boreal species, and the peat properties of the *acrotelm* (the top portion of peat, which is partially living and is periodically saturated due to a fluctuating water table) and the *catotelm* (the lower portion of peat, which is fully saturated and anaerobic; Ingram, 1978; Clymo, 1984). It synthesizes known peatland-fire-climate feedbacks that could increase burn severity and the propensity for peatland fires in the future, addressing current understanding and gaps in knowledge. To improve understanding of complex and interrelated feedbacks, we examine peatland feedbacks through the framework of those that occur a) prior to wildland fire to either increase or decrease burn severity; and b) in the years immediately following fire, which may either increase peatland resiliency or sensitivity, thereby altering future fire regimes. Finally, we discuss the implications of peatland-fire feedbacks to the climate system. We also present conceptual feedback diagrams of peatland processes related to wildland fire, hydro-climate, and ecosystem change, which may be incorporated into models of boreal peatland-fire-climate drivers and environmental characteristics that either maintain resilience or predispose peatlands to greater impacts from fire.

2. Pre-fire feedbacks affecting variability in burn severity

Burn severity varies both spatially and temporally as a result of any number of factors. Complex interactions related to burn severity include the weather at the time of fire: high wind speeds, prolonged warm conditions, and drying can spread fire rapidly through dry litter and understory vegetation to tree canopies (Bradshaw et al., 1984). Burn severity is also related to spatial variations in vegetation species and forest structural characteristics (e.g., Alonzo et al., 2017; Whitman et al., 2018), as well as surficial geology (Aldous et al., 2015) and variations in local topography, which influence local moisture levels and the flammability of the soil organic layer. This is due, in part, to variations in energy receipt and water accumulation within soils (e.g., Lukenbach et al., 2017). Peat, a fuel source for wildland fire (Benscoter and Wieder, 2003), provides suitable conditions for smouldering fires, which produce similar carbon dioxide (CO_2) emissions but significantly more carbon monoxide (CO) and methane (CH_4) than flaming fires (French et al., 2002). Smouldering fires can also ignite in colder, wetter conditions, and persist for weeks to years, despite precipitation (Rein, 2013). Here, we describe peatland interactions and feedbacks that affect burn severity: a) soil properties; and, b) vegetation structures and species. These are critical for understanding how climate-mediated and other (e.g. anthropogenic) disturbances could alter peatland function and resiliency vs. sensitivity to fire in the future.

2.1. Soil properties: the relationship between hydrology, bulk density, and burn severity

Soil moisture is a primary control on the likelihood of peat ignition (Frandsen, 1997), as well as the depth and extent of burn (Rein et al., 2008; Fig. 1). While vegetation, microtopography, and geology influence organic soil moisture locally (e.g., Benscoter and Wieder, 2003; Petrone et al., 2008; Wilkinson et al., 2018b), they do not appear to improve predictive models of depth of peat burn (Kohlenberg et al., 2018). Instead, the spatial variability of combustion and C losses results from variations in local hydrology and living/decomposed peat structural characteristics (e.g., Miyanishi and Johnson, 2002; Benscoter et al., 2011; Sherwood et al., 2013).

Lowered water tables and increases in water table fluctuations increase depth of burn by reducing soil moisture, increasing bulk density ('red' positive feedback arrow, Fig. 1), and improving conditions for tree and shrub growth (Sherwood et al., 2013; Lukenbach et al., 2015; 'blue' positive feedback arrow, Fig. 1). An increase in depth to water table may increase soil tension, thereby reducing the soil's

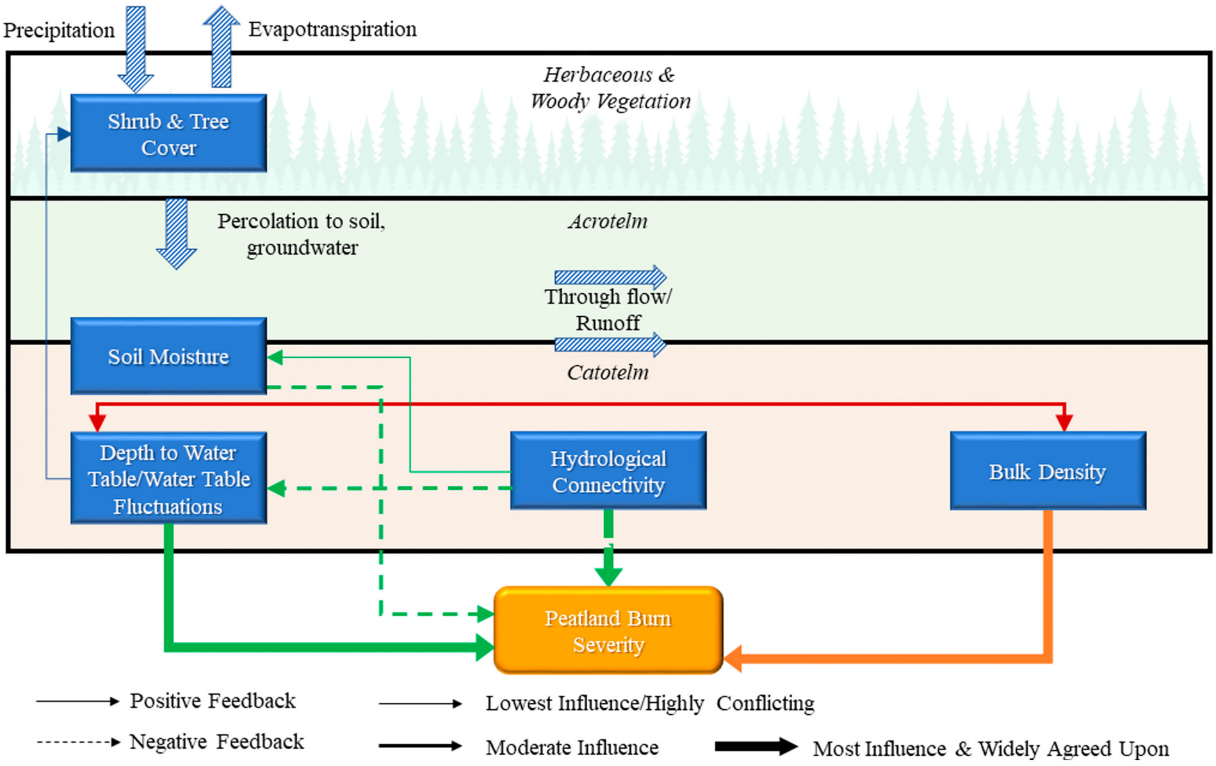

Fig. 1. A conceptual diagram of positive and negative feedback mechanisms as they relate to peatland soil properties (hydrology and bulk density) and peat wildland fire. Major water fluxes are also included (wide, patterned arrows). Note that the diagram is not to scale and is not meant to represent horizontal spatial variations within a peatland.

capacity to replace evaporated moisture (e.g., Lukenbach et al., 2015). Spatial variations in depth of burn are influenced by hydrological connectivity and groundwater movement or, alternatively, peatland fragmentation, which increases the edge to area ratio of peatlands, exposing them to greater proximal water use from surrounding forests ('green' positive and negative feedback arrows, Fig. 1). For example, Hokanson et al. (2016) found that the greatest depth of burn (50 cm, average) occurred along bog margins where the water table fluctuated substantially due to ephemeral groundwater connectivity to upland forests. Further, Lukenbach et al. (2015) found that depth of burn ranged from an average of 8 cm in peatland middles ($n = 580$) to an average of 42 cm in peatland margins ($n = 340$), illustrating the potential for greater depth of burn into peatlands with increased peatland fragmentation.

Variation in water table and soil moisture is enhanced by localised warming/drying of peatland soils. For example, Kohlenberg et al. (2018) found that within 0.012 $\mathrm{m^{-3}}$ samples, depth of burn more than tripled from field moisture levels to air-dried to oven-dried samples, while fuel consumption increased by ~61% in air-dried samples versus those left at field moisture. Oven-dried peat, which may be used as a proxy for hot, dry conditions, resulted in an average increase in total fuel consumption of 14.2%, emphasizing the importance of bulk density and hydrological conditions during peat fires. However, it is interesting to note that when controlling for other factors, the actual rate of downward spread in smouldering peat fires may increase at greater levels of soil moisture (Huang and Rein, 2017). Rein et al. (2008) found that for peat to ignite, soil gravimetric water content must be below 125 ± 10%, while Benscoter et al. (2011) found that the average surface gravimetric water content of samples in which ignition occurred was 61 ± 44%. Smouldering of over seven hours occurred in peat with up to 100% moisture content, regardless of bulk density, indicating that moisture content was the main control on the propagation of smouldering within soils containing variable amounts of organic matter. These studies' results are to be expected: reduction in soil moisture results in deeper peat burns, longer duration of peat burn, and peat that is more readily ignitable.

Depth of burn and subsequent soil C emissions are directly related to dry bulk density, defined as the weight of soil (dried) per given volume. Bulk density influences the maximum soil moisture at which combustion can occur (Benscoter et al., 2011; Kohlenberg et al., 2018), impacting both peatland hydrological conditions (Lukenbach et al., 2015) and depth of burn (Kohlenberg et al., 2018; Fig. 1). Higher bulk densities can result in greater water table fluctuations (Lukenbach et al., 2015; 'red' positive feedback arrow, Fig. 1), which are linked to greater depth of peat burn (Hokanson et al., 2016; 'orange' positive feedback arrow, Fig. 1). Further, increased bulk density also provides an environment for combustion at higher moisture levels (Kohlenberg et al., 2018), as the increase in energy supplied by denser, and therefore added content of peat, results in greater burn severity (Benscoter et al., 2011). For example, Benscoter et al. (2011) found that combustion occurred at lower maximum gravimetric water content in peat with a bulk density of <40 kg $\mathrm{m^{-3}}$ than that with a bulk density of >40 kg $\mathrm{m^{-3}}$ (187% and 295%, respectively). While increased bulk densities may result in greater water table variability, temporal variations in hydrology may also lead to spatial variations in bulk density ('red' positive feedback arrow, Fig. 2), and bulk density may also increase through compaction and increased aerobic decomposition (Waddington et al., 2015; Granath et al., 2016; Fig. 1), which could alter fire propagation in peatlands. Conversely, Prat-Guitart et al. (2016) found that an increase in bulk density could slow lateral propagation of smouldering burn in peat blocks at 100% moisture or greater. While there was more energy produced in combustion as bulk density increases, the energy was less than that required to overcome high soil moisture levels. With the exception of these atypical findings, most studies demonstrate the potential for accelerated changes in bulk density, resulting from, and causing further, water table

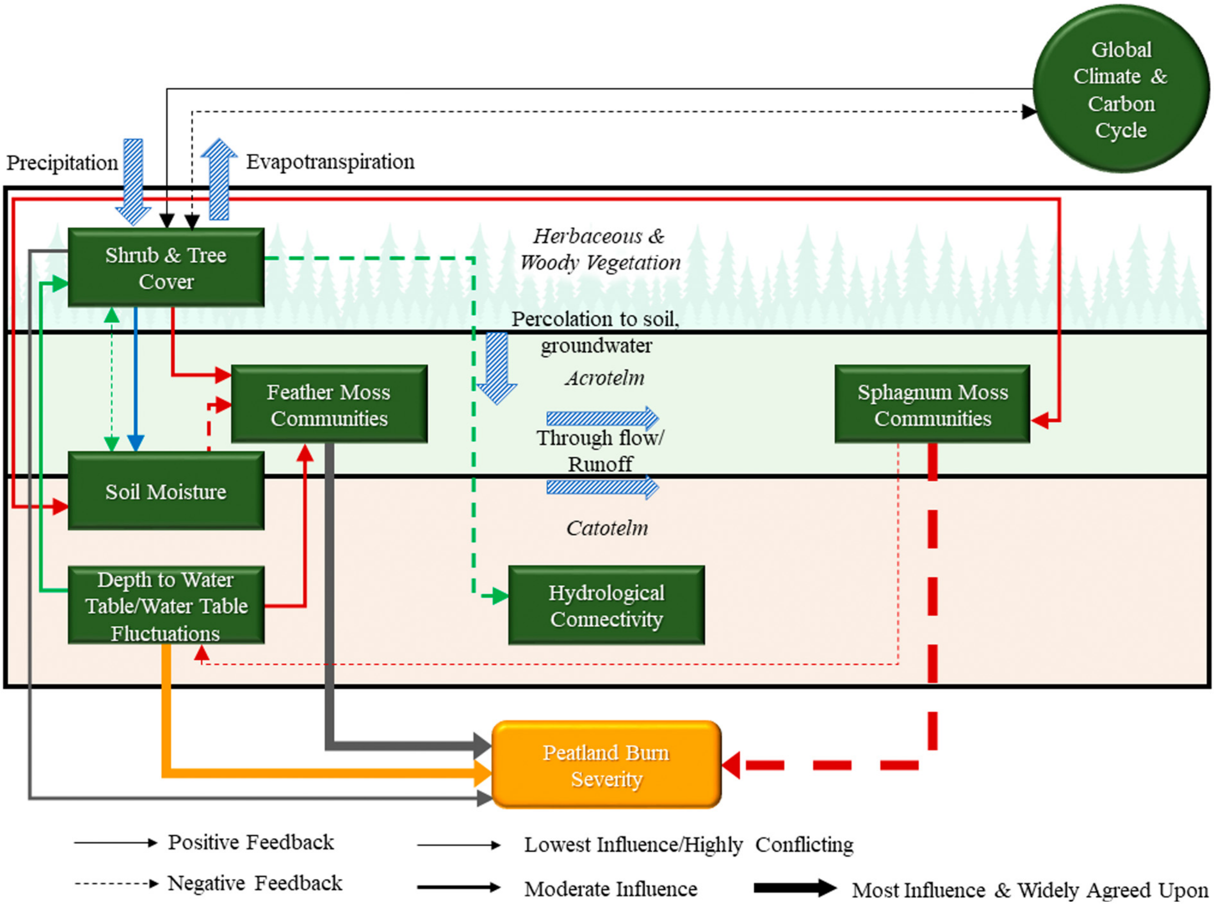

Fig. 2. A conceptual diagram of positive and negative feedback mechanisms as they relate to vegetation distribution, structure, and peat wildland fire. Major water fluxes are also included (wide, patterned arrows). Note that the diagram is not to scale and is not meant to represent horizontal spatial variations within a peatland.

fluctuations and moisture reduction (Lukenbach et al., 2015; Lukenbach et al., 2017), subsequently altering fire propagation patterns associated with anthropogenic and climate-mediated disturbance.

Natural peatlands that are artificially modified or drained may be analogous to future peatland conditions under climate change scenarios (Kettridge et al., 2015). Peatlands are commonly drained for forestry, road/infrastructure development, horticulture, and oil extraction, resulting in changes in peatland hydrological connectivity (Lieffers and Macdonald, 1990; Cleary et al., 2005; Rooney et al., 2012; Nieminen et al., 2018). Drained and/or disturbed peatlands are prone to greater smouldering periods and increased depth of burn (Granath et al., 2016). For example, Wilkinson et al. (2018a) found that depth of burn was significantly greater in heavily drained areas (36.9 cm ± 29.6 cm) compared with moderately drained (6.4 cm ± 5.0 cm) and undrained (2.5 cm ± 3.5 cm) peatlands. Similar results were also found in Turetsky et al. (2011), who observed an almost three-fold increase in depth of burn from undisturbed to drained peatlands. Thus, deep peat fires found in drained peatland analogues illustrate the potential for significant impacts to the C-climate system and drying of peatlands in the future. Granath et al. (2016) estimated C losses of 21 kg m^{-2} from 30 cm deep burns (water table at 40 cm) to over 35–40 kg m^{-2} when water table is lowered to 80 cm. This is equivalent to 600–1000 years of C sequestration. Turetsky et al. (2011) found that wildland fire released 2.0 ± 0.5 kg C m^{-2} from undrained peatlands and 16.8 ± 0.2 kg C m^{-2} from drained peatlands. Similar to drained peatlands, deep burns resulting in large C emissions may be observed in undisturbed peatlands that are drying naturally (Granath et al., 2016). Lowered water tables expose deeper, compressed peat to smouldering, and consequently, higher C emissions per unit burned. Despite these results, many studies have not accounted for the variability of depth of burn and relation to C loss during combustion between peatland middles and margins, potentially underestimating C loss from boreal peatlands within the global C-climate cycle. This illustrates the importance of peatland hydrological connectivity and the implications of peatland fragmentation ('green' positive and negative feedback arrows, Fig. 1).

2.2. Variability in vegetation distribution and structure: influences on burn severity

Ecological and vegetative processes controlling depth to water table in peatlands are non-linear, complex, and interacting (Waddington et al., 2015). Here we examine vegetation-related feedback mechanisms that directly and indirectly influence peatland fire severity within mature ecosystems. Vegetation feedback mechanisms associated with biomass losses from wildland fire include afforestation and shrubification, as well as changes to moss productivity and community over time (Fig. 2).

Increased depth to water table associated with climate warming or other disturbances (Holmgren et al., 2015) can encourage the encroachment of shrubs ("shrubification") into peatlands (Weltzin et al., 2003), potentially resulting in afforestation (Waddington et al., 2015; 'green' positive feedback arrow, Fig. 2). This may result in a positive soil drying feedback, where drying occurs due to transpiration ('green' negative feedback arrows, Fig. 2), which further lowers the water table and enhances shrub/tree growth (Lieffers and Macdonald, 1990; Murphy et al., 2009; Waddington et al., 2015; 'green' positive feedback arrow, Fig. 2). Alternatively, increased shading from trees may reduce evapotranspiration from the moss surface, partly mitigating increased interception and evapotranspiration fluxes associated with shrubification (Kettridge et al., 2013; 'blue' positive feedback arrow, Fig. 2) and reducing burn severity. Changes to the structure of vegetation can increase wildland fire fuels and can alter the hydrological connectivity of the landscape (Thompson et al., 2019; 'grey' positive feedback arrows, Fig. 2), thereby increasing fire risk and post-fire burn severity (e.g., Wilkinson et al., 2018a). Kettridge et al. (2015) suggest that ecological tipping points may exist when drying is significant enough that wildland fire results in deep burning (Wilkinson et al., 2018a; 'orange' positive feedback arrow, Fig. 2). These processes have been observed in temperate peatlands in the U.K. (Davies et al., 2013). For example, Wilkinson et al. (2018a) examined the effects of peatland drainage on afforestation and subsequent burn severity ('grey' positive feedback arrows, Fig. 2). It was found that drainage significantly increased tree growth, contributing to the positive feedback mechanism between afforestation and water table reduction ('green' positive feedback arrow, Fig. 2). Increased productivity also resulted in greater tree canopy cover (approximately 20% for undrained, 30% for moderately drained, and 70% for heavily drained peatlands). Wilkinson et al. (2018a) observed that tree cover further reduced the amount of precipitation that reached the peat surface ('blue' positive feedback arrow, Fig. 2) and noted a threshold shift to a greater depth of burn during wildland fire. Variations in vegetation structures and foliage cover could have significant and complex implications for peatland maintenance vs. drying. Increased evapotranspiration due to shrubification and afforestation is enhanced by interception of precipitation, evaporation from leaves and branches, and reduced overall throughfall (Baisley, 2012; Thompson et al., 2014; Waddington et al., 2015). Not only does a reduction in precipitation reaching the peat surface affect burn severity via a decrease in soil moisture, but it may also result in increased burn severity by lessening the ability of precipitation to extinguish, or at least minimize the further spread of, smouldering in peat. The ability of rainfall to extinguish smouldering peat depends on intensity rather than only duration, and it must reach a threshold to have an impact (Lin et al., 2020). Low-intensity rain (<4 mm hr^{-1}) is unlikely to have any extinguishing impact (Lin et al., 2020); it is important to consider how greater canopy cover can reduce the intensity of rainfall.

While a general increase in shrubs or trees may result in further positive evapotranspiration-drying feedbacks, afforestation of an already shrubby peatland may counteract this if tree shading reduces shrub growth and maintenance (Waddington et al., 2015), as, under some instances, evapotranspiration may be greater in shrubby peatlands than in treed peatlands (Strilesky and Humphreys, 2012). For example, treed peatlands dominated by black spruce (*Picea mariana*) will have lower evapotranspiration and gross ecosystem photosynthesis than open/shrubby peatlands, as *P. mariana* has lower transpiration and photosynthetic rates. *P mariana* has low stomatal conductance, which also decreases as vapour pressure deficit increases (Dang et al., 1997), so a transition from shrubs to trees may result in reduced evapotranspiration, reduced water loss, and improved peatland resilience to wildland fire.

Sphagnum mosses, particularly *Sphagnum fuscum*, which dominate peatland hummocks, retain moisture in dead hyaline cells and reduce soil temperature, thereby acting as a natural fire retardant in peatlands. When the depth to water table increases, hummock *Sphagnum* species increase hyaline cell area (Bu et al., 2013; Fig. 2), increasing water storage capacity, maintaining surface moisture, and improving water storage capacity such that the potential for combustion is reduced ('red' positive and negative feedback arrows, Fig. 2). Micro-topographic hollows are dominated by a diverse range of more flammable mosses, such as *Sphagnum angustifolium*, *Sphagnum magellanicum*, and feather moss (Kellner and Halldin, 2002; Benscoter et al., 2005). A decline in water table position or soil moisture, or increased shrubification and afforestation may result in a transition from *Sphagnum*-dominated moss communities to forest/upland species such as feathermoss (e.g., Bisbee et al., 2001; Breeuwer et al., 2009; Wilkinson et al., 2018a; 'red' positive and negative feedback arrows, Fig. 2). Feathermoss species have lower moisture requirements than *Sphagnum* and thrive under shadier conditions (Bisbee et al., 2001). However, because feathermoss has a lower moisture content for the same height above the water table, they tend to burn more severely (Wilkinson et al., 2018a; Fig. 2). This could enhance future wildland fire burn severity within peatlands and surrounding transitional boundaries.

Fig. 3 illustrates the combined feedbacks of the dominant pre-fire factors influencing the loss of biomass from C-rich peatland soils illustrated in Figs. 1 and 2 without highlighted feedbacks (used for the understanding of connections described above). Enhanced fragmentation of wetlands associated with drying, and also disturbance from natural resources extraction, will likely contribute to increased fire severity within peatlands in the future. This may occur as a result of reduced hydrological connectivity and a reduction of the ability of peatlands to maintain moisture conditions required for future fire resilience. Drying could enhance shrubification and positive feedbacks associated with water losses from evapotranspiration, resulting in a net increase of C fluxes to the atmosphere associated with combustion and microbial respiration.

3. Post-fire feedbacks and their influence on peatland ecosystem change

Wildland fire and burn severity in peatlands may critically impact feedback mechanisms, which, in the years immediately following fire, can enhance or diminish peatland resiliency to climate-mediated changes or future wildland fire regimes. Here we describe what is currently understood with regards to the immediate post-fire environment with regards to a) energy balance; b) soil properties, including bulk density and hydrological feedbacks; and c) vegetation regeneration.

3.1. Energy balance

Boreal peatlands that have not recently burned have lower sensible heat fluxes, higher latent heat fluxes, and higher albedo (even through the growing season) than do boreal forests (Helbig et al., 2020). Boreal peatlands play an important role in local climates by cooling summer air temperatures by up to 1.7–2.5 °C (Helbig et al., 2020). As such, understanding how wildland fire impacts the energy balance of these peatlands in the years immediately following the fire is important in understanding energy partitioning into latent and sensible heat exchanges and interactions between evaporative losses, hydrology, and vegetative regeneration (Fig. 4).

In the period immediately following a moderate to severe fire, the ground surface receives increased incident shortwave radiation and reduced shading due to a loss of trees. This can result in a shift in the proportion of latent and sensible energy fluxes, which may result in significantly greater surface evaporation in burned peatlands than in unburned (~50%; Thompson et al., 2014; 'orange' positive feedback arrow, Fig. 4). However, these positive feedbacks may be alleviated by negative feedback mechanisms such as reduced transpiration due to a loss of trees and changes in albedo associated with increased winter snow cover. While Thompson et al. (2014) found that evaporation increased from burned peatlands, once the reduction in transpiration due to a loss of trees was accounted for, the difference in evapotranspiration between burned and unburned peatlands was negligible. An increase in winter albedo and an increase in outgoing longwave radiation also mitigates increased shortwave radiation received by burned peatlands in the first few years post-fire ('red' negative feedback arrows Thompson et al., 2015). Further, rapid regrowth of shrubs within burned peatlands mitigated the impact of a loss of canopy on radiation at the moss surface ('blue' negative feedback arrow, Fig. 4). Shrub growth likely reduces evaporation from the scorched ground surface as well as open water within small hummocks and ground cover

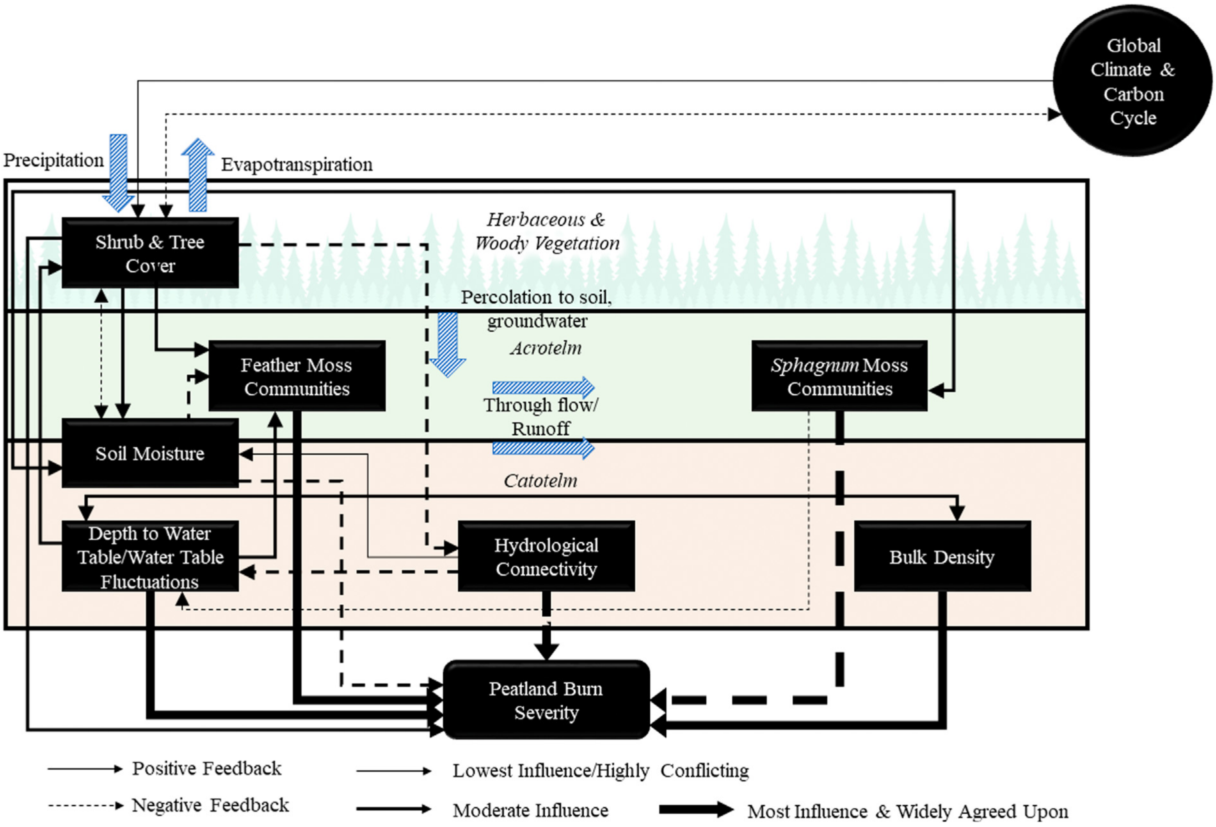

Fig. 3. The combination of soil, hydrological, and vegetation influences (Figs. 1, 2) on pre-fire positive and negative feedback mechanisms and relationships affecting peatland burn severity. Major water fluxes are also included (wide, patterned arrows). Note that the diagram is not to scale and is not meant to represent horizontal spatial variations within a peatland.

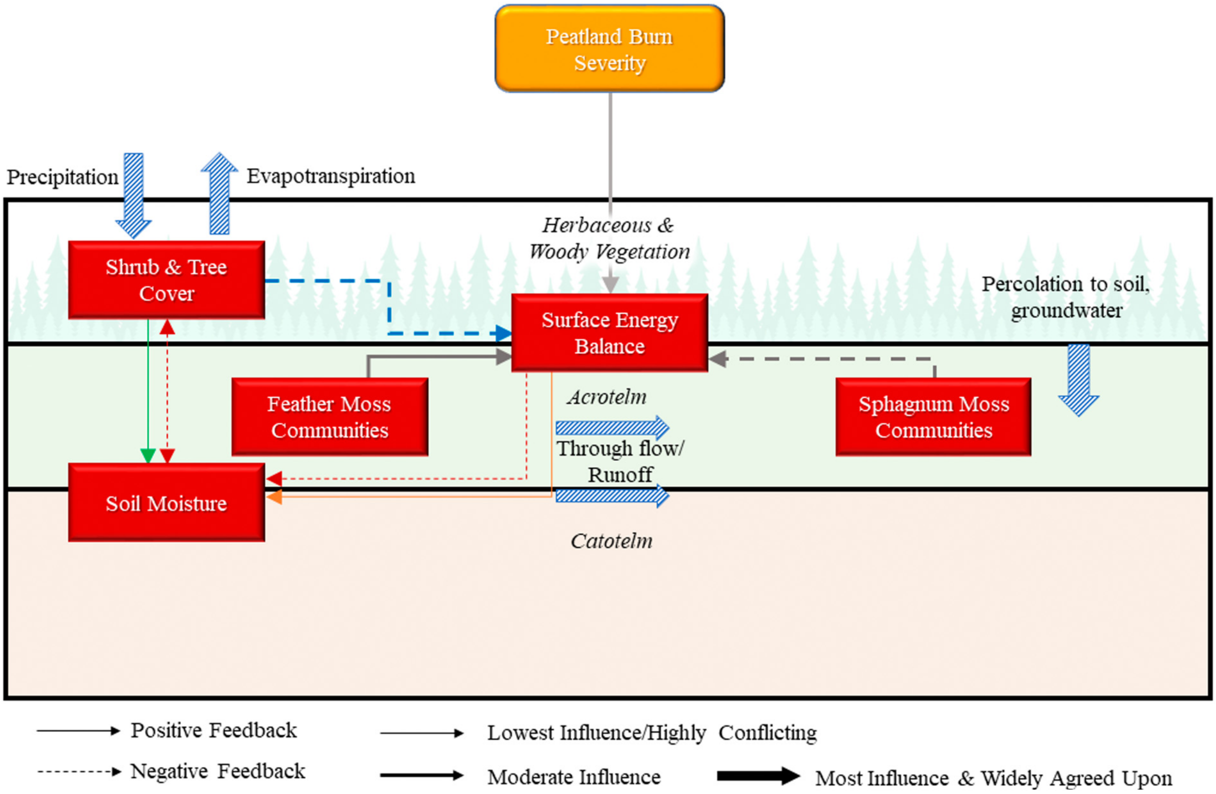

Fig. 4. A conceptual diagram of positive and negative feedback mechanisms as they relate to energy balance in an immediately post-fire peatland. Major water fluxes are also included (wide, patterned arrows). Note that the diagram is not to scale and is not meant to represent horizontal spatial variations within a peatland.

vegetation, resulting in greater moisture retention (Kellner, 2001; 'green' positive feedback arrow, Fig. 4).

Surface temperatures are also affected by moss species type and microtopography (Kettridge et al., 2012). *S. fuscum* hummocks maintain pre-fire temperatures ('grey' negative feedback arrow, Fig. 4), and while the surface temperatures of hollows may be significantly greater than that of hummocks ('grey' positive feedback arrow, Fig. 4), these differences are restricted to surface layers. Low soil moisture and retention of sensible heat at the burned peat surface results in warming of the laminar surface temperature, while also insulating the sub-surface peat to a depth of ~1–2 cm. Kettridge et al. (2012) found that at approximately 1 m below the peat surface, burned and unburned peatland temperatures were similar. However, following wildland fire in sporadic permafrost environments, Gibson et al. (2018) found warmer soil thermal regimes and expansion of heat into the active layer (seasonally thawed soil). They hypothesize that the combined effects of deeper active layers, thermokarst bog expansion, and warmer soils will significantly increase rates of decomposition and C emissions, while thermokarst bog expansion could also result in net cooling, *Sphagnum* community enhancement, and possible net C sequestration. Further, during the period following fire, singed feather mosses may become hydrophobic, thereby reducing latent heat exchange (Kettridge et al., 2017; 'red' negative feedback, Fig. 4).

3.2. Soil properties: hydrological and bulk density feedbacks

Combustion of peatlands may result in a positive or negative feedback response relative to the hydrological conditions of the peatland in the short-term post-fire, depending on environmental factors including pre-fire hydrology (e.g., Kettridge et al., 2015; Lukenbach et al., 2017), vegetation (e.g., Flannigan et al., 2009; Waddington et al., 2015) and burn severity (e.g., Lukenbach et al., 2016). Regarding hydrology, if peatlands are undrained (Kettridge et al., 2015) or are well-connected to groundwater sources (Lukenbach et al., 2017), post-fire water tables may remain at similar pre-fire levels and stability, enhancing recovery and moss regeneration. Alternatively, if peatlands are not well-connected to groundwater sources, or have been drained, increased depth of burn results in a lowered and more fluctuating water table in the years following the fire (Sherwood et al., 2013; Thompson et al., 2014; Lukenbach et al., 2017; 'red' positive and negative feedback arrows, Fig. 5). For example, peatlands that are poorly hydrologically connected may experience deeper, more severe burning, resulting in elevation loss ('red' positive and negative feedback arrows, Fig. 5), exposure of high bulk density peat, and, subsequently, more dynamic hydrology ('grey' positive feedback arrows, Fig. 5). Pre-fire surface peat with low bulk density has a high specific yield, which is important for moderating water table fluctuations (Thompson and Waddington, 2013a). Wildland fire results in the exposure of deeper peat with higher bulk density to the surface, especially in hollows. This denser peat has higher water retention and lower specific yield, which results in a less stable, "flashier" water table that fluctuates more readily with small weather changes (Thompson and Waddington, 2013a; 'grey' positive feedback arrows, Fig. 5). Particularly when peatlands are poorly connected to groundwater and the surrounding peatland complex, this can result in increased flooding during wet conditions and greater water table draw-down during dry periods, in the years following wildland fire (Thompson et al., 2014).

The importance of hydrological connectivity in post-wildland fire hydrological impacts is especially apparent when considering peatland margins. When comparing the post-fire hydrological conditions of poorly connected versus well-connected peatland margins, Lukenbach et al. (2017) found that poorly-connected peatlands had a less stable water table, whereas the well-connected peatlands' water table was moderated. Peatland margins that are well-connected within the

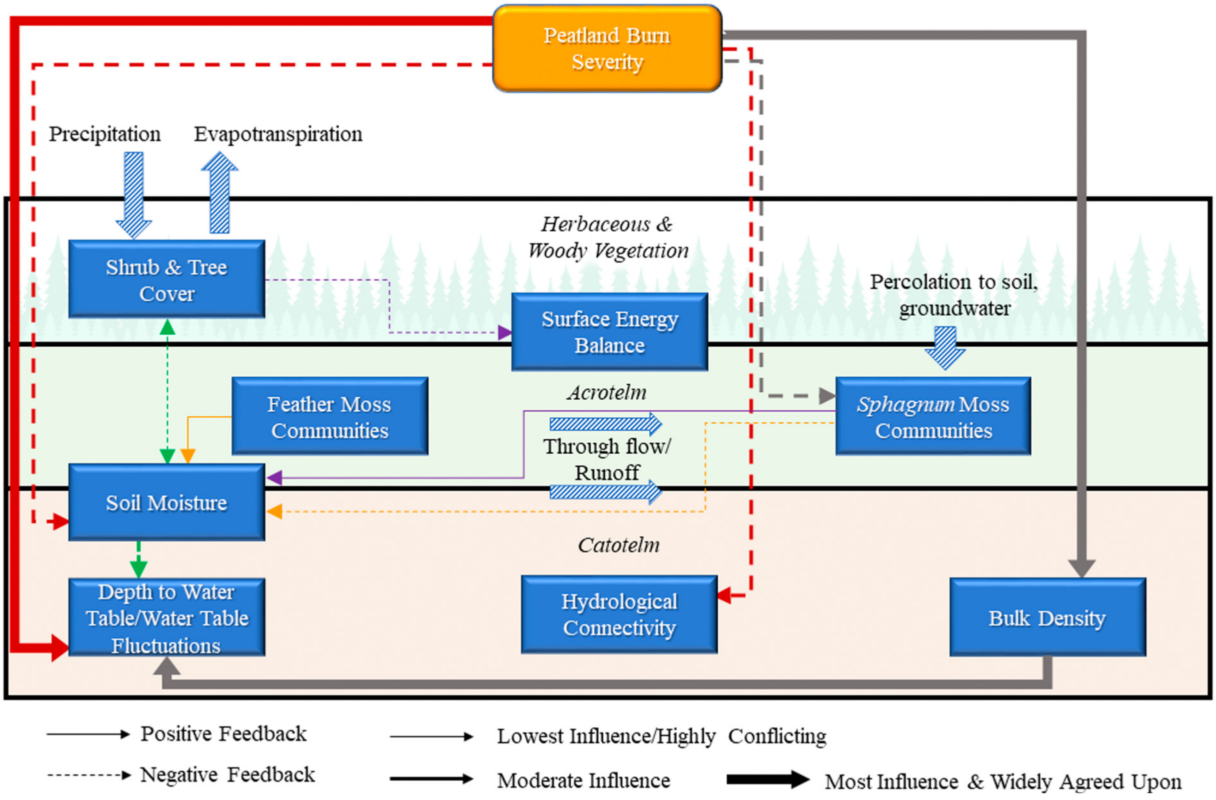

Fig. 5. A conceptual diagram of positive and negative feedback mechanisms as they relate to post-fire burn severity and soil properties (hydrology and bulk density). Major water fluxes are also included (wide, patterned arrows). Note that the diagram is not to scale and is not meant to represent horizontal spatial variations within a peatland.

peatland complex have lower depth of burn (like that of peatland middles). The deep burning in the margins of poorly connected peatlands not only result in a greater elevation loss, but enhance peat exposure to high bulk density and low specific yield.

Peatlands may have different hydrological responses following wildland fire, depending on their vegetation and/or microtopography and the severity of burn (e.g., Thompson and Waddington, 2013b). In peatlands dominated by *Sphagnum*, evapotranspiration may increase after a wildland fire, resulting in drier peatlands (Thompson et al., 2014) and an increased risk of recurring fire. Particularly in *S. fuscum*-dominated hummocks, there is a greater increase in pore-water pressure than in hollows, suggesting that despite the limited depth of burn, and the apparently low burn severity of hummocks relative to hollows, the hydrological impacts may be more severe. This is demonstrated by increased soil moisture losses post-fire ('orange' negative feedback arrow, Fig. 5), increased moisture tension, limited *Sphagnum* growth, and reduced post-fire regeneration (Thompson and Waddington, 2013b).

However, changes to evapotranspiration may also result in negative hydrological feedbacks (Thompson and Waddington, 2013b). For example, lower severity burning resulting in residual feathermoss may become hydrophobic, increasing soil moisture retention (Wilkinson et al., 2020; 'orange' positive feedback arrow, Fig. 5). As burn severity increases, hydrophobicity rises to a point where vegetation is thoroughly combusted, exposing the underlying peat (Wilkinson et al., 2020). This may reduce the risk of subsequent fires, the potential for vegetation regime shift, and/or the possibility of excess C release due to drying peat (Kettridge et al., 2014). Further, while other studies as described previously found that low severity burn of *Sphagnum* increases evapotranspiration, others have found that it may also increase the water repellency of *Sphagnum* (Kettridge et al., 2014), resulting in a negative feedback such that evapotranspiration is reduced, water storage is increased, and propensity for future burn is reduced ('purple' positive feedback arrow and 'grey' negative feedback arrow, Fig. 5).

Further mitigating potential increases in evapotranspiration from burned *Sphagnum* communities, post-combustion feathermoss evapotranspiration is much lower than that of *Sphagnum* and may be less than the evaporation from a non-vegetated environment (Kettridge et al., 2017). If treed peatlands are burned, the loss of trees and post-fire forb and shrub succession may result in a lower net loss of moisture in the post-fire peatland environment (Thompson et al., 2015; 'green' negative feedback arrows, Fig. 5). A loss of canopy will also increase the amount of precipitation reaching the soil and will reduce the evaporation that occurs on the canopy before it reaches the peat surface (via interception). Fewer trees and shrubs will also reduce evapotranspiration (Baisley, 2012; Waddington et al., 2015; Wilkinson et al., 2018a; 'purple' negative feedback arrow, Fig. 5). Because evapotranspiration is the dominant flux of water from boreal peatlands (Petrone et al., 2006), reduced transpiration is essential in maintaining peat moisture, and therefore reducing the susceptibility of peatlands from future wildland fire (Kettridge et al., 2017).

Regarding post-fire bulk density, Thompson and Waddington (2013a) found that surface bulk density was significantly greater in burned than in unburned peatlands (85 kg m^{-3} and 56 kg m^{-3}, respectively). Increased post-fire bulk density can result in enhanced water table variability, which in turn, can further increase bulk density and the probability of greater depth of burn in future fires (Waddington et al., 2015; Granath et al., 2016); 'grey' positive feedback arrows, Fig. 5). Changes in post-fire bulk-density can also have significant implications for post-fire moisture by reducing saturated hydraulic conductivity (Whittington and Price, 2006) and specific yield, which controls the rate of water table decline per unit of water loss (Price, 1997). Greater bulk density with depth, especially in post-fire peatlands, allows for increased water retention by peat found above the water

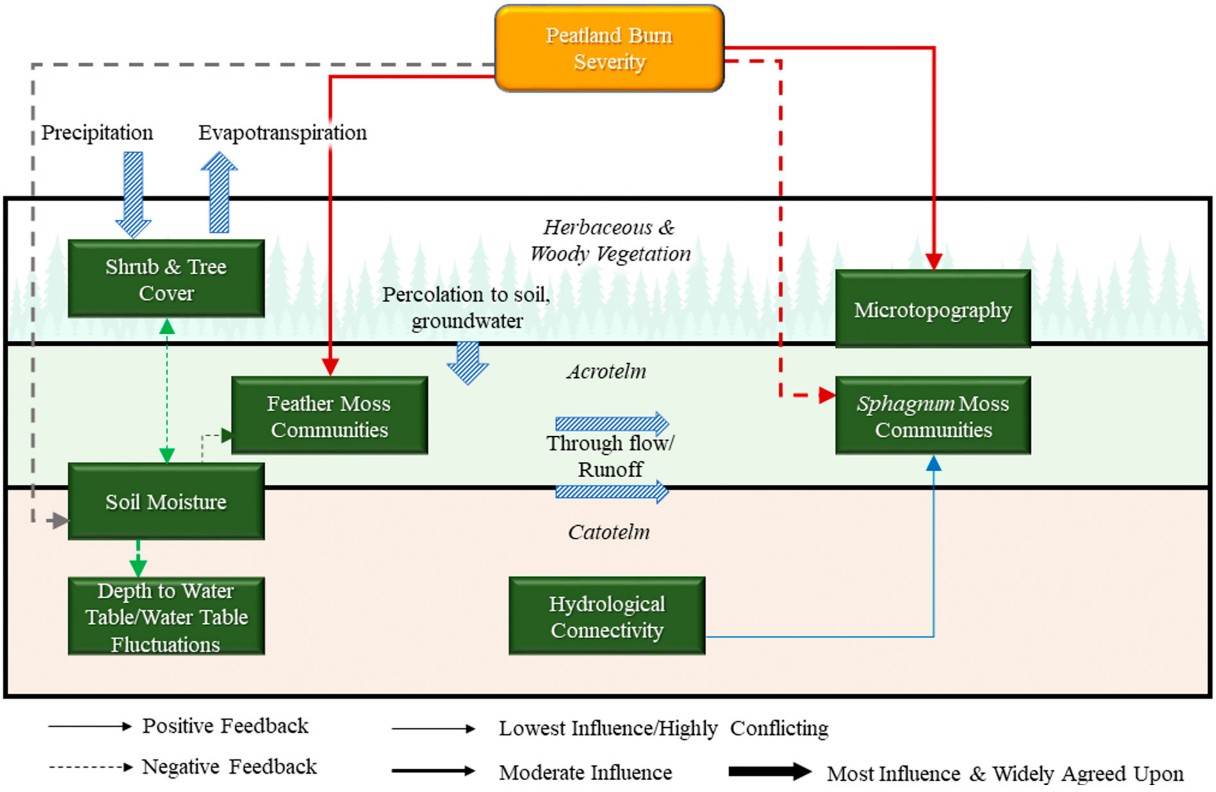

Fig. 6. A conceptual diagram of positive and negative feedback mechanisms as they relate to post-fire burn severity and vegetative regeneration. Major water fluxes are also included (wide, patterned arrows). Note that the diagram is not to scale and is not meant to represent horizontal spatial variations within a peatland.

table (Thompson and Waddington, 2013a). Finally, the positioning and bulk density within hollows vs. hummocks also varies following wildland fire. For example, Thompson and Waddington (2013a) found that post-fire bulk density was greater in hollows (where burn severity and loss of C-rich soils are often greater) than in hummocks (95 kg m^{-3} and 45 kg m^{-3}, respectively).

3.3. Shrubification and change to ground cover vegetation

The alteration of microtopography by wildland fire is an important determinant of post-fire vegetation regeneration and peatland resilience. Microtopography is a primary control of moss and lichen composition associated with variations in hydrology and energy balance (Vitt, 1990), which may result in a positive fire/species feedback response associated with different moisture levels and decomposition rates. Variations in ground cover species can also result in differences in peat bulk density, further enhancing variations in microtopography (Benscoter et al., 2015; 'red' positive and negative feedback arrows, Fig. 6). Benscoter et al. (2015) found that the post-fire local microtopography elevation range between hummocks and hollows was nearly double that of pre-fire in a boreal peatland. Therefore, if wildland fire did not occasionally enhance local microtopograhical variations, peatlands would become more vertically homogeneous (Benscoter and Vitt, 2008; Rowe et al., 2017), resulting in successional changes and potentially lower diversity of vegetation species (Benscoter and Vitt, 2008). Following fire, hollows remain hollows; however, hummocks may be equally likely to become hollows as they are to remain hummocks (Benscoter et al., 2005). Whether a microtopographic feature is changed or maintained is dependent on the local spatial variability of the depth of burn (burn severity). If burn severity is relatively low, hummocks may regenerate faster than hollows due to remaining *Sphagnum* fragments (Clymo and Duckett, 1986). However, if burn severity is high, hummocks can become hollows, and *Sphagnum* regeneration would be limited (Benscoter et al., 2005). This highlights the importance of fire severity and spatial variations in depth of burn for determining peatland succession and the overall form of boreal peatlands in the future (Fig. 6).

Regarding the influence of microtopography on post-fire vegetation communities, *S. fuscum* typically regenerates on hummocks, while hollows are often characterised by a greater variety of post-fire species (Benscoter et al., 2005) due to greater variability of moisture conditions. *Sphagnum* regeneration on hummocks is supported if burn severity is low or if peatlands are hydrologically well-connected ('blue' positive feedback arrow, Fig. 6); however, if burn severity increases, and/or peatlands are disconnected from groundwater and the surrounding peatland complex, the functionality of this negative feedback mechanism will be reduced. *Sphagnum* hummocks may not regenerate, resulting in the migration of feathermoss into hummocks (Lukenbach et al., 2016; Lukenbach et al., 2017) or the replacement of *Sphagnum* communities with upland species and, subsequently, enhanced peatland drying (e.g., Johnston et al., 2015; Miller et al., 2015; 'red' negative feedback arrow, Fig. 6).

Post-fire water table variability within peatland margins may also promote a regeneration trajectory similar to that of uplands, as indicated by the growth of vegetation species such as aspen (*Populus tremuloides*; Lukenbach et al., 2017; Depante et al., 2019; 'green' negative feedback arrows, Fig. 6). As these are not peat-forming species, they may affect the C sink capacity of the peatland and could increase transpiration. This may result in a positive feedback response in which increased drying results in further growth of upland vegetation and possible transition to an upland as opposed to a wetland ecosystem ('green' negative feedback arrows, Fig. 6). The process feedbacks of post-fire peatland establishment associated with energy exchanges (Fig. 4), burn severity, hydrological and topographical influences (Fig. 5), and vegetation community establishment (Fig. 6) are summarised in Fig. 7.

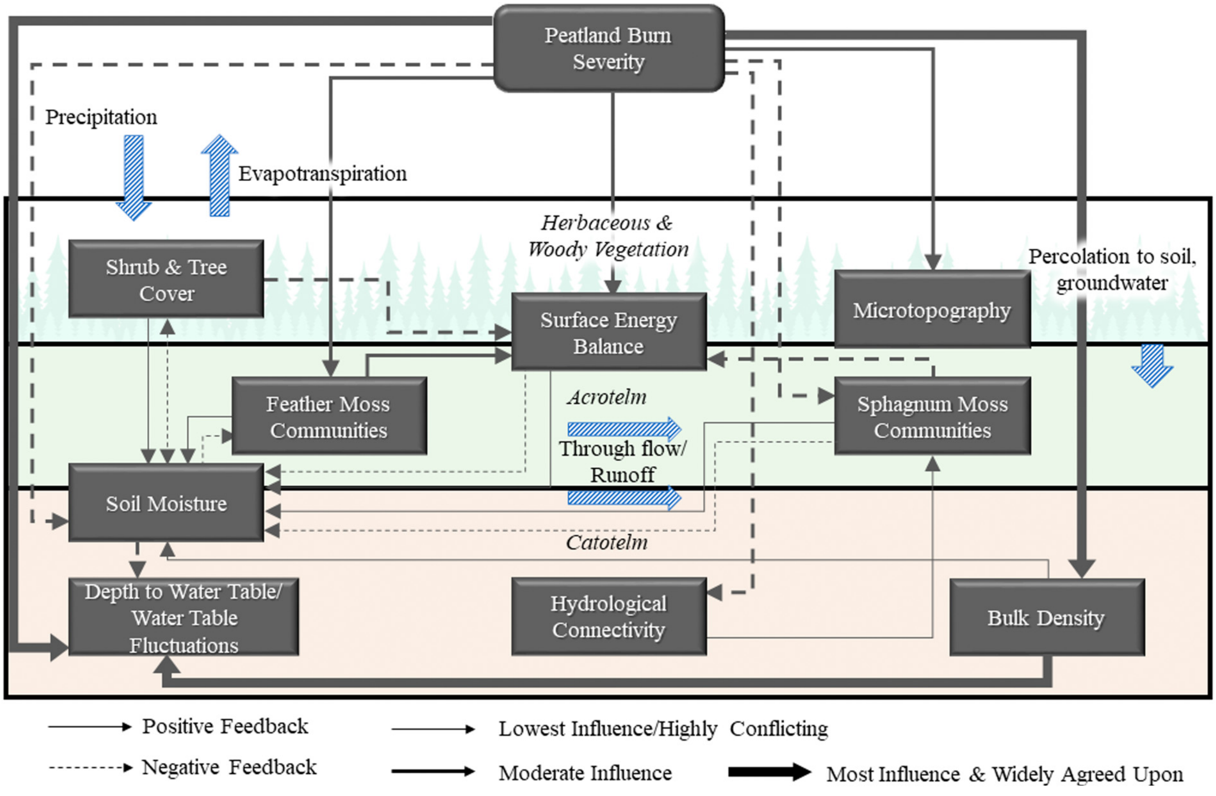

Fig. 7. A conceptual feedback diagram with water fluxes summarizing post-fire positive and negative feedback mechanisms and relationships affected by peatland burn severity, hydrology, and vegetation described in Figs. 4-6. Major water fluxes are also included (wide, patterned arrows). Note that the diagram is not to scale and is not meant to represent horizontal spatial variations within a peatland.

4. Peatland fire linkages to the climate system

Due to the vast C stores of northern peatlands, changes in hydrology and burn regimes will significantly influence peatland C cycling and implications to the global C cycle (Camill et al., 2009; Turetsky et al., 2011). Climatic warming and changes to the period of snow-cover in northern regions are causing major ecological shifts within boreal peatlands (e.g., Chasmer and Hopkinson, 2017 within the discontinuous permafrost zone), affecting both the directionality and strength of peatland-atmosphere C fluxes (Helbig et al., 2017). Further, C emissions from peatland fires are predicted to increase associated with projected climatic shifts (e.g., Kohlenberg et al., 2018; Wilkinson et al., 2018a; 'red' positive feedback arrow, Fig. 8). Smouldering peat releases more C during peatland wildland fire than does the burning of the forested overstory (Benscoter et al., 2011), while near equivalent amounts of C are released in the years following wildfire due to net balances of decreased gross primary production (Harden et al., 2000) and enhanced ecosystem decomposition/respiration (e.g., Auclair and Carter, 1993; Kasischke et al., 1995; O'Neill et al., 1997; Harden et al., 2000), exacerbating positive C-climate feedback cycle (Kasischke et al., 1995; Stocks et al., 1996; van der Werf et al., 2010; Fig. 7). Such changes could shift peatlands from a gradual sink for atmospheric C to a source (Loisel and Yu, 2013).

It is worth noting that while this paper focuses on C emissions during peat combustion, which is mostly CO_2 (Hu et al., 2018), CO and CH_4 are also emitted in greater proportions than in flaming fires. In reviewing the literature, Hu et al. (2018) found that average emissions factors in boreal and temperate peatland fires were 1133.8 g kg^{-1} CO_2, 179.4 g kg^{-1} CO, and 8.1 g kg^{-1} CH_4. The ratios of these C gasses will fluctuate depending on the soil's bulk density and moisture content (Kohlenberg et al., 2018). Dry peat results in an increase in flaming and greater CO_2 emissions, whereas wet peat emits more CO (Hu et al., 2019), which may be of concern when considering the negative impacts of CO on human health (Hinwood and Rodriguez, 2005). As the strength of combustion and oxidization declines with moisture content, the ratio of $CO:CO_2$ increases. While these are important metrics, especially when considering air quality, the loss of specific C gasses is not addressed in this paper.

The extent to which North American boreal peatland fires affect global C and climate systems by re-introducing C sequestered over several millennia to the atmosphere, and the response of peatland C emissions to climatic warming, remains unclear. Because of the complexity of the combustion of organic peatland soils, spatial variations of depth of burn, and the large proportion of C emitted relative to other ecosystem components (Benscoter and Wieder, 2003), accurate quantification of C emissions can be challenging (van der Werf et al., 2010). This may result in the large variability in depth of burn, particularly between margins and middles, left unaccounted for (e.g., Thompson and Waddington, 2014; Kohlenberg et al., 2018). For example, Harden et al. (2000) found that the boreal ecosystem C losses from wildfire were three to ten times greater than those used in general circulation models. Wu et al. (2015) found that peatlands, in general, are not well represented within earth systems models, and while they were incorporated into the Canadian Land Surface Scheme v3.6 and Canadian Terrestrial Ecosystem Model v2.0, wildland fire and its impacts of C loss were not represented. Other studies have modelled C loss while assuming a maximum depth of peat burn of 15 cm (e.g. van der Werf et al., 2010), which underestimates depth of burn measurements identified using field sampling and airborne lidar data within boreal peatlands (e.g., Granath et al., 2016; Hokanson et al., 2016; Chasmer et al., 2017). If depth of burn is underestimated within C emissions models, then C losses from peatland fires are also significantly underestimated. The proportion of the landscape that is subject to such deep burning, however, remains unclear. Improved accuracy of C emissions estimations requires quantification of the proportion of deep to shallow burns associated with burn severity and a better understanding of the distribution of deep burns for statistical analyses and C budget modelling.

Peatland-climate feedback mechanisms are complex, and there are many uncertainties regarding the prediction of peatland fires in the

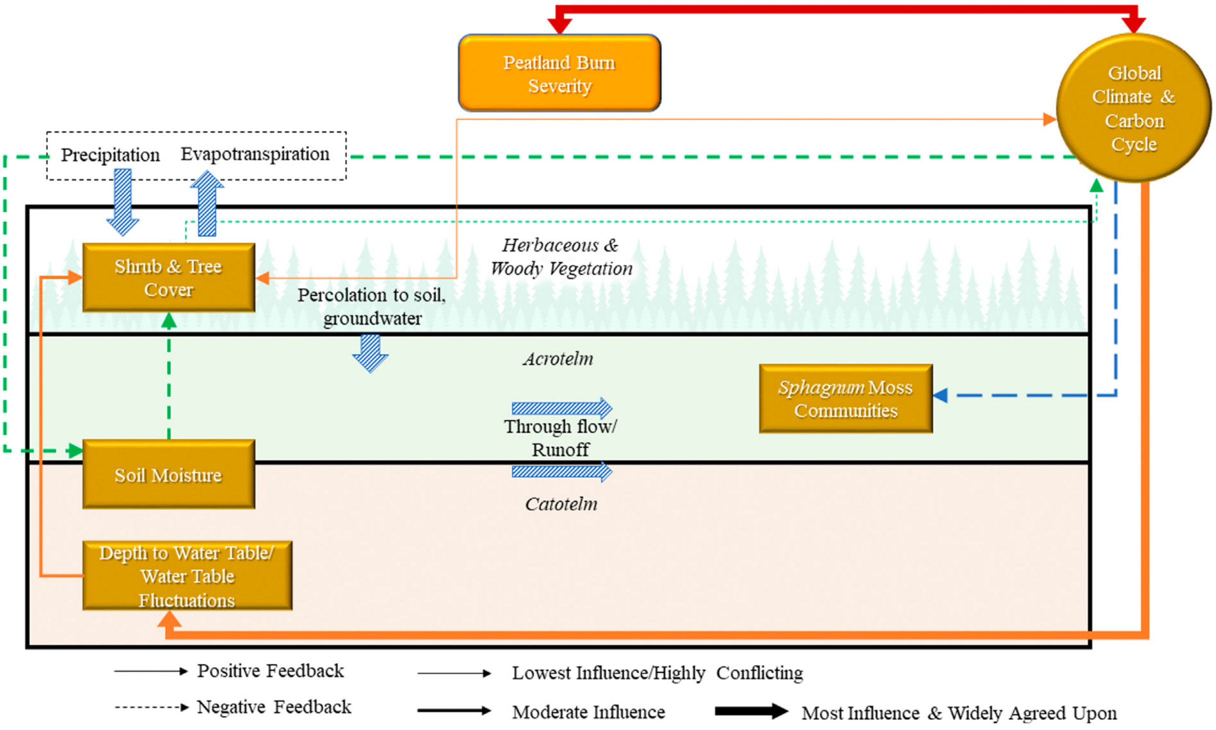

Fig. 8. A conceptual diagram of positive and negative feedback mechanisms as they relate to the global C-climate cycle and peat wildland fire. Major water fluxes are also included (wide, patterned arrows). Note that the diagram is not to scale and is not meant to represent horizontal spatial variations within a peatland.

future (e.g., Camill et al., 2009). It is possible that, while a warming climate may increase wildland fire frequency, severity, and/or extent (Flannigan et al., 2005), resulting in greater C emissions (Turetsky et al., 2011; 'orange' positive feedback arrows, Fig. 8), the opposite could also occur. For example, increased shrubification of peatlands following fire will result in a pulse of increased net primary production (NPP), resulting in a negative C-climate feedback, potentially mitigating C emissions from peat combustion (Camill et al., 2009; Fan et al., 2013; Loisel and Yu, 2013; 'green' negative feedback arrows, Fig. 8). Further, an increase in surface air temperature and length of growing season prolongs the period of C sequestration, resulting in net uptake (Fan et al., 2013; Loisel and Yu, 2013), while an increase in air temperature may also increase heterotrophic respiration. In some cases, a warming climate may also result in a transition from fen to bog within some boreal peatlands and an increase in *Sphagnum* production (Loisel and Yu, 2013; 'blue' negative feedback arrow, Fig. 8), both of which also promote increased C uptake. Finally, increased sequestration from historically wetter peatlands, such as fens, may offset C emissions of already-drier peatlands (Loisel and Yu, 2013). However, a shift from wetter to dryer peatlands may increase fire severity and the likelihood of ignition, further reducing fire return intervals. The long-term implications of increasing fire frequency are uncertain. If vegetation regeneration was not considered, the shortening of fire intervals by half could result in a net source of C from peatlands (Wieder et al., 2009); however, with more frequent fires, while deciduous trees may flourish, the quantity of conifers, surface organic material, and herbaceous plant species will likely decrease (Whitman et al., 2019). Shortened fire return intervals may not allow for regeneration of current stands, reducing fuel load (Johnstone et al., 2016), and possibly decreasing burn severity and C emissions from future wildland fires, despite their increased frequency.

The relationship between peatland vegetation communities in the post-fire ecosystem and impacts on C emissions may be mitigated by the regeneration of peatland mosses and vascular vegetation (Camill et al., 2009). Still, this enhanced regeneration could have other implications for peatland function and ecosystem services. For example, an increase in NPP or shifting vegetation communities could increase fire fuel sources, increasing the probability of ignition and spread. Further, Fan et al. (2013) suggest that peatland C sinks may transition to sources in the latter part of the 21st century as projected warming may increase respiration beyond what is sequestered through primary production, amplifying positive C-climate-fire feedback cycles (e.g., Kettridge et al., 2017).

5. Discussion of peatland feedbacks as related to resiliency and vulnerability to wildland fire

The processes and feedback mechanisms related to peatland fires and climatic change are complex and uncertain; however, the recent proliferation of research on these important topics helps to clarify our understanding of peatland-fire interactions. Here, we provide a summary of key characteristics and feedback mechanisms that affect the resiliency of peatlands to wildland fire (Fig. 9a), as well as a comprehensive conceptual of all interactions discussed throughout the review (Fig. 9b).

The most resilient peatlands are hydrologically well-connected to both the larger peatland complex and groundwater system, resulting in a moderated water table. They have not been anthropogenically altered (compacted, drained, or harvested), and therefore maintain stable soil moisture and low bulk density. They are not fragmented and have low margin:middle area ratios (e.g. Lukenbach et al., 2015). These peatlands have a thick surface layer of mosses, keeping surface bulk density low and moisture retention high, and a high proportion of hummock-dominating species, such as *Sphagnum fuscum*, which holds moisture even during drought, lowers surface temperatures, and limits encroachment of upland species (e.g. Kettridge et al., 2012; Bu et al., 2013). Highly resilient peatlands may have black spruce as a dominant tree species, as low stomatal conductance will help maintain peat moisture (Dang et al., 1997). Following fire, *Sphagnum* mosses prevalent in resilient peatlands will help mitigate the lowering of the water table and reduction of soil moisture.

The most vulnerable peatlands have been fragmented or disturbed and are more hydrologically isolated. Thus, their water tables are highly temporally variable, resulting in increased bulk density and conditions that support shrubification, particularly in the margins(e.g. Lukenbach et al., 2015; Hokanson et al., 2016). Aspens may dominate the margins, encroaching into the peatlands and promoting a transition to an upland ecosystem (e.g. Lukenbach et al., 2017; Depante et al., 2019). Fragmentation results in a high margin:middle area ratio, which increases the rate of shrubification, fuels for fire, and burn severity. These peatlands may have burned severely in the past, resulting in a loss of hummocks and hummock-forming moss species. A transition from *S. fuscum* and other hummock-forming species to feathermoss and other hollow species due to either previous wildland fire or drying and afforestation may increase the risk of subsequent high severity fires (e.g. Bisbee et al., 2001; Breeuwer et al., 2009; Wilkinson et al., 2018a). Previous fires may have been severe, increasing bulk density, resulting in unstable water tables and increased risk of severe burns (e.g. Thompson and Waddington, 2013a; Waddington et al., 2015; Granath et al., 2016; Fig. 9a).

6. Recommendations

Modelling and mapping peatlands based on the key attributes described in the previous section may allow for a better understanding of future wildland fire scenarios within the boreal and improved estimations of boreal peatlands' contribution to the global C-climate cycle. We also suggest that research focuses on improving estimates of wildland fire C emissions of the boreal region. By more accurately quantifying C emissions, the contribution of wildland fire to the global C-climate cycle can be better understood. We propose that better integration of process understanding and scaling of changes in peatlands through a combination of remotely sensed data and hydro-ecological and wildland fire models is necessary. In utilizing these multi-disciplinary approaches, we can better understand the coupling of boreal peatland-fire interactions and boreal peatlands' contribution to global climate change and climate forcing mechanisms.

7. Conclusion

In this review, we have synthesized knowledge of peatland-wildland fire feedback mechanisms and how they interact with the C-climate feedback cycle (Fig. 9b). While this is by no means an exhaustive list, this review provides an overview of the dominant processes and feedbacks and explanations as to their relative connections. It is clear that positive and negative feedbacks are numerous and complex and may act against one another, entirely or partially mitigating the effect of another, or may compound the effects, resulting in enhanced fire risk and C-climate forcing. The extent of the effects of these feedbacks also varies across peatlands, regions, and through time. However, we can conclude that over larger areas, climatic warming will result in greater fire frequency, extent, and severity in the boreal region, which will increase peatland C losses due to fire, as well as alter peatland condition and the ecosystem services that northern communities rely on. Initially, increased C emissions from wildland fire may be offset by increased NPP; however, this is temporary and may eventually result in further increases of C loss through enhanced decomposition and ecosystem respiration. Climatic warming and anthropogenic disturbance may also reduce peatland resiliency to wildland fire through reduced hydrological connectivity. While there are undoubtedly negative feedback mechanisms initiated following peatland fires, the dominant feedbacks are predominantly positive (Figs. 1–8). It is clear that increases in wildland fire activity in boreal peatlands will result in greater C losses to the

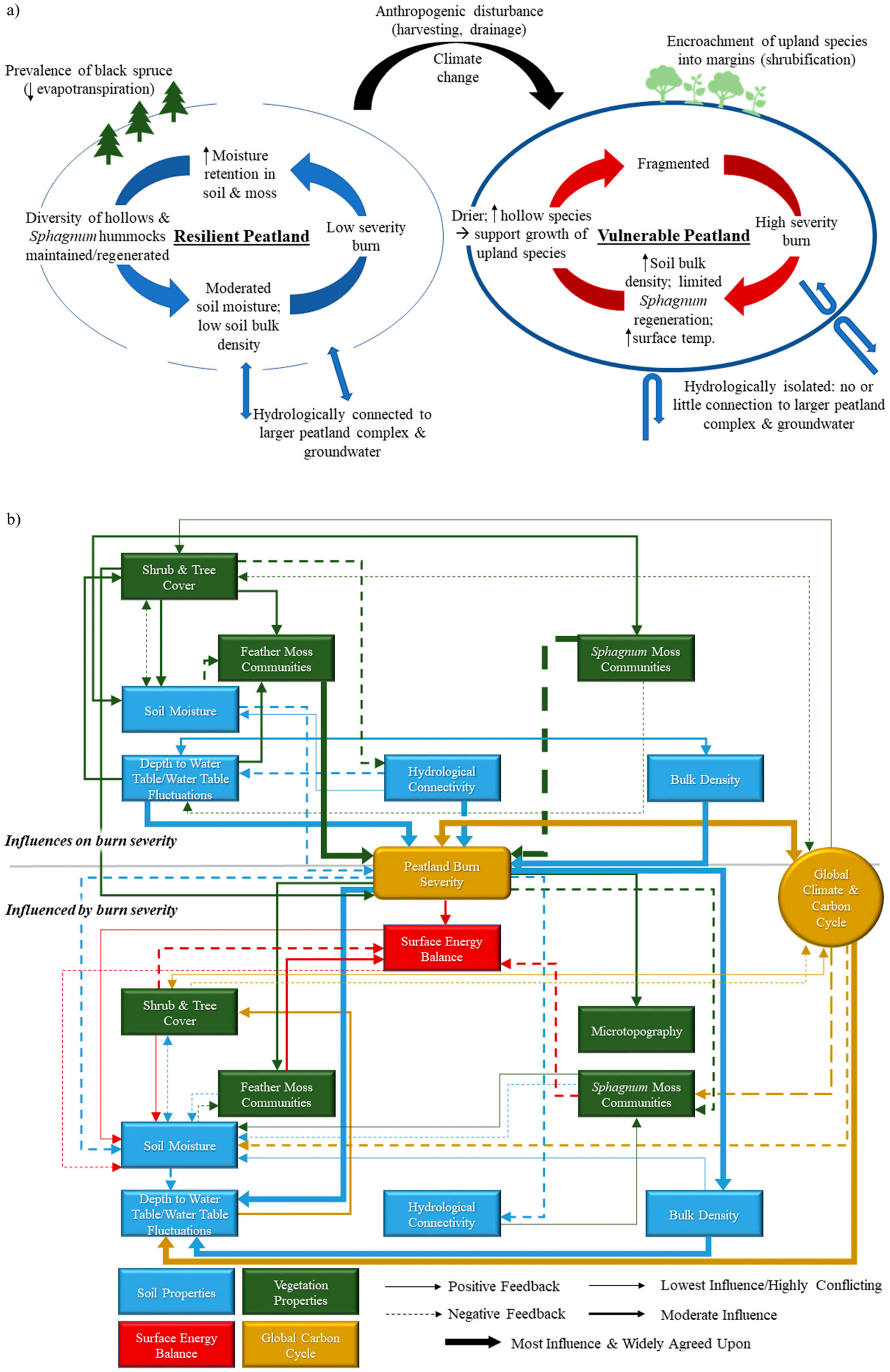

Fig. 9. Conceptual models of a) feedbacks within resilient vs. sensitive peatlands; and b) cumulative positive and negative feedback mechanisms related to peatland-fire interactions and effects on the global C-climate cycle.

atmosphere, enhancing climate warming and resulting in a positive feedback mechanism.

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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