


RESEARCH ARTICLE

The role of hummocks in re-establishing black spruce forest following permafrost thaw

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Funding information

Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant; NSERC Undergraduate Student Research Award; ArcticNet

Abstract

Northwestern Canada's discontinuous permafrost landscape is transitioning rapidly due to permafrost thaw, with the conversion of elevated, forested peat plateaus to low-lying, treeless wetlands. Increasing hydrological connectivity leads to partial drainage of previously-isolated bogs, which have been observed to subsequently develop hummock microtopography. However, the role of microtopographic features in the future trajectory of the transitioning landscape is unclear, including their potential controls on tree re-establishment. In order to understand the role of hummocks in landscape change, research was conducted at the Scotty Creek Research Station, Northwest Territories, to measure hummock and black spruce tree physical characteristics, and assess tree and hummock spatial coverage in peat plateaus, collapse scar bogs and the advanced transitional feature known as treed bogs. Canopy coverage in all landforms and wetland hummock areal coverage was assessed using a LiDAR (Light Detection and Ranging) canopy gap fraction model and multispectral imagery. Hummocks, which are not underlain by permafrost but contain seasonal ice, support the establishment of black spruce trees due to favourable soil moisture conditions. Hummock flank moisture in treed bogs is intermediate between those of dry peat plateaus and inundated collapse scar bogs. Black spruce trees on peat plateaus and in treed bogs are significantly taller and of greater circumference than those in collapse scar bogs. The spatial distribution of hummocks and canopy coverage of black spruce trees in treed bogs collectively suggest that these features may play an important role in the advanced stages of permafrost thaw-driven transition of the discontinuous permafrost landscape.

KEYWORDS

black spruce, hummock microtopography, landscape change, transitioning wetlands

1 | INTRODUCTION

The mosaicked landscape of northwestern Canada's discontinuous permafrost zone is undergoing a rapid transition as a result of climate change-induced permafrost thaw (Jorgenson & Osterkamp, 2005; Lara et al., 2016; Quinton et al., 2019). This landscape is comprised of peat plateaus, underlain by ice-rich permafrost, interspersed with

permafrost-free wetlands including channel fens and collapse scar bogs (Chasmer, Hopkinson, Quinton, Veness, & Baltzer, 2014; Hayashi, Quinton, Pietroniro, & Gibson, 2004; Quinton, Hayashi, & Chasmer, 2011). Forested peat plateaus are elevated topographically above the sparsely treed wetlands by approximately 0.5 to 1.5 m (Wright, Hayashi, & Quinton, 2009). Given the hydraulic gradient from the peat plateaus towards the surrounding wetlands, plateaus shed

water relatively quickly to the low-lying bogs and fens (Wright et al., 2009), which store (bogs) or convey (channel fens) water across the landscape (Hayashi et al., 2004). As warming air temperatures thaw and degrade the underlying permafrost, plateaus subside and become inundated by adjacent wetlands (Quinton et al., 2011), resulting in alterations to the hydrology (Connon, Quinton, Craig, & Hayashi, 2014; Haynes, Connon, & Quinton, 2018) and ecology (Jorgenson, Racine, Walters, & Osterkamp, 2001) of the landscape.

Expansion of wetland area at the expense of permafrost terrain influences the surface and subsurface routing of water through the landscape (Connon et al., 2014). Long-term mean annual flow records monitored throughout the Northwest Territories have demonstrated a significant increase in streamflow, particularly in the southern portions of the region (St. Jacques & Sauchyn, 2009). Such flow increases cannot be attributed to increased precipitation, which has remained virtually unchanged over the same period (Connon et al., 2014; Haynes et al., 2018). As the permafrost that impounded water and prevented its drainage thaws, basin runoff increases due to increased hydrological connectivity throughout the basin (Connon et al., 2014; Haynes et al., 2018). Specifically, as bogs that were hydrologically isolated develop a connection to the basin drainage network through 'bog capture' (Connon et al., 2014), they release a portion of their stored water; a process that continues until the bog water table is lowered to a new equilibrium elevation (Haynes et al., 2018). As such, this loss of storage and concomitant contribution to basin runoff is transient in nature. However, since such wetlands remain hydrologically connected following their transient contribution, they continue to contribute to basin discharge through in situ runoff generation and conveyance of runoff from upstream sources (Haynes et al., 2018).

Permafrost loss also influences the form and community composition of ecosystems, including the establishment, growth and survival of vegetation (Jorgenson et al., 2001). The rapid transition from relatively dry peat plateaus to inundated wetlands results in the loss of black spruce canopy due to the intolerance of black spruce to flooding (Islam & Macdonald, 2004). However, field observations suggest that the subsequent partial, transient drainage of such wetlands enables the re-establishment of a black spruce forest, although without permafrost (Carpino, Berg, Quinton, & Adams, 2018; Chasmer &

Hopkinson, 2017; Disher, 2020). Such actively draining wetlands often referred to as 'treed bogs' (National Wetlands Working Group (NWWG), 1988; Figure 1b,c) are an emerging feature as the discontinuous permafrost landscape changes with thawing and have been overlooked by studies that classify landform units according to their hydrological function and black spruce cover; commonly mistaken for peat plateaus during remote sensing analyses. Considering the accelerated permafrost thaw observed over recent decades and that treed bogs form following substantial change to ground that recently contained permafrost, a wide coverage of treed bogs may indicate a rapidly transitioning landscape.

Treed bogs have hydrological, ecological and geophysical characteristics distinct from peat plateaus, collapse scar bogs and channel fens (NWWG, 1988; Figure 1b,c), are permafrost-free and occupy a lower elevation than peat plateaus. The soil moisture content and hydrological response of treed bogs are intermediate between that of plateaus and collapse scar bogs (Disher, 2020). Treed bogs have been posited as an advanced stage of climate warming-induced landform change, given the re-establishment of black spruce in these features (Disher, 2020; Figure 1b,c). Such re-establishment following permafrost thaw-induced loss has been reported in localized areas of discontinuous permafrost (Chasmer & Hopkinson, 2017) as well as at the broader scale in the southern region of discontinuous permafrost (Carpino et al., 2018). The prevalence of these forested, permafrost-free wetlands in that region lends support for these features being at a more advanced phase of wetland transition, considering a latitudinal space-for-time proxy. Despite the widespread occurrence of treed bogs throughout the discontinuous permafrost zone, encompassing both the extensive-discontinuous and sporadic-discontinuous regions, the mechanisms driving their development remain poorly understood.

In the discontinuous permafrost zone, newly-formed collapse scar bogs isolated from the drainage network due to surrounding permafrost barriers, and which remain saturated throughout the year, exhibit very little variation in surface microtopography (Figure 1a). In contrast, field observations suggest that partial drainage of wetlands co-occurs with an increase in microtopographic variation, mainly resulting from the development of hummocks (Haynes et al., 2018; Quinton et al., 2019). The rate of peat formation in the different microforms in



FIGURE 1 (a) Collapse scar bog, recently formed as a result of permafrost loss, with minimal microtopographic variation and dominance of lawn and aquatic *Sphagnum* species, (b) hummock microtopography in a developing treed bog, with *Picea mariana* seedlings located on topographically-elevated hummocks and (c) juvenile treed bog, with hummock microtopography colonized by *Sphagnum* species that tolerate drier conditions and the re-establishment of *Picea mariana*

boreal peatlands, including wet depressions such as pools and dry features such as hummocks, is largely controlled by the local water table depth (Belyea & Clymo, 2001; Waddington et al., 2015). Hummocks are mounds of organic soil resulting from the production of fast-growing *Sphagnum* species above the water table (Zoltai, 1993), and the subsequent decomposition and compression of organic matter derived from the mosses and vascular plants as accumulated peat (Clymo, 1984). As the hummock form grows vertically, the increasing separation of the hummock surface from the water table enables the development of an unsaturated layer (Diamond, McLaughlin, Slesak, & Stovall, 2019; Strack, Waddington, Rochefort, & Tuittila, 2006). The relatively dry surfaces of hummocks as compared to the low-lying inter-hummock areas facilitate black spruce seedling establishment and growth (Camill, 1999; Figure 1b), with fine roots concentrated in hummocks (Iversen et al., 2018). Consequently, although tree and shrub presence and growth vary spatially throughout bogs, the highest density of biomass in boreal peatlands occurs in association with hummocks (Iversen et al., 2018). However, the mechanisms governing the development of hummocks with a changing permafrost

landscape and the potential influences on vegetation establishment throughout the trajectory of change are not well understood in the discontinuous permafrost zone.

The overall objective of this study is to improve the understanding of the processes controlling the re-establishment of black spruce forest following permafrost thaw in the discontinuous permafrost landscape. This will be accomplished through the following specific objectives: (a) evaluate the physical and ecohydrological characteristics of hummocks in the rapidly changing landform types of the region, including peat plateaus, permafrost-free collapse scar bogs with sparse tree cover and permafrost-free treed bogs; (b) define and compare the tree canopy coverage and the proportion of area occupied by hummocks using remote sensing techniques to assess the prominence of these microforms in the transitioning wetlands of this landscape; (c) refine the classification of landform types in this environment in order to assess the proportion of the transitioning landscape that is occupied by treed bogs and is therefore posited to be at an advanced stage of thaw-induced change; and (d) present an ecohydrological conceptual model that defines the role of and mechanistic

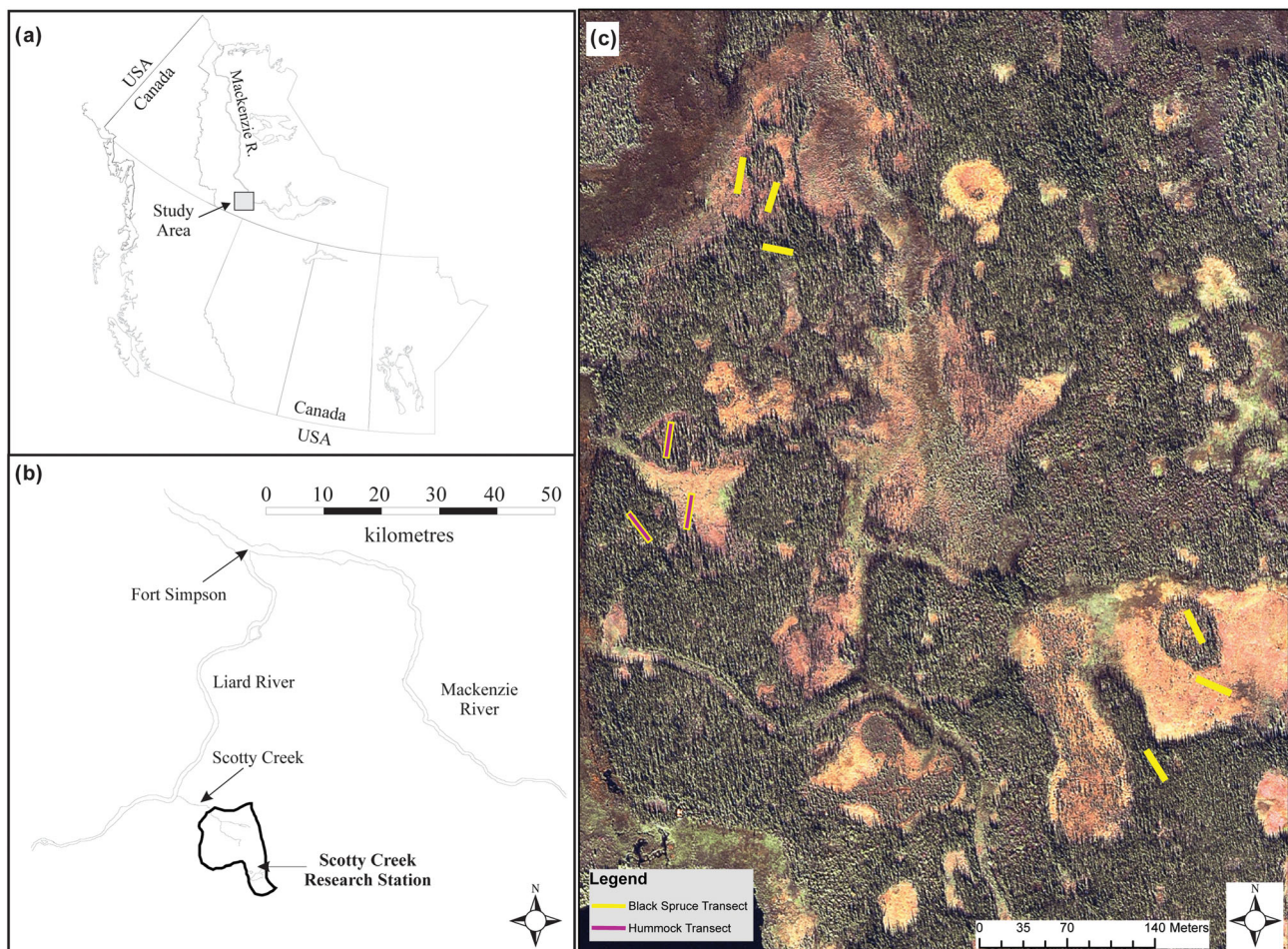


FIGURE 2 (a) Location of study area in northwestern Canada, (b) location of the Scotty Creek Research Station in the lower Liard River valley, 50 km south of Fort Simpson, NWT, and (c) nine transects (each 30 m in length) delineated in the headwaters region of the Scotty Creek watershed along which black spruce (yellow lines, $N = 9$) and hummock (purple, $N = 3$) characteristics were measured. Each of the three selected locations comprised a peat plateau, treed bog and collapse scar bog

understanding of wetland transition in the process of forest re-establishment.

2 | STUDY SITE

This research was conducted at the Scotty Creek Research Station (61.44°N, 121.25°W), located approximately 50 km south of Fort Simpson, Northwest Territories (Figure 2a,b). This site is located within the sporadic-discontinuous permafrost zone. The portion of the Scotty Creek watershed gauged by the Water Survey of Canada covers approximately 152 km² (Quinton & Baltzer, 2013; Quinton, Hayashi, & Pietroniro, 2003) comprised heterogeneous upland moraines (48%), raised permafrost plateaus (20%), ombrotrophic bogs (19%), channel fens (12%) and lakes (2%; Chasmer et al., 2014). Given the relatively warm temperature of permafrost (near 0°C) in this area (Jorgenson et al., 2001), the landscape is vulnerable to permafrost thaw-induced change (Quinton et al., 2011). The elevated peat plateaus underlain by permafrost are forested with a canopy of black spruce (*Picea mariana*) trees with an understory of ericaceous shrubs (e.g., *Rhododendron groenlandicum*), lichens (*Cladonia* spp.) and mosses (*Sphagnum* spp.). Channel fens are dominated by floating vegetative mats of predominantly sedges (*Carex* and *Eriophorum*) with tamarack (*Larix laricina*) and birch (*Betula glandulosa*) trees scattered throughout the fens (Garon-Labrecque, Léveillé-Bourret, Higgins, & Sonnentag, 2015). Bogs in this basin are vegetated with ericaceous shrubs including leatherleaf (*Chamaedaphne calyculata*), bog rosemary (*Andromeda polifolia*) and small cranberry (*Vaccinium oxycoccos*; Garon-Labrecque et al., 2015). The dominant bryophyte species in the bogs include *Sphagnum balticum* and *S. magellanicum* (Garon-Labrecque et al., 2015) as well as *S. riparium* particularly in the wettest sites including recent permafrost thaw-induced collapse scar features (Gibson et al., 2018; Pelletier et al., 2017). Peat deposits in the Scotty Creek watershed range from 2 to 8 m in depth (McClymont, Hayashi, Bentley, & Christensen, 2013).

3 | METHODS

3.1 | Hummock and black spruce characteristics

The focus area for this study was the headwaters of the Scotty Creek basin, characterized predominantly by peatland landform types including permafrost plateaus, channel fens and bogs, including both those connected to and those isolated from the drainage network. Three sites were selected over a 0.6-km² area of the basin headwaters, each of which comprised a peat plateau, a collapse scar bog and a treed bog. The treed wetland sites were selected based on an initial field survey conducted in conjunction with Disher (2020) that identified these treed, low elevation features as distinct from peat plateaus and collapse scar wetlands. A subsequent preliminary supervised landform classification identified further treed wetlands within proximity to the first site. The three monitored sites were ultimately selected based on

the presence of an adjacent peat plateau, treed wetland and collapse scar wetland to facilitate the direct comparison of these landforms while limiting spatial variability. In each of the three landform types in each of the three sites, a 2 m by 30 m belt transect was established, with a total of nine delineated transects (Figure 2c). Each transect was comprised of a linear series of points spaced at 5-m intervals. The transects across plateaus were set back at least 5 m from the plateau edge to avoid the incorporation of dying black spruce trees along the transitioning plateau perimeters into this analysis, as suggested by Higgins and Garon-Labrecque (2018). Ten living black spruce trees dispersed evenly along each belt transect were selected for measurements of tree height and circumference at the root-crown interface (given the small nature of the trees in this environment). For trees that were in excess of 1 m tall, height was measured using a clinometer. Tree measurements were collected in May to June 2018.

In addition to black spruce tree measurements, hummocks were randomly selected for intensive measurements along the belt transects in each of the three landform types at one site (Figure 2c). Hummock measurements were taken in August 2018. Five hummocks with trees actively growing on the hummock surface (one or multiple trees) and five hummocks without trees were selected for characterization along each transect in each of the plateau, treed bog and collapse scar bog at one site. The perimeter, height and length along two perpendicularly bisected axes were measured for each of the 30 monitored hummocks. A frost probe was used to assess the presence of seasonal ice in each hummock. Soil moisture was measured on each hummock using a portable HydroSense II soil water sensor (with CS658 20 cm probe; Campbell Scientific). Soil moisture measurements for each hummock were collected both at the surface ($n = 4$ per hummock) as well as around the hummock flank ($n = 4$). As the Hydrosense II soil water sensor is calibrated for determining volumetric water content (VWC) in mineral soils, measurements of soil water collected in period were converted to VWC using the organic soil calibration algorithms developed for the NASA Arctic Boreal Vulnerability Experiment (ABOVE). These calibration equations were determined for a range of organic soils including those from boreal bogs and fens in the Northwest Territories (similar to the approach of Bourgeau-Chavez, Garwood, Riordan, Koziol, & Slawski, 2010). To convert the hummock soil moisture measurements to VWC, the calibration coefficients for a boreal bog were applied.

3.2 | Landform classification

To determine the prominence and extent of the landforms characteristic of the discontinuous permafrost landscape (collapse scar bog, peat plateau, channel fen, mineral upland) as well as the newly-identified treed bog landform within an approximately 17 km² area of the peatland-dominated headwaters portion of the Scotty Creek basin, a supervised image classification using a support vector machine (SVM) algorithm was utilized. Using a fusion approach to ensure the differentiation between forested peat plateaus and treed bogs both with black spruce canopies, the supervised classification

was completed using WorldView-3 8-band multispectral imagery and an object-based analysis of Light Detection and Ranging (LiDAR) data and its subsequent derived products including a digital elevation model (DEM), canopy height model (CHM) and canopy gap fraction model. The WorldView-3 imagery was collected in 2018 at a resolution of 2 m. The LiDAR data used in this classification were collected in 2010 for the Scotty Creek basin, with a resolution of 1 m (see Chasmer, Quinton, Hopkinson, Petrone, & Whittington, 2011, for processing details).

The full classification approach and assessment of accuracy are presented and explained in detail in Disher (2020). Briefly, given that it is difficult to discern channel fens and treed bogs from other landform types based solely upon canopy characteristics, the classification of these features relied upon both spectral and topographic properties. The classification of the upland, although minimal in the headwaters portion of the Scotty Creek basin, was conducted using canopy characteristics (i.e., CHM and canopy gap fraction products).

To assess the accuracy of the classification, training sites were selected for each of the landform types included in the analysis. As these validation sites were selected from aerial imagery, 25 sites were chosen for the peat plateau, channel fen and collapse scar bog landforms given the ease with which these classes can be visually determined. For the treed bog class, only 10 training sites were used in the accuracy analysis to ensure that only sites for which field validation had been conducted were included. Given the unbalanced number of training sites for each of the landform types being classified, the SVM approach was chosen as the optimal classification technique. This method is also less susceptible to correlated bands (Foody & Mathur, 2004).

In an effort to reduce potential discrepancies within the classification, open water present within the area of interest was masked out of the final imagery. To minimize noise and 'speckle' of the classified spectral product, a low pass filter (3×3) and boundary clean tool were utilized. The topographic position index (TPI) was used to de-trend the DEM and identify topographically-elevated features. This index uses neighbourhood-based focal statistics to assess the mean elevation within a specified area. A circular neighbourhood (with a diameter of 125 m) was deemed most appropriate to discern high and low elevation features. For each landform type, thresholds for the TPI and CHM were determined (see Disher, 2020). The overall accuracy of the classification as well as misclassification rates were assessed using a confusion matrix on the final classified raster for each landform type (see Disher, 2020).

3.3 | Tree canopy gap fraction

In order to determine potential variation in canopy density across landforms, an analysis of a canopy gap fraction model was completed. Canopy gap fraction is defined as the probability of a ray of light passing through the canopy without encountering any plant element (Danson, Hetherington, Morsdorf, Koetz, & Allgöwer, 2007). The gap fraction model for Scotty Creek was created using a combination of in

situ data collection and LiDAR data collected over the basin (see Chasmer et al., 2011, for collection and processing details). To determine the mean canopy gap fraction for each landform within the study area, the classification described above was overlain with the gap fraction product using a zonal statistics tool (Esri, Redlands, California), and the mean gap fraction was determined for the total area of each classified landform.

3.4 | Hummock spatial coverage

Hummocks can be identified through high-resolution imagery as a result of the spectral differences (most notably colour) that exist between *Sphagnum* species (Gibson et al., 2018). Specifically, hummock species such as *S. fuscum* can be easily identified by their deeper colouring, which appears in sharp contrast to surrounding aquatic and lawn species. While their visual appearance allows for imagery to be used, hummocks can also be identified in high-resolution digital terrain models (DTMs) such as those created using a Remotely Piloted Aircraft System (RPAS). Given that hummocks are well suited to geomatics analyses these methods were used to estimate the current distribution of hummocks within the 0.6 km² region where the targeted fieldwork was completed. Multispectral 8-band (2 m resolution) WorldView-3 imagery collected in 2018 was used alongside a DTM (0.05 m resolution), which was created using a RPAS. In this study, an eBee X equipped with a senseFly SODA 3D mapping camera was used, and all image processing was completed in Pix4DMapper. The RPAS was flown over eight ground control points (GCPs) and the consistency between the field geolocation (i.e., true GCP location) and mapped geolocation (i.e., GCP location determined in Pix4DMapper) was calculated. The root mean square georeferencing error across the 8 GCPs was 0.04 m. The accuracy of the DTM product was also determined in Pix4DMapper where an average ground sampling distance (GSD) of 0.02 m was recorded for the project, which corresponded to a horizontal (x, y coordinates) accuracy of 0.02–0.04 m, and a vertical (z coordinate) accuracy of 0.02–0.06 m. The DTM product was then spatially aggregated from the original 0.05-m resolution to match the 2-m resolution of the WorldView-3 imagery.

An unsupervised Principle Component Analysis (PCA) classification was completed on the WorldView-3 imagery using the ArcGIS suite of products. Five components were identified in the classification, one of which represented the targeted hummock-dominated terrain. This product was then reclassified into three classes to estimate the bog area with and without hummocks and also classified the remaining landforms (e.g., peat plateau, channel fen and mineral upland) as 'other'. The 'other' category was isolated and removed from the classified product leaving a binary raster (i.e., with or without hummock terrain) that overlaid and corresponded with the boundaries identified in the landform classification of collapse scar and treed bogs. The DTM created for this study was masked to those same boundaries and the Slope Tool in ArcGIS was used to reveal fine scale changes across the surface of bog landforms. As collapse scar and

treed bogs were the only landforms represented within the new DTM boundaries, moderate slopes were most likely indicative of hummock terrain. As such, areas with a slope $<10^\circ$ were considered unlikely to be hummock terrain and were conditionally removed. Similarly, any areas with extreme slopes $>70^\circ$ were identified as trees rather than hummocks. The presence of these trees was confirmed using the optical eBee camera (~ 0.02 m resolution). The hummocks present in the unsupervised classification and the hummocks identified using the DTM were compared ($>90\%$ agreement) and combined to create the final estimate of hummock distribution.

3.5 | Statistical analyses

All statistical analyses were performed using R statistical software (R Core Team, 2017) with $\alpha = 0.05$. All data were tested for normality (Shapiro–Wilk W test) and heteroscedasticity and were successfully log-transformed to achieve normality when parametric assumptions were not met. Significant differences in hummock physical and hydrological characteristics, including the lengths of two perpendicularly-bisected axes, perimeter and height as well as surface and flank soil moisture, were assessed individually with two-way analyses of variance (ANOVAs) to determine any significant direct and interactive effects of the landform type and tree presence. One-way ANOVAs with post-hoc Tukey tests were subsequently applied to the hummock physical and hydrological characteristics to determine significant differences among the six conditions. To assess potential significant differences in black spruce height and circumference among the three landform types (peat plateau, treed bog and collapse scar bog), one-way ANOVAs with post-hoc Tukey tests were performed.

4 | RESULTS

4.1 | Hummock physical and ecohydrological characteristics

No significant differences in hummock dimensions (length along two perpendicular axes and perimeter) were observed among the three landform types including those hummocks with and without trees present (Figure 3). Specifically along the N–S axis, there were no significant differences ($p = 0.73$) in hummock length among any of the landform types both with and without black spruce tree growth, with no significant influence of landform type ($p = 0.33$), tree presence ($p = 0.62$) or interactive effect of these two factors ($p = 0.88$; Figure 3a). The average N–S axis length of hummocks located in collapse scar wetlands was 2.0 ± 0.5 m for those with trees and 1.9 ± 0.9 m for those without trees. On plateaus, the N–S hummock axis length averaged 1.8 ± 0.5 m for those with trees and 1.8 ± 0.8 m for those without trees. For treed wetlands, hummock N–S axis lengths averaged 1.7 ± 0.5 m for those with trees and 1.4 ± 0.6 m for hummocks without trees. Along the E–W hummock axis, there was

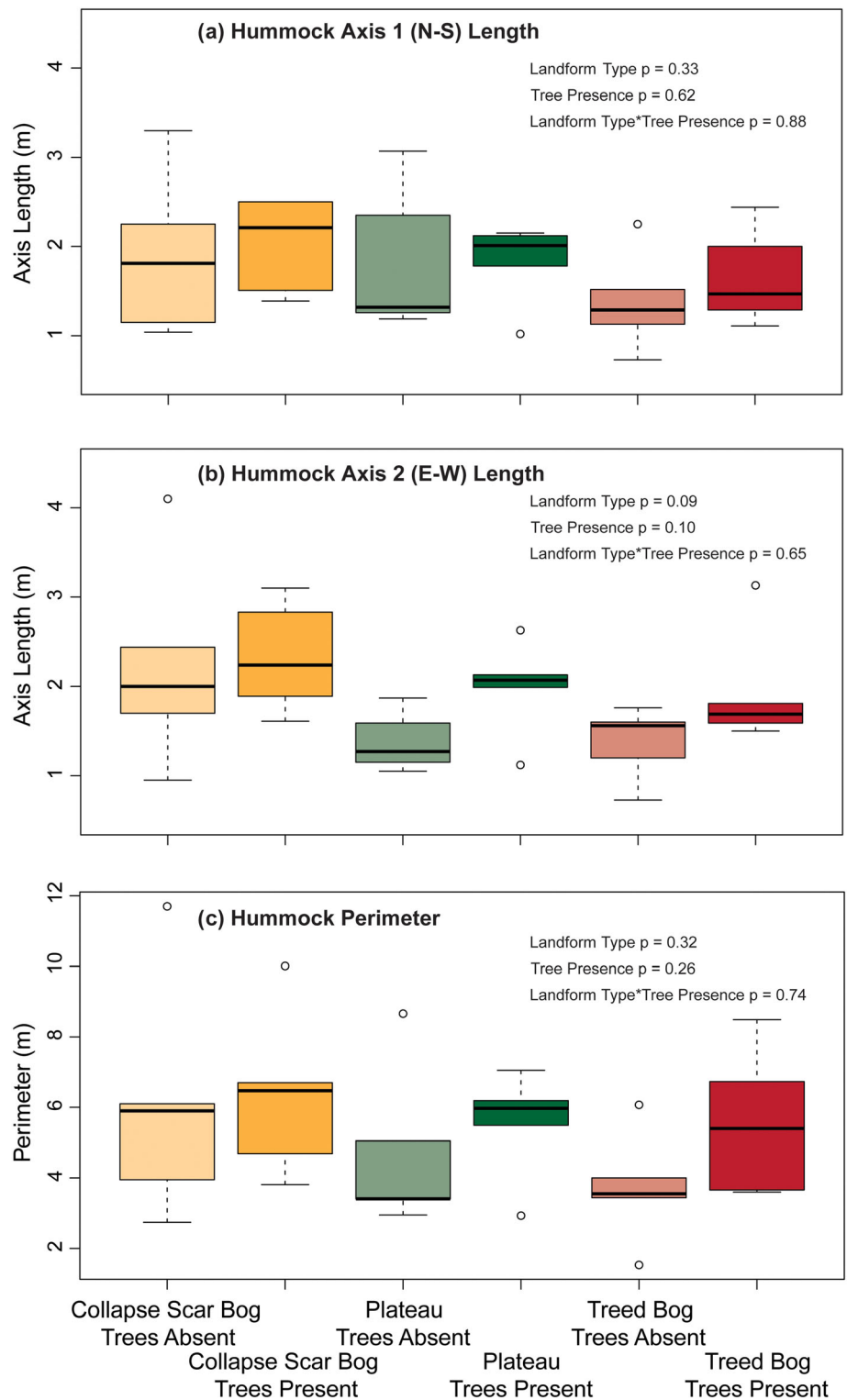
no significant influence of landform type ($p = 0.10$) or tree presence ($p = 0.09$) and no significant interaction of these direct effects ($p = 0.65$; Figure 3b). No significant differences ($p = 0.14$) were observed among the collapse scar wetland (2.3 ± 0.6 m with trees, 2.2 ± 1.2 m without trees), treed wetland (1.9 ± 0.7 m with trees, 1.4 ± 0.4 m without trees) and peat plateau (2.0 ± 0.5 m with trees, 1.4 ± 0.3 m without trees) landform types (Figure 3b). The perimeter of hummocks located in treed wetlands, both with (5.6 ± 2.1 m) and without (3.7 ± 1.6 m) black spruce trees, was not significantly different ($p = 0.52$) from the perimeter of hummocks on peat plateaus (5.5 ± 1.6 m with trees, 4.7 ± 2.4 m without trees) and in collapse scar wetlands (6.3 ± 2.4 m with trees, 6.1 ± 3.4 m without trees; Figure 3c).

There was, however, a significant difference in the height of hummocks upon which trees were located as compared to those without trees present ($p = 0.01$; Figure 4). Hummocks with trees present were observed to be significantly taller than those without trees (Figure 4). This trend was consistent across all three landform types, as there was no significant interaction between landform type and the presence of trees ($p = 0.76$; Figure 4). The disparity in hummock heights of those with trees as compared to those without trees appears most evident in the treed bog (0.50 ± 0.10 m with trees, 0.38 ± 0.13 m without trees) as well as the collapse scar bog (0.47 ± 0.04 m with trees, 0.35 ± 0.10 m without trees), with a less obvious distinction on the peat plateau (0.49 ± 0.12 m with trees, 0.43 ± 0.11 m without trees). There was no significant difference in hummock height among landform types ($p = 0.58$).

Significant influences of both landform type ($p < 0.0001$) and tree presence ($p < 0.0001$) on the surface soil moisture of hummocks were observed, although not in a clear systematic fashion (Figure 5a). Rather, the direction of the individual impacts of landform type and tree presence on surface moisture is dependent upon the interacting factor (interaction $p < 0.001$). Surface soil moisture was highest on hummocks located in the treed bog upon which no trees were present ($VWC = 26.9 \pm 10.7$), significantly higher (all $p < 0.0001$) than the surface soil moisture measured on hummocks both with and without trees present on the plateau ($VWC = 12.5 \pm 3.2$ with trees, 13.5 ± 3.1 without trees) and in the collapse scar bog ($VWC = 11.9 \pm 1.8$ with trees; 17.9 ± 7.2 without trees) as well as those also located in the treed bog with trees present ($VWC = 14.5 \pm 3.4$; Figure 5a). Surface soil moisture was significantly elevated on hummocks in the collapse scar bog from which trees were absent ($VWC = 17.9 \pm 7.2$) as compared to hummocks with trees in both the collapse scar bog ($VWC = 11.9 \pm 1.8$; $p = 0.02$) and peat plateau ($VWC = 12.5 \pm 3.2$; $p = 0.04$; Figure 5a).

Similar to hummock surfaces, soil moisture measured around the flanks of the hummocks was significantly dependent upon landform type ($p < 0.0001$), although the effect of tree presence was marginal ($p = 0.09$; Figure 5b). No interactive effect of landform type and tree presence on flank soil moisture was observed ($p = 0.12$). There were no significant differences (all $p > 0.05$) in flank soil moisture among the collapse scar bog with ($VWC = 43.3 \pm 15.3$) and without ($VWC = 46.6 \pm 11.1$) trees and

FIGURE 3 Hummock length along (a) N-S and (b) E-W axes (Axis 1 and Axis 2, respectively) and (c) hummock perimeter (all measured in metres) in the three landform types (collapse scar bog (yellow), peat plateau (green) and treed bog (red)) including those with ('trees present'; darker colours) and without ('trees absent'; lighter colours) trees growing on each hummock. Two-way ANOVA results are presented in each plot. No statistically significant differences observed among the six groups for any of these measurements. The bottom and top of the boxplots represent the 25th and 75th quantiles, respectively, while the whiskers represent the range of data



the treed bog without trees present on the hummocks ($VWC = 37.2 \pm 14.6$; Figure 5b). Hummocks in the treed bog with black spruce trees ($VWC = 27.2 \pm 8.9$) are intermediate in flank soil moisture between the relatively dry elevated peat plateau ($VWC = 15.5 \pm 4.7$ with trees, 15.0 ± 5.9 without trees) and the low-lying collapse scar bog (Figure 5b).

4.2 | Black spruce canopy—Gap fraction and tree characteristics

The different landform types of the Scotty Creek basin support tree canopies of varying density and therefore canopy gap fraction (Figure 6). Of the landforms undergoing rapid climate-induced

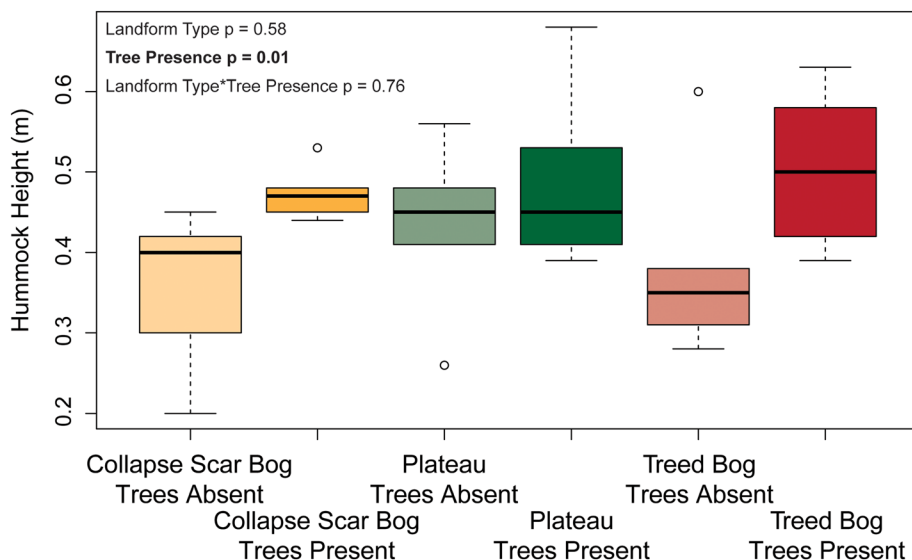


FIGURE 4 Hummock height measured in metres, in the three landform types (collapse scar bog (yellow), peat plateau (green) and treed bog (red)) including those with ('trees present'; darker colours) and without ('trees absent'; lighter colours) trees growing on each hummock. Significant two-way ANOVA results are presented in bold font in the plot. No statistically significant differences observed among the six groups. The bottom and top of the boxplots represent the 25th and 75th quantiles, respectively, while the whiskers represent the range of data

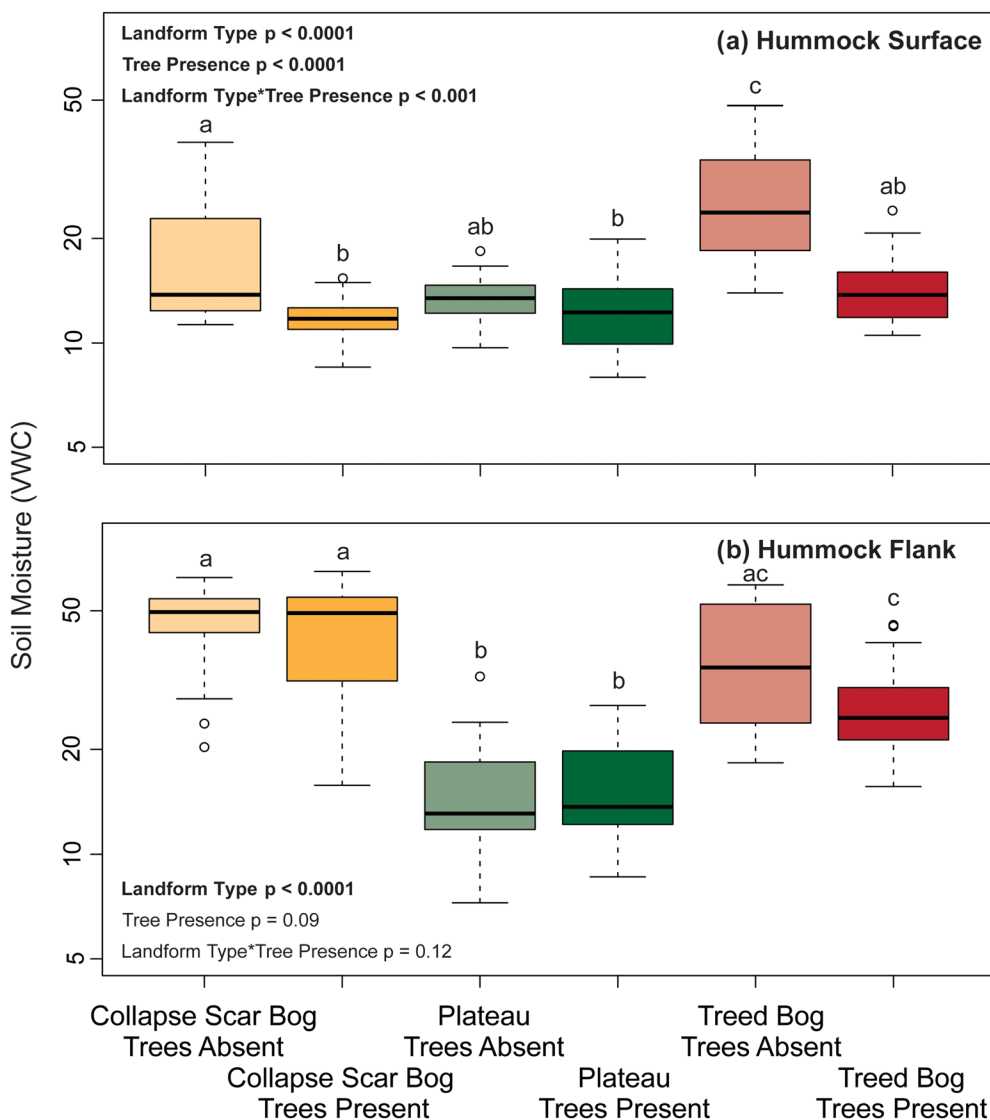


FIGURE 5 Mean soil moisture (expressed as volumetric water content, VWC) measured on the surface (a) and around the flank (b) of hummocks in each of the three landform types (collapse scar bog (yellow), peat plateau (green) and treed bog (red)) including those with ('trees present'; darker colours) and without ('trees absent'; lighter colours) trees growing on each hummock. Data in both plots are presented on a logarithmic scale. Significant two-way ANOVA results are presented in bold font in each plot. Letters denote statistically similar groups. The bottom and top of the boxplots represent the 25th and 75th quantiles, respectively, while the whiskers represent the range of data

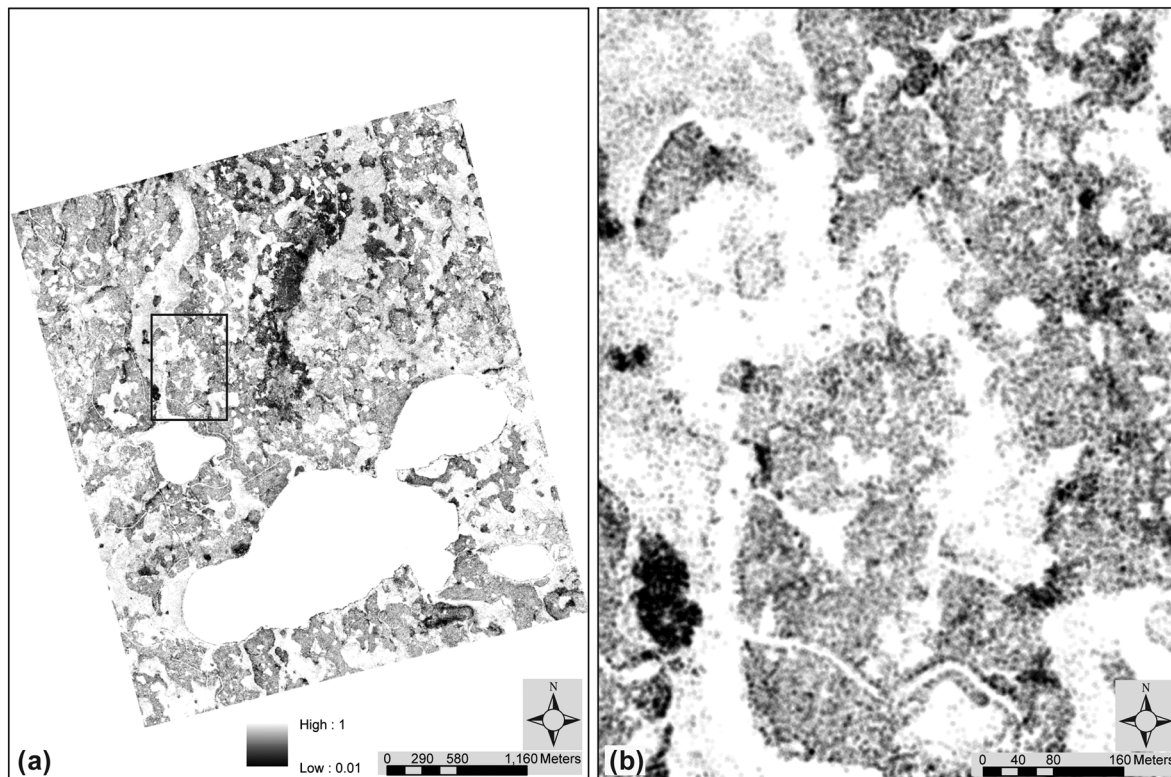


FIGURE 6 (a) Canopy gap fraction over approximately 17 km² of the peatland-dominated headwaters portion of the Scotty Creek basin. (b) Enlarged image of the 0.6 km² area outlined in black in (a), illustrating the canopy coverage of peat plateaus, treed bogs and collapse scar bogs in the area of individual hummock and black spruce field measurements

changes, peat plateaus have the lowest canopy gap fraction (82.2%), and therefore the densest canopy cover, of the landform types (Table 1). The greater canopy cover in treed bogs (with a gap fraction of 93.9%) as compared to collapse scar bogs is evidenced by the higher canopy gap fraction of collapse scar bogs (98.7%). Although peat plateaus and treed bogs both have black spruce canopy cover, there is a difference in the canopy gap fraction that differentiates these two forested landform types (Table 1; Figure 6). Channel fens had a canopy gap fraction (93.2%) similar to that of treed bogs. Although not prominent in the headwaters region of the Scotty Creek basin, mineral uplands had the lowest canopy gap fraction at 60.3% (Table 1).

In addition to the canopy coverage in each of the landform types in the Scotty Creek basin, significant differences in the size of

individual black spruce trees were observed. Black spruce trees located in collapse scar bogs were significantly shorter than those present on peat plateaus and in treed bogs ($p < 0.001$; Figure 7a). The height of black spruce trees in collapse scar bogs averaged 1.6 ± 1.2 m as compared to 3.0 ± 2.6 m in treed bogs and 4.6 ± 3.7 m on peat plateaus. Similarly, the circumference of black spruce trees in collapse scar bogs (0.13 ± 0.08 m) was significantly smaller ($p < 0.001$) than that of trees in treed bogs (0.22 ± 0.09 m) and on peat plateaus (0.26 ± 0.1 m; Figure 7b). The size of black spruce trees in treed bogs appears to be intermediate between those in collapse scar bogs and peat plateaus. However, no significant difference in either tree height ($p = 0.14$) or circumference ($p = 0.99$) was observed between those present on peat plateaus and in treed bog landscape features.

TABLE 1 Percentage of the classified 17 km² of the basin headwaters occupied by each landform type as well as the mean canopy gap fraction for each landform type over the same area

Landform type	Area (%)	Canopy gap fraction (%)
Peat plateau	40	82.2
Channel fen	32	93.2
Treed bog	12	93.9
Collapse scar bog	12	98.7
Upland	3	60.3

4.3 | Landform classification and hummock spatial coverage

In the changing landscape of the Scotty Creek basin, peat plateaus occupy the greatest area of all the landform types; representing 40% of the classified 17 km² area of the basin headwaters (Table 1). Channel fens are present in 32% of this classified area. Mineral uplands represent only 3% of the headwaters portion of the basin. Treed wetlands and collapse scar wetlands each occupy 12% of this landscape (Table 1). Using the drone DTM in concert with the multispectral

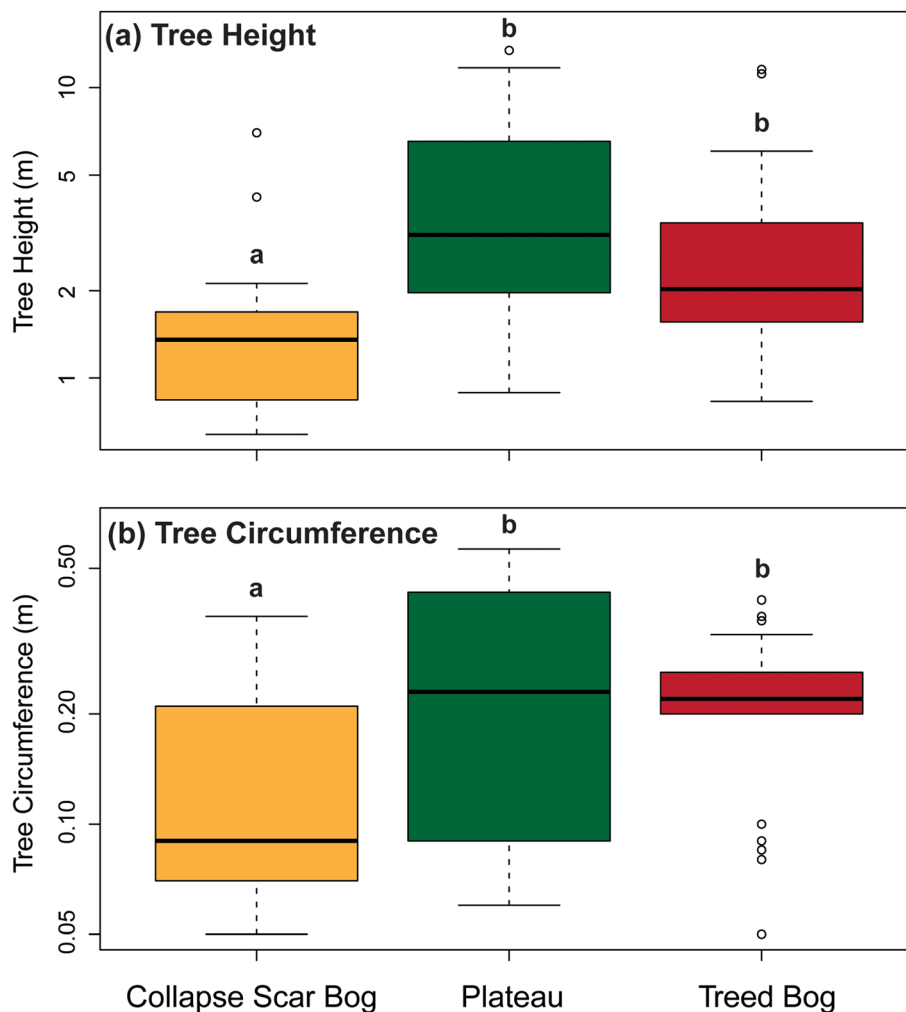


FIGURE 7 Black spruce tree height (a) and circumference (b), both in metres, measured in the collapse scar bog (yellow), peat plateau (green) and treed bog (red) landform types ($N = 30$ trees per landform type). Data in both plots are presented on a logarithmic scale. Letters denote statistically similar groups. The bottom and top of the boxplots represent the 25th and 75th quantiles, respectively, while the whiskers represent the range of data

imagery, hummock area was determined to account for approximately 21% of the total treed bog area and nearly 44% of the area in collapse scar wetlands.

5 | DISCUSSION

5.1 | Hummock physical and ecohydrological characteristics

The likely factor driving afforestation of the black spruce canopy in the rapidly-transitioning discontinuous permafrost zone of northwestern Canada is the formation of hummock microtopography (Camill, 1999). Although present to varying extents in each of the treed bog, peat plateau and collapse scar bog landform types in terms of areal coverage, the physical dimensions (length along two perpendicular axes and perimeter) of hummock microforms (both with and without black spruce tree growth) do not differ among the characteristic discontinuous permafrost landform types. Although these lateral characteristics are not observed to directly contribute to the establishment and growth of black spruce trees on hummocks in this environment, the relationship between hummock height and tree presence may suggest that this process, particularly in the collapse

scar and treed bog landform types, may be influenced by the height of hummocks. The influence of hummock height on black spruce establishment and growth may occur either directly by the stability provided by a greater depth of peat or indirectly via the influence of hummock height on soil moisture.

Hummock soil moisture differed in each of the three landform types and exhibited significant differences for those microforms with and without black spruce trees, suggesting that hummock soil moisture may play a role in controlling the occurrence of black spruce in the transitional wetland features of the discontinuous permafrost landscape. Given the intermediate nature of the flank soil moisture of hummocks in the treed bog and the presence of tree canopy in these landscape features, it can be suggested that hummocks in treed bogs provide an environment appropriate for the establishment of black spruce trees. Saturated soil suppresses respiration of black spruce roots (Islam & Macdonald, 2004), and therefore, conversion of peat plateaus in this region to inundated wetlands through permafrost loss and ground subsidence results in widespread tree mortality along the margins undergoing transition (Jorgenson et al., 2001). The elevated ground surface afforded by hummock microtopography on the order of 0.20 to 0.68 m, and therefore increasingly aerated and drier soils as compared to the surrounding wetland soils, provides a suitable ecohydrological environment for the successful establishment and growth

of black spruce seedlings; eventually promoting broad-scale afforestation in these rapidly-changing environments (Carpino et al., 2018; Chasmer & Hopkinson, 2017).

5.2 | Black spruce canopy across landform types

Despite distinct differences between peat plateaus and treed bogs in terms of permafrost presence, topographic position and hydrological characteristics (Disher, 2020), both of these landform types support black spruce canopies of similar height but of differing tree densities. This is likely due in part to the geophysical characteristics of both peat plateaus and treed bogs that facilitate sufficient soil aeration to prevent anaerobic stress to the roots of vascular vegetation including black spruce, thereby promoting establishment and growth of vegetation in these landforms. Due to the presence of permafrost beneath peat plateaus, these landscape features have limited capacity to store water and an elevational difference of approximately 1 to 2 m as compared to the adjacent wetlands, creating a hydraulic gradient. Therefore, peat plateaus rapidly shed the majority of water received from precipitation, contributing runoff to surrounding wetlands and ultimately to basin runoff (Wright, Quinton, & Hayashi, 2008). The comparatively dry soils of peat plateaus provide a suitable environment to support a canopy of black spruce. The destabilization and subsequent inundation of the soil with permafrost degradation and loss beneath peat plateaus results in black spruce mortality along the margins undergoing active conversion to inundated wetland (Jorgenson et al., 2001) due to inhibited root respiration and the lack of adaptive capacity of black spruce to survive in flooded conditions (Islam & Macdonald, 2004). Consequently, collapse scar bogs formed as a result of permafrost thaw are virtually treeless landforms, as suggested by the high canopy gap fraction percentage in collapse scar bogs (98.7%; Table 1). In contrast, treed bogs support a black spruce canopy, although not as dense as that found on peat plateaus (Figure 6, Table 1) but of similar tree height and circumference (Figure 7). The hummock microtopography present in wetland features appears to support the establishment and growth of black spruce trees in this landscape. Hummocks in boreal peatlands are known to be suitable settings for vascular plants given the distinction in soil moisture on these features from the hydrologically-induced anaerobic conditions of inundated peat soils (Diamond et al., 2019; Strack et al., 2006). Therefore, the network of hummock microforms interspersed with saturated hollows likely provide an appropriate environment for the afforestation of a black spruce canopy, similar to that lost with permafrost thaw-induced plateau subsidence.

5.3 | Prevalence of treed bogs in the changing landscape

The peatland-dominated headwaters of the Scotty Creek basin are undergoing rapid landscape change with the extensive conversion of topographically-elevated, ice-rich permafrost plateaus to low-lying,

inundated wetlands including channel fens and hydrologically-transitioning bogs; those isolated from as well as those that have developed connections to the basin drainage network. Only 3% of the landscape is upland mineral soil-dominated moraine (Table 1); a permafrost-free landform that dominates in the northern portion of the basin nearer the drainage outlet (Chasmer et al., 2014) and remains virtually unchanged as compared to the dynamic landscape transition observed in the southern headwaters. Peat plateaus continue to comprise the largest proportion of the headwaters region of the Scotty Creek basin, with 40% of the landscape classified as forested peatland and elevated above the surrounding low-lying wetlands (Table 1; Figure 8). Although this classification based on the 2018 WorldView-3 imagery is limited to the headwaters region spanning approximately 17 km², the fraction of peat plateau area, and hence the percentage of the terrain underlain by permafrost, has continued to decline as compared to the most recent analysis conducted by Connon et al. (2014), which determined 47.5% plateau area over a representative 6 km² of the basin headwaters in 2010. Channel fens occupy 32% of the basin headwaters (Table 1; Figure 8), which act to convey water from precipitation, primary runoff from plateaus and those bogs advanced in the hydrological transition that have developed connections to the drainage network and direct it to the basin outlet (Connon et al., 2014; Hayashi et al., 2004; Haynes et al., 2018). With considerable permafrost loss, the contributing area of the drainage network has expanded at the expense of peat plateau area.

In addition to the impacts of permafrost loss on the channel fens, the bogs in this landscape are also experiencing rapid change. Approximately 12% of the Scotty Creek basin headwaters area is in the form of collapse scar bogs (Figure 8), with sparse black spruce tree cover. Spatially, collapse scar wetlands are predominately located in zones of recent plateau collapse and inundation (Figure 8), identified from historical aerial photography and remote sensing imagery (Chasmer et al., 2014; Quinton et al., 2011). Newly-formed collapse scar bogs in this basin are typically colonized by *Sphagnum riparium* (Gibson et al., 2018; Pelletier et al., 2017) as well as other bryophyte species including *S. balticum*, *S. fuscum* and *S. magellanicum* to lesser extents (Garon-Labrecque et al., 2015). The spectral characteristics of the bryophyte cover in collapse scar bogs and the virtual lack of black spruce tree cover facilitate the classification of these landforms, aiding the differentiation between collapse scar bogs and other low-lying wetlands including channel fens and treed bogs. Posited to be at an advanced stage along the trajectory of change in this landscape (Carpino et al. under review; Disher, 2020) as has been suggested in boreal wetland regions of Canada (NWWG, 1988), treed bogs occupy a similar proportion of the headwaters area as collapse scar bogs (12%; Table 1). These landforms are characterized by the dominance of *Sphagnum* moss species more tolerant of drier conditions including *S. magellanicum* and *S. fuscum* (Garon-Labrecque et al., 2015); those that typically thrive on hummock microforms in boreal peatlands (Diamond et al., 2019). Spatially, treed bogs appear to be located predominantly along the periphery of wetlands connected to the drainage network and other zones that are relatively dry (including centrally in dome-like bogs) as compared to adjacent collapse scar

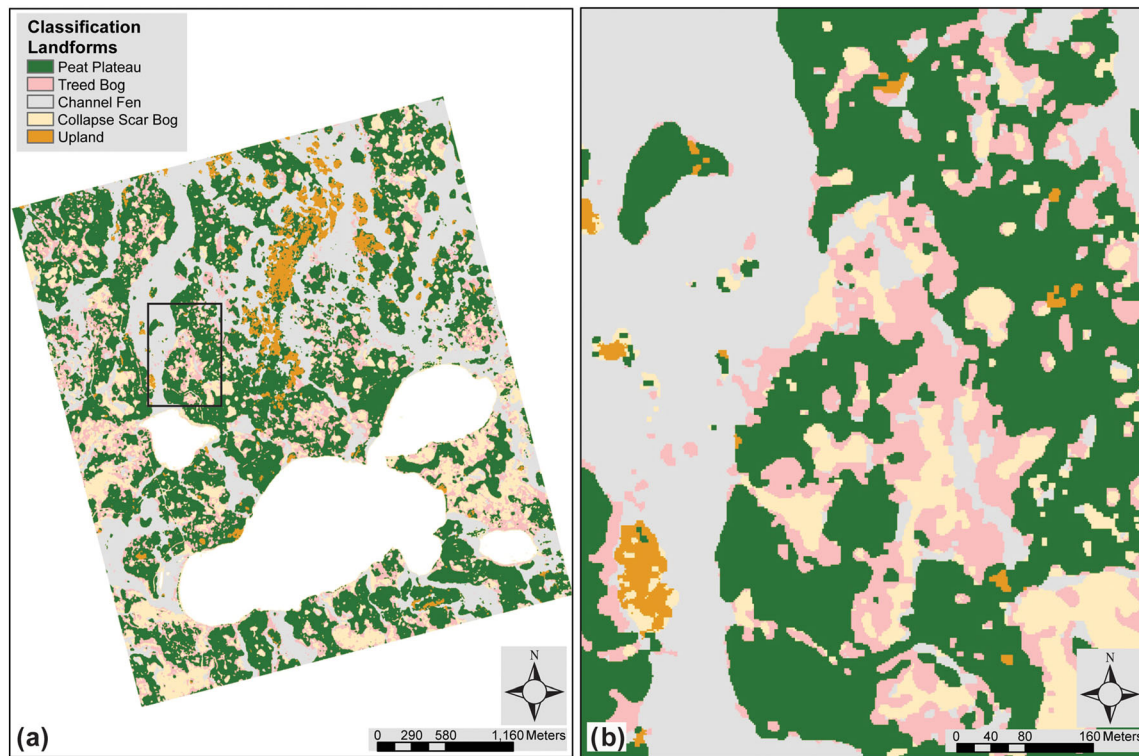


FIGURE 8 (a) Landform classification over approximately 17 km² of the peatland-dominated headwaters portion of the Scotty Creek basin. (b) Enlarged image of the 0.6 km² area of study outlined in black in (a), illustrating the spatial distribution of treed bogs in this landscape

bogs, likely dependent upon drainage patterns (Figure 8b). As bogs develop connections to the drainage network due to the loss of intervening permafrost barriers, these wetlands contribute their stored water to runoff, resulting in the decline in wetland water levels (Haynes et al., 2018). Increasingly dry conditions in previously-isolated wetlands, as stored water is lost to drainage, may promote afforestation in these landforms (Chasmer & Hopkinson, 2017), as observed at the southern boundary of the discontinuous-sporadic permafrost zone (Carpino et al., 2018). The successful establishment and growth of black spruce seedlings is likely supported by the development of hummock microtopography in treed bogs, resulting from rapid growth and accumulation of peat due to the drier conditions.

The treed bog landform has not been previously included in classifications of the Scotty Creek basin (such as Chasmer et al., 2014). Rather, due to the presence of black spruce canopy in these features, area currently attributed to treed bogs was likely included in the classification of peat plateau area. Permafrost in the boreal region is known to be present beneath forested peat plateaus (Vitt, Halsey, & Zoltai, 1994). It is therefore likely that previous values of permafrost areal coverage, which relied purely on assessments of forest cover, have been overestimated due to the inclusion of treed bogs. Classification approaches that merge the utility of spectral differentiation with a LiDAR-derived digital elevation model facilitate the determination of treed bogs in this changing landscape. The differences in the dominant *Sphagnum* moss species present in treed bogs as compared to collapse scar bogs and channel fens result in distinct spectral

characteristics (Gibson et al., 2018). Additionally, although treed bogs have black spruce canopy cover, they are of lower elevation than peat plateaus due to the lack of permafrost underlying these landforms (Disher, 2020). Therefore, topographical and vegetation spectral differences as compared to peat plateaus and collapse scar bogs, respectively, differentiate treed bogs when classifying the mosaic of landforms in this discontinuous permafrost basin. Given that recent research has identified these areas of black spruce afforestation as distinct landforms (Chasmer & Hopkinson, 2017) and determined unique hydrological and geophysical characteristics of treed bogs (Disher, 2020), treed bogs may play an important role in the trajectory and hydrology of this dynamic transitioning landscape.

5.4 | Formation of treed bogs in the transitional discontinuous permafrost landscape

The processes driving peat formation and the development of hummock microtopography include production, decomposition and compression of organic matter from *Sphagnum* mosses and vascular plants in peatlands (Clymo, 1984). Spatial variation in the height of the peatland surface above the water table plays a controlling role in vascular plant and moss production, subsequent litter deposition and decomposition facilitated by increasing aeration and drainage as litter accumulates, and ultimately compression of buried organic matter (Waddington et al., 2015). The net primary production (NPP) of lawns

and small hummock microforms is known to vary over short time-scales largely as a function of surface soil moisture (Belyea & Clymo, 2001; Malmer & Wallén, 1993). In dry periods, the areal coverage of hummocks is known to expand (Belyea & Clymo, 2001). Therefore, as collapse scar bogs become connected to the drainage networks in discontinuous permafrost basins with the loss of intervening barriers, the reduction in stored water and subsequent drying of the surface peat promotes the development of hummock-hollow microtopography (Figure 9). Following prolonged periods of drying, particularly in areas experiencing sustained drainage, the development of treed bog landforms that support a black spruce canopy intermediate in density between that of peat plateaus and collapse scar wetlands may be catalyzed by hummock formation. The patterning of black spruce tree establishment in the transitioning environments of saturated, virtually-treeless collapse scar wetlands as well as treed wetlands further along the trajectory of change appears to be confined predominantly to hummock microforms (Figure 9). In boreal peatlands, the roots of black spruce trees penetrate deeper into the

soil when water tables are low, while in wet environments roots are confined primarily to hummock microforms (Iversen et al., 2018; Liefers & Rothwell, 1987; Waddington et al., 2015).

Recent research has demonstrated notable differences in the hydrology of treed bogs, resulting in characteristics distinct from peat plateaus and collapse scar wetlands (Disher, 2020). Such differences in hydrological characteristics, including soil moisture and stormflow responses, may be important when considering the availability and sustainability of freshwater resources in this rapidly transitioning landscape. The increasing prevalence of hummock microforms in this environment will likely affect the movement of water, as hummocks are known to have a lower hydraulic conductivity than hollows and consequently retard runoff as they act as barriers to flow (Belyea & Clymo, 2001; Foster, King, & Glaser, 1983). The hydrological impacts of hummock formation and potential feedbacks on landscape change, including flowpath tortuosity and water storage dynamics warrant comprehensive examination (Figure 9). The influence of hummock-hollow microtopography on the hydrology of wetlands in this

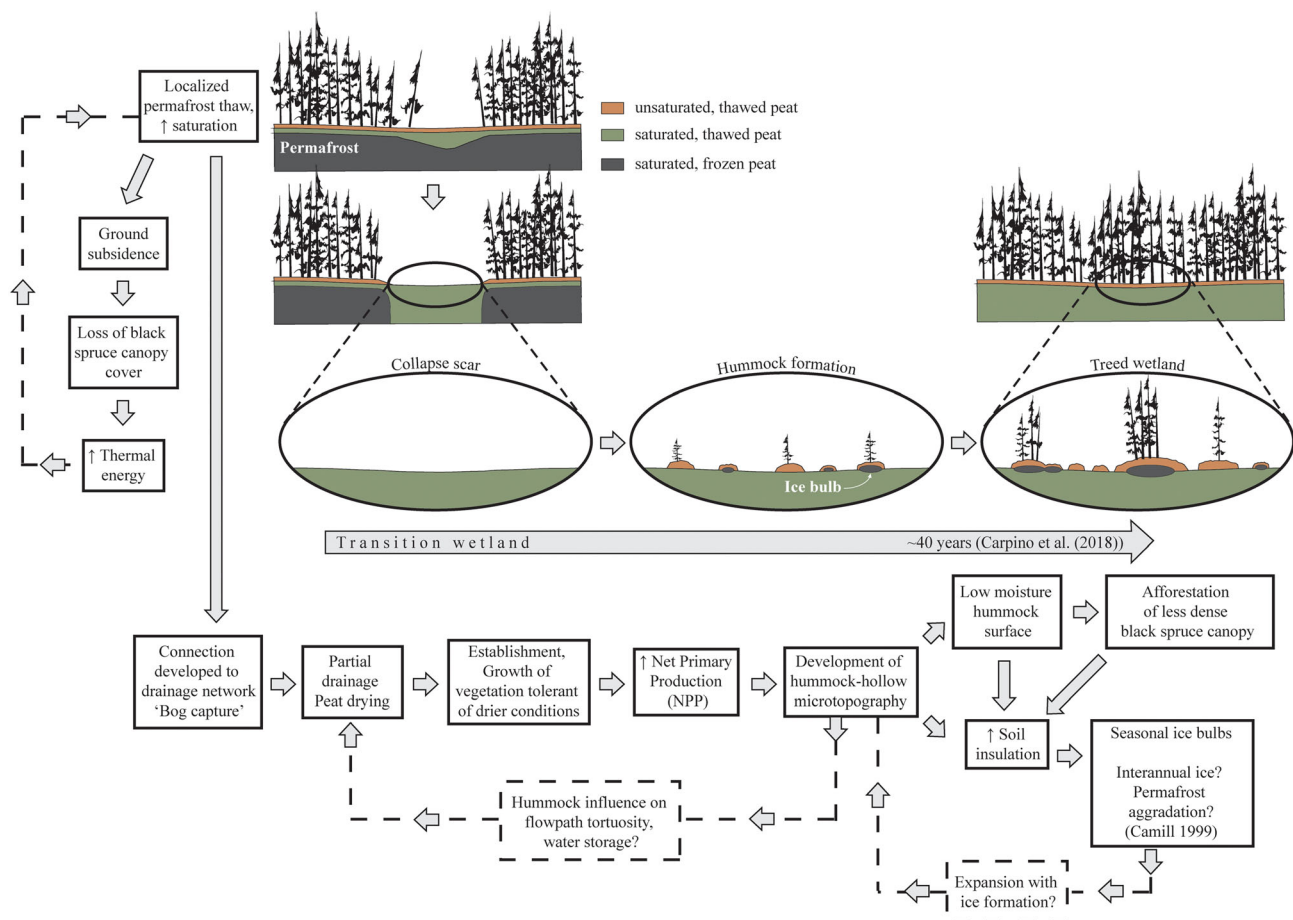


FIGURE 9 The mechanistic trajectory of transitioning wetlands initiated with the formation of collapse scar bogs with the loss of underlying permafrost. Grey arrows represent direct mechanisms, while dashed lines represent potential feedbacks. As collapse scars become connected to the basin drainage network, partial drainage promotes the development of hummock microtopography. The ecohydrological impacts of hummock development may act as a positive feedback, reinforcing the stability and growth of hummock microforms. Thermal insulation by the unsaturated peat of hummocks may support seasonal ice bulbs. The aerobic surfaces of hummocks promote re-establishment of black spruce, catalyzing the formation of treed wetlands, and ultimately the return of low-lying black spruce forests with no underlying permafrost likely due to warming air temperatures

landscape may facilitate a positive feedback effect (Belyea & Clymo, 2001; Diamond et al., 2019), reinforcing the growth and stability of hummock microforms through the support of vascular plants including ericaceous shrubs and comparatively fast-growing *Sphagnum* species such as *S. magellanicum* and *S. fuscum* that thrive in drier conditions (Figure 9).

Considering the trajectory of permafrost thaw-induced change in the discontinuous permafrost zone (Carpino et al. under review), a significant proportion of the landscape appears to be undergoing rapid change; reinforced by the result of approximately 21% of total treed bog area and nearly 44% of collapse scar wetland area being occupied by hummocks. As hummock area was often obscured by tree coverage, particularly in the treed bog environments, the value of hummock areal coverage is anticipated to be underestimated using this approach. Nonetheless, the overall average estimate of approximately 30% of bogs (both treed and collapse scar combined) covered by hummock microforms is considerable. Additionally, the large fraction of collapse scar bog area occupied by hummocks suggests that a more substantial proportion of the landscape is undergoing rapid landform change towards the re-establishment of black spruce cover, beyond purely the treed bog environments as hypothesized.

It has been suggested that peat accumulation in the form of hummocks may promote the aggradation of permafrost due to the insulative properties of peat and the re-establishment of black spruce; altering the energy dynamics of the landscape (Camill, 1999; Figure 9). Spatial variability in thaw depth was observed to be significantly impacted by hummock microforms and their associated vegetation resulting from thermal insulation facilitated by peat deposits (Higgins & Garon-Labrecque, 2018). Carpino et al. (2018) concluded that the return to a forest-dominated landscape occurred in approximately 40 years (Figure 9). The successional change in landforms and their associated vegetative cover to the point of permafrost formation has been estimated to occur on the order of 80 years (Camill, 1999); much more rapidly than permafrost plateau formation estimated to have taken 600 years (Zoltai, 1993). Although no permafrost was found to be present beneath the hummocks monitored in this study, some seasonal ice was located in the hummocks at the time of measurements in August (Figure 9). Further monitoring of the hummock ice would be necessary to confirm if this ice persists interannually. The variability in thaw depth and potential promotion of ice formation due to the insulation afforded by hummocks (Higgins & Garon-Labrecque, 2018) may have the potential to act as a positive feedback and further contribute to the vertical growth of hummock microtopography through expansion upon freezing (Figure 9); similar to the observed effects of ice formation on the development of mineral earth hummocks in the Canadian Arctic and Subarctic (Tarnocai & Zoltai, 1978) and peat plateaus at the southern boundary of the discontinuous permafrost zone (Zoltai, 1972). This potential positive feedback mechanism of ice formation on hummock growth requires further examination, particularly to assess its influence relative to the controls on NPP and organic matter accumulation known to drive

hummock development in boreal peatlands (Belyea & Clymo, 2001). Despite the presence of small-scale seasonal ice bulbs under some hummock microforms, it is unlikely that broad-scale permafrost aggradation will occur (Figure 9), as has been previously suggested by Camill (1999), given the trajectory of climate change-induced warming in northwestern Canada (Richter-Menge, Overland, Mathis, & Osborne, 2017).

5.5 | Future work

The processes resulting from rapid wetland transition have the potential to significantly impact the availability and sustainability of freshwater resources for northern communities. Further research is warranted to develop a mechanistic process understanding of the ecohydrological changes occurring at the advanced stages of climate change-induced landscape change in the discontinuous permafrost environment. Landscape transition involves the complex dynamic interplay between hydrological, geophysical, thermal and ecological mechanisms. The relative strength and direction of impact of these numerous processes and associated feedbacks have not been quantified (Figure 9). Although the trajectory of transition and associated hydrological and thermal dynamics in the plateau-wetland complexes of the discontinuous permafrost zone have been examined (Carpino et al. under review), the timescales of these mechanistic changes have been proposed based on literature and observations of recent change captured by aerial imagery. Ecohydrological modelling of the processes and feedbacks involved in permafrost thaw-induced wetland transition would greatly enhance the mechanistic understanding of this changing environment.

ACKNOWLEDGEMENTS

We wish to thank the Dehcho First Nations, including the Liidlii Kue First Nation, Jean-Marie River First Nation and Sambaa K'e First Nation, for their support and acknowledge that the Scotty Creek Research Station is located on Treaty 11 land. We acknowledge funding support from ArcticNet for the Dehcho Collaborative on Permafrost as well as a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to W.Q. and an NSERC Undergraduate Student Research Award to J.S. The 2010 Light Detection and Ranging (LiDAR) data and gap fraction product were provided by L. Chasmer and C. Hopkinson, University of Lethbridge. We sincerely thank Dr. Mike Waddington, McMaster University, for his constructive comments and suggestions, which greatly improved the scope and clarity of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

- Belyea, L. R., & Clymo, R. S. (2001). Feedback control of the rate of peat formation. *Proceedings of the Royal Society of London B*, 268, 1315–1321. <https://doi.org/10.1098/rspb.2001.1665>
- Bourgeau-Chavez, L. L., Garwood, G. C., Riordan, K., Koziol, B. W., & Slawski, J. (2010). Calibration algorithm development for selected water content reflectometers to burned and non-burned organic soils of Alaska. *International Journal of Wildland Fire*, 19, 961–975. <https://doi.org/10.1071/WF07175>
- Camill, P. (1999). Peat accumulation and succession following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Écoscience*, 64, 592–602. <https://doi.org/10.1080/11956860.1999.11682561>
- Carpino, O. A., Berg, A. A., Quinton, W. L., & Adams, J. R. (2018). Climate change and permafrost thaw-induced boreal forest loss in northwestern Canada. *Environmental Research Letters*, 13, 084018. <https://doi.org/10.1088/1748-9326/aad74e>
- Carpino, O. A., Haynes, K. M., Connon, R., Craig, J., Devoie, É., & Quinton, W. L. (under review). The trajectory of landcover change in peatland complexes with discontinuous permafrost, northwestern Canada. *Hydrology and Earth System Sciences – Discussions*. <https://doi.org/10.5194/hess-2020-411>
- Chasmer, L., & Hopkinson, C. (2017). Threshold loss of discontinuous permafrost and landscape evolution. *Global Change Biology*, 23, 2672–2686. <https://doi.org/10.1111/gcb.13537>
- Chasmer, L., Hopkinson, C., Quinton, W., Veness, T., & Baltzer, J. (2014). A decision-tree classification for low-lying complex land cover types within the zone of discontinuous permafrost. *Remote Sensing of Environment*, 143, 73–84. <https://doi.org/10.1016/j.rse.2013.12.016>
- Chasmer, L., Quinton, W., Hopkinson, C., Petrone, R., & Whittington, P. (2011). Vegetation canopy and radiation controls on permafrost plateau evolution within the discontinuous permafrost zone, Northwest Territories, Canada. *Permafrost and Periglacial Processes*, 22, 199–213. <https://doi.org/10.1002/ppp.724>
- Clymo, R. S. (1984). The limits to peat bog growth. *Philosophical Transactions of the Royal Society B*, 303, 605–654.
- Connon, R. F., Quinton, W. L., Craig, J. R., & Hayashi, M. (2014). Changing hydrologic connectivity due to permafrost thaw in the lower Liard River valley, NWT, Canada. *Hydrological Processes*, 28, 4163–4178. <https://doi.org/10.1002/hyp.10206>
- Danson, F. M., Hetherington, D., Morsdorf, F., Koetz, B., & Allgöwer, B. (2007). Forest canopy gap fraction from terrestrial laser scanning. *IEEE Geoscience and Remote Sensing Letters*, 4, 157–160. <https://doi.org/10.1109/LGRS.2006.887064>
- Diamond, J. S., McLaughlin, D. L., Slesak, R. A., & Stovall, A. (2019). Pattern and structure of microtopography implies autogenic origins in forested wetlands. *Hydrology and Earth System Sciences*, 23, 5069–5088. <https://doi.org/10.5194/hess-23-5069-2019>
- Disher, B. S. (2020). *Characterising the hydrological function of treed bogs in the zone of discontinuous permafrost*. M.Sc. Thesis, Wilfrid Laurier University, Waterloo. 72 pp
- Foody, G. M., & Mathur, A. (2004). Toward intelligent training of supervised image classifications: Directing training data acquisition for SVM classification. *Remote Sensing of Environment*, 93, 107–117. <https://doi.org/10.1016/j.rse.2004.06.017>
- Foster, D. R., King, G. A., Glaser, P. H., & Wright, H. E. Jr. (1983). Origin of string patterns in boreal peatlands. *Nature*, 306, 256–258. <https://doi.org/10.1038/306256a0>
- Garon-Labrecque, M.-È., Léveillé-Bourret, É., Higgins, K., & Sonnentag, O. (2015). Additions to the boreal flora of the Northwest Territories with a preliminary vascular flora of Scotty Creek, Canadian Field Naturalist, 129, 349–367.
- Gibson, C. M., Chasmer, L. E., Thompson, D. K., Quinton, W. L., Flannigan, M. D., & Olefeldt, D. (2018). Wildfire as a major driver of recent permafrost thaw in boreal peatlands. *Nature Communications*, 9, 3041. <https://doi.org/10.1038/s41467-018-05457-1>
- Hayashi, M., Quinton, W. L., Pietroniro, A., & Gibson, J. J. (2004). Hydrologic functions of wetlands in a discontinuous permafrost basin indicated by isotopic and chemical signatures. *Journal of Hydrology*, 296, 81–97. <https://doi.org/10.1016/j.jhydrol.2004.03.020>
- Haynes, K. M., Connon, R. F., & Quinton, W. L. (2018). Permafrost thaw induced drying of wetlands at Scotty Creek, NWT, Canada. *Environmental Research Letters*, 13, 114001. <https://doi.org/10.1088/1748-9326/aae46c>
- Higgins, K. L., & Garon-Labrecque, M.-È. (2018). Fine-scale influences on thaw depth in a forested peat plateau landscape in the Northwest Territories, Canada: Vegetation trumps microtopography. *Permafrost and Periglacial Processes*, 29, 60–70. <https://doi.org/10.1002/ppp.1961>
- Islam, M. A., & Macdonald, S. E. (2004). Ecophysiological adaptations of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) seedlings to flooding. *Trees—Structure and Function*, 18, 35–42. <https://doi.org/10.1007/s00468-003-0276-9>
- Iversen, C. M., Childs, J., Norby, R. J., Ontl, T. A., Kolka, R. K., Brice, D. J., ... Hanson, P. J. (2018). Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat. *Plant and Soil*, 424, 123–143. <https://doi.org/10.1007/s11104-017-3231-z>
- Jorgenson, M. T., & Osterkamp, T. E. (2005). Response of boreal ecosystems to varying modes of permafrost degradation. *Canadian Journal of Forest Research*, 35, 2100–2111. <https://doi.org/10.1139/x05-153>
- Jorgenson, M. T., Racine, C. H., Walters, J. C., & Osterkamp, T. E. (2001). Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change*, 48, 551–579. <https://doi.org/10.1023/A:1005667424292>
- Lara, M. J., Genet, H., McGuire, A. D., Euskirchen, E. S., Zhang, Y., Brown, D. R. N., ... Bolton, W. R. (2016). Thermokarst rates intensify due to climate change and forest fragmentation in an Alaskan boreal forest lowland. *Global Change Biology*, 22, 816–829. <https://doi.org/10.1111/gcb.13124>
- Lieffers, V. J., & Rothwell, R. L. (1987). Rooting of peatland black spruce and tamarack in relation to depth of water table. *Canadian Journal of Botany*, 65, 817–821. <https://doi.org/10.1139/b87-111>
- Malmer, N., & Wallén, B. (1993). Accumulation and release of organic matter in ombrotrophic bog hummocks—Processes and regional variation. *Ecography*, 16, 193–211. <https://doi.org/10.1111/j.1600-0587.1993.tb00210.x>
- McClymont, A. F., Hayashi, M., Bentley, L. R., & Christensen, B. S. (2013). Geophysical imaging and thermal modeling of subsurface morphology and thaw evolution of discontinuous permafrost. *Journal of Geophysical Research*, 118, 1826–1837. <https://doi.org/10.1002/jgrf.20114>
- National Wetlands Working Group (NWWG). (1988). *Wetlands of Canada, C. Tamocai (Ed.). Ecological land classification series, no. 24. Sustainable development branch, Environment Canada, Ottawa, Ontario, and Poly-science publications Inc (p. 452). Quebec: Montreal.*
- Pelletier, N., Talbot, J., Olefeldt, D., Turetsky, M., Blodau, C., Sonnentag, O., & Quinton, W. L. (2017). Influence of Holocene permafrost aggradation and thaw on the paleoecology and carbon storage of a peatland complex in northwestern Canada. *The Holocene*, 27, 1391–1405. <https://doi.org/10.1177/0959683617693899>
- Quinton, W., Berg, A., Braverman, M., Carpino, O., Chasmer, L., Connon, R., ... Sonnentag, O. (2019). A synthesis of three decades of hydrological research at Scotty Creek, NWT, Canada. *Hydrology and Earth System Sciences*, 23, 1–25. <https://doi.org/10.5194/hess-23-1-2019>
- Quinton, W. L., & Baltzer, J. L. (2013). The active-layer hydrology of a peat plateau with thawing permafrost (Scotty Creek, Canada). *Hydrogeology Journal*, 21, 201–220. <https://doi.org/10.1007/s10040-012-0935-2>
- Quinton, W. L., Hayashi, M., & Chasmer, L. E. (2011). Permafrost thaw-induced land-cover change in the Canadian subarctic: Implications for water resources. *Hydrological Processes*, 25, 152–158. <https://doi.org/10.1002/hyp.7894>

- Quinton, W. L., Hayashi, M., & Pietroniro, A. (2003). Connectivity and storage functions of channel fens and flat bogs in northern basins. *Hydrological Processes*, 17, 3665–3684. <https://doi.org/10.1002/hyp.1369>
- R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org/>
- Richter-Menge, J., Overland, J. E., Mathis, J. T., and Osborne, E. (Eds.). (2017). Arctic Report Card 2017, available at: <http://www.arctic.noaa.gov/Report-Card>
- St. Jacques, J. M., & Sauchyn, D. J. (2009). Increasing winter baseflow and mean annual streamflow from possible permafrost thawing in the Northwest Territories, Canada. *Geophysical Research Letters*, 36, L01401. <https://doi.org/10.1029/2008GL035822>
- Strack, M., Waddington, J. M., Rochefort, L., & Tuittila, E. S. (2006). Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water level drawdown. *Journal of geophysical research—Biogeochemistry*, 111, G02006. <https://doi.org/10.1029/2005JG000145>
- Tarnocai, C., & Zoltai, S. C. (1978). Earth hummocks of the Canadian Arctic and Subarctic. *Arctic and Alpine Research*, 10, 581–594. <https://doi.org/10.2307/1550681>
- Vitt, D. H., Halsey, L. A., & Zoltai, S. C. (1994). The bog landforms of continental Western Canada in relation to climate and permafrost patterns. *Arctic and Alpine Research*, 26(1), 13.
- Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K., & Moore, P. A. (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology*, 8, 113–127. <https://doi.org/10.1002/eco.1493>
- Wright, N., Hayashi, M., & Quinton, W. L. (2009). Spatial and temporal variations in active layer thawing and their implication on runoff generation in peat-covered permafrost terrain. *Water Resources Research*, 45, W05414. <https://doi.org/10.1029/2008WR006880>
- Wright, N., Quinton, W. L., & Hayashi, M. (2008). Hillslope runoff from an ice-cored peat plateau in a discontinuous permafrost basin, Northwest Territories, Canada. *Hydrological Processes*, 22, 2816–2828. <https://doi.org/10.1002/hyp.7005>
- Zoltai, S. C. (1972). Palsas and peat plateaus in central Manitoba and Saskatchewan. *Canadian Journal of Forest Research*, 2, 291–302. <https://doi.org/10.1139/x72-046>
- Zoltai, S. C. (1993). Cyclic development of permafrost in the peatlands of northwestern Alberta, Canada. *Arctic and Alpine Research*, 25, 240–246. <https://doi.org/10.1080/00040851.1993.12003011>

How to cite this article: Haynes KM, Smart J, Disher B, Carpino O, Quinton WL. The role of hummocks in re-establishing black spruce forest following permafrost thaw. *Ecohydrology*. 2021:e2273. <https://doi.org/10.1002/eco.2273>