RESEARCH ARTICLE

Permafrost thaw in boreal peatlands is rapidly altering forest community composition

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Abstract

1. Boreal peatlands are frequently underlain by permafrost, which is thawing rapidly. A common ecological response to thaw is the conversion of raised forested plateaus to treeless wetlands, but unexplained spatial variation in responses, combined with a lack of stand-level data, make it difficult to predict future trajectories of boreal forest composition and structure.

2. We sought to characterize patterns and identify drivers of forest structure, composition, mortality and recruitment in a boreal peatland experiencing permafrost thaw. To do this, we established a large (10 ha) permanent forest plot (completed in 2014), located in the Northwest Territories, Canada, that includes 40,584 mapped and measured trees. In 2018, we conducted a comprehensive mortality and recruitment recensus. We also measured frost table depth, soil moisture, soil humification and organic layer thickness within the plot between 2012 and 2018, and used habitat association tests to link these variables to forest characteristics and dynamics.

3. Forest composition and structure varied markedly throughout the plot and were strongly governed by patterns in permafrost presence and organic layer thickness. Overall, there was a net loss of trees from the plot at a rate of 0.7% year^{-1}. Mortality of black spruce, the dominant tree species, was more than double that of recruitment and was strongly associated with permafrost thaw. In contrast, recruitment of larch was over four times greater than mortality, and occurred primarily in low-lying, permafrost-free wetlands with mineral soil near the surface.

4. *Synthesis*. The trends in tree demography and underlying drivers suggest that spruce-dominated permafrost plateaus will be converted into larch-dominated wetlands as permafrost thaw progresses in boreal peatlands, particularly in areas where mineral soil is near the surface. In the longer term, thaw could increase the hydrologic connectivity of the landscape, resulting in widespread drainage and re-vegetation by spruce, but we did not find evidence that this is occurring yet. Given the increasing rates of permafrost thaw, and positive feedbacks between thaw and forest change, we predict that larch abundance will continue to increase in boreal peatlands over the coming decades, leading to shifts in ecosystem function, wildlife habitat, albedo and snow dynamics.

1 | INTRODUCTION

The boreal forest is the second largest forested biome in the world, and approximately 25%–30% of it is composed of peatlands (Gorham, 1991). Boreal peatlands store vast amounts of carbon (Kurz et al., 2013; Tarnocai et al., 2009) and provide critical habitat for wildlife (Bradshaw et al., 1995). They are characterized by poor drainage, sparse forest canopies, thick organic soils (>40 cm) and the presence of sporadic (10%–50% coverage) or discontinuous (50%–90% coverage) permafrost (~30% of the boreal forest is underlain by permafrost; Gauthier et al., 2015; Helbig et al., 2016; National Wetlands Working Group, 1997). This permafrost plays a critical role in governing hydrological and ecological processes (Baltzer et al., 2014; Connon et al., 2014). Near its southern limits, it is relatively warm (near 0°C), making it vulnerable to rapid thaw with even minor amounts of climate warming or disturbance (Gibson et al., 2018; Tarnocai, 2006). As a result, boreal peatlands are poised to undergo rapid land cover change in the near future, and there is evidence that this change is already underway (Helbig et al., 2016). Given these changes and the importance of boreal peatlands as carbon stores, wildlife habitat, and to the livelihoods and cultures of local inhabitants, understanding potential post-thaw forest trajectories is critical.

A frequent outcome of permafrost thaw in boreal peatlands is the conversion of raised forested plateaus to treeless wetlands (Baltzer et al., 2014; Carpino et al., 2018; Osterkamp et al., 2000; Vitt et al., 2000). Permafrost often elevates the ground surface above the surrounding wetlands in these systems due to the volumetric expansion of water as it freezes. These raised permafrost 'plateaus' are well drained and densely treed compared to the surrounding wetlands. As thaw progresses, plateaus subside, resulting in local flooding and forest loss (Baltzer et al., 2014; Quinton et al., 2011). This process has accelerated in recent decades, reaching rates as rapid as half a percent per year (Baltzer et al., 2014). However, trajectories of forest response to thaw are not always consistent, and in some cases different tree species have shown contrasting responses, leading to an increase in the dominance of one species over another (Lara et al., 2016).

There are several abiotic and biotic factors that could be mediating forest response to thaw, including soil properties. The build-up of undecomposed organic matter in northern peatlands frequently prevents plants from accessing nutrients in the underlying mineral material. In areas where mineral material occurs near the surface, tree recruitment rates can be notably higher than they are in surrounding areas (Préfontaine & Jutras, 2017). These higher recruitment rates suggest that the nutritional benefits of near-surface mineral soil layers could be capable of counteracting some of the

mortality resulting from plateau subsidence and flooding in permafrost peatlands. It is also possible that permafrost plateaus underlain by mineral soil will experience less subsidence and therefore undergo lower rates of forest loss, since they generally contain less pore space (and therefore less frozen water) than permafrost composed of organic material. Alternatively, the more frequent presence of large ice lenses in mineral compared to organic layers could drive rapid subsidence in the former if/when the thaw front reaches these lenses (Paul et al., 2020).

Species-specific nutrient and moisture requirements are also likely to affect trajectories of forest change. North American boreal peatlands typically consist of a combination of *Picea mariana* (black spruce), *Larix laricina* (eastern larch) and *Betula spp.* (birch; Islam et al., 2003; Lara et al., 2016). Eastern larch is more flood-tolerant than black spruce (Islam & Macdonald, 2004; Montague & Givnish, 1996), suggesting it may begin to replace black spruce as permafrost thaw proceeds. However, it is also more nutrient demanding (Islam & Macdonald, 2005), which could limit this process to nutrient-rich sites. Birch can be highly vulnerable to the effects of ground subsidence because it tends to be most abundant along plateau-wetland edges (Lara et al., 2016; Osterkamp et al., 2000). However, its rapid growth rate and propensity to reproduce vegetatively (Bret-Harte et al., 2002) could give it a competitive edge over conifers when gaps form in the canopy.

Due in part to the remote nature of boreal peatlands, forest response to permafrost thaw has primarily been quantified using remotely sensed imagery (Baltzer et al., 2014; Chasmer & Hopkinson, 2017; Helbig et al., 2016; Jorgenson et al., 2010). These methods can quantify land cover change across broad spatial extents, but cannot elucidate dynamic processes or differential responses of tree species (Baltzer et al., 2014; Helbig et al., 2016; Lara et al., 2016). A few studies have used dendrochronology to quantify growth responses to changing permafrost conditions (Sniderhan & Baltzer, 2016; Sniderhan et al., 2020; Zhang et al., 2019), but these methods cannot capture fine-scale demographic dynamics. There is also a network of permanent forest plots in the Northwest Territories (Gillis et al., 2005), but they exclude trees <5 cm in diameter (which are very common in peatlands), contain no spatial information and are small (400 m^2). Large forest dynamics plots provide an opportunity to examine fine-scale spatial patterns in mortality and recruitment of individual species across local gradients in edaphic conditions, thereby enhancing our understanding of warming-induced land cover change (Anderson-Teixeira et al., 2015).

Pronounced variation in rates and trajectories of change, combined with a lack of species-specific recruitment and mortality data at high latitudes make it difficult to anticipate forest

response to permafrost thaw in boreal peatlands. To address this uncertainty, we used forest structure and dynamics data coupled with measurements of key abiotic variables to characterize recent forest change in a unique 10-ha mapped forest plot. The plot (established between 2012 and 2014) encompasses a mosaic of rapidly thawing permafrost plateaus and permafrost-free wetlands, and traverses a strong gradient in organic layer thickness. We asked (a) How do forest structure, mortality and recruitment vary spatially and among species within this boreal peatland? (b) What are the abiotic controls on forest composition, structure, mortality and recruitment? (c) To what extent has recent permafrost thaw driven mortality and recruitment of the dominant species? Our results establish direct links between abiotic variables and fine-scale forest dynamics, information that is necessary to improve predictions of future forest composition and structure in permafrost peatlands.

2 | MATERIALS AND METHODS

2.1 | Study site

The study site is located at Scotty Creek (61°18′38″N, 121°17′36″W), a 152 km² basin located approximately 50 km south of Fort Simpson, Northwest Territories, Canada. This area is a boreal peatland that has not experienced stand-replacing wildfire in over a century (based on mean tree age; Sniderhan & Baltzer, 2016) and has minimal human disturbance. Mean annual air temperature in Fort Simpson (169 m a.s.l.) is −2.8°C and the total annual precipitation is 388 mm, approximately 60% of which falls as rain (1981–2010 climate normals; Environment and Climate Change Canada). Since plot establishment (beginning in 2012), annual average temperature has consistently exceeded this longer-term average while annual precipitation has fluctuated around this average (see Appendix 1). Permafrost in the area is sporadic discontinuous, occupying ~45% of the landscape; this results in a mosaic of raised forested permafrost plateaus, permafrost-free wetlands (ranging from nutrient-rich fens to ombrotrophic bogs) and lakes (Quinton et al., 2011).

Soils in the 10-ha area encompassed by the Scotty Creek ForestGEO plot are a mix of Organic Soils (in permafrost-free wetlands) and Organic Cryosols (atop permafrost plateaus) according to the Canadian System of Soil Classification, meaning they are composed exclusively of organic material in the upper 50 cm and are sometimes underlain by permafrost (ground that has remained frozen for at least 24 consecutive months). Organic material ranges from moderately humified atop permafrost plateaus or in nutrient-rich fens (pH of 6.5) to completely undecomposed in acidic bogs (pH of 4.5–5; Fafard, 2014). Organic soils are underlain by mineral soils of varying thickness that were deposited during the last glaciation (approximately 10,000 years ago; Aylesworth & Kettles, 2000) and are comparatively rich in nutrient cations. Generally, the thickness of the overlying organic soil (up to 8 m; Braverman &

Quinton, 2016) prohibits plant access to nutrient-rich mineral soil, but in areas with particularly thick glacial deposits, mineral soil can be found within 50 cm of the surface. Mineral soils in the plot have a highly consistent texture (sandy loam) and are easily distinguishable from the overlying organic soils (i.e. the boundary is highly abrupt, see Appendix 2).

2.2 | Plot initiation and recensus

An 800 m (east-west) by 120 m (north-south) forest plot was established between 2012 and 2014 as part of the Smithsonian Forest Global Earth Observatory (ForestGEO), a global network of 72 methodologically identical permanent plots (Anderson-Teixeira et al., 2015). These plots support spatially explicit investigations of forest dynamics across local environmental gradients (e.g. Furniss et al., 2017; Harms et al., 2001) and comparative studies at the global scale (e.g. Allen et al., 2010; Chisholm et al., 2014; Chu et al., 2018; Lutz et al., 2018). The Scotty Creek plot is the only boreal forest plot in the network. It is the most northerly, experiences the most extreme (cold and dry) climate and climate change, and has the second lowest woody biomass of all plots (Anderson-Teixeira et al., 2015; Lutz et al., 2018). Elevation varies by <2 m within the plot, and relates strongly to permafrost conditions.

In 2012, 287 aluminium posts were installed at 20-m intervals throughout the Scotty Creek ForestGEO plot using a GNSS receiver (Leica Viva GS10, Leica Geosystems AG, Heerbrugg, CH) with differential correction via an on-site base station (horizontal accuracy of 8–15 mm), dividing the plot into 240 20 m × 20 m grid cells. Between 2012 and 2014, every live stem with a diameter at breast height (hereafter abbreviated as DBH and defined as the diameter of the tree at a height of 1.3 m above the ground) ≥1 cm was tagged, measured and mapped following standard ForestGEO protocols (Condit, 1998). Stems were identified to species except in the case of shrub species that exhibited high rates of introgressive hybridization (*Salix* and *Betula* spp.) and were considered species complexes (Porsild & Cody, 1990). For *Salix* and *Betula* spp., identification was to genus except in the case of the tree form of *Betula neoalaskana* Sarg., for which unhybridized trees were clearly identifiable. Multi-stemmed individuals were common due to the high rates of clonal reproduction in shrub taxa. These individuals were identified using a single numeric tag corresponding to the entire genet and individual stems were uniquely identified within that genet using lettered tags.

In summer 2018, we conducted a complete mortality and recruitment recensus. For each tree, we recorded its status (alive or dead). We recorded probable cause of mortality for all dead stems; this included waterlogging (dead stem was either standing or had fallen over in, or was immediately adjacent to fully saturated soil), falling over (stem fell over from below breast height, likely due to blowdown, but was not located in or immediately adjacent to standing water), physical damage (main stem snapped off above breast height), browsing (evidence of heavy browsing) or biological/unknown

(dead stem was standing and cause of death was unknown, but likely attributable to fungal decay, insect damage or senescence). Finally, we tagged, measured, mapped and identified all new stems with DBH ≥ 1 cm as described for the original census, hereafter referred to as 'recruits'.

2.3 | Abiotic variables

We measured key abiotic variables at 20-m intervals throughout the plot (i.e. adjacent to each of the 287 aluminium posts) between 2012 and 2018. We obtained volumetric soil water content measurements from the top 5 cm of soil using TDR (time domain reflectometry) probes (ThetaProbe, Delta-T Devices and Stevens Hydra Probe, Stevens Water Monitoring Systems Inc.) on 19 July 2012. We subsequently adjusted these measurements using site-specific calibrations (Warren, 2015). We also obtained soil moisture measurements from subsections of the plot on two additional days in 2012, 4 days in 2013 and 1 day (at multiple depths) in 2017 (total of eight sets of measurements). These repeated measurements correlated strongly with the 19 July 2012 measurements (Appendix 3). We therefore considered the 19 July 2012 measurements to be representative of spatial patterns in soil moisture, and used them in all subsequent analyses. We measured snow depth between March 21 and 26, 2013 using a GPS automatic snow depth probe with ±5 cm accuracy (Snow-Hydro LLC). Spatial patterns of snow accumulation are likely consistent among years in this area, since more snow tends to accumulate atop forested permafrost plateaus than in surrounding wetlands due to reduced wind speeds in the former (Haughton, 2018). Snow depth was re-measured on a subset of 50 (out of 287) posts in 2015 and measurements correlated positively with the 2013 dataset ($r = 0.33$, unpublished data), confirming that the 2013 measurements likely capture predominant patterns. Finally, we measured organic layer thickness (using a 1.5 m auger), fibric layer thickness (the upper horizon of organic soils that is lighter in colour and less humified than the underlying 'humic' layer) and peat humification at a depth of 5 cm (using the qualitative von Post scale; von Post, 1922) between 5 and 8 August 2018.

We measured frost table depth as depth to refusal using a 2-m steel rod on 19 July 2012 and 5 August 2018, and on multiple dates (27 May, 31 May and 27 August) across the westernmost 500 m of the plot in 2013. To quantify changes in frost table depth between 2012 and 2018, we first adjusted the values to make them comparable, since active layers were not measured at their seasonal maximum in either year due to logical constraints of the remote field site. To perform this adjustment, we used the difference in frost table depth between 31 May and 27 August 2013 (in cm), and the difference in thawing degree days (TDD, derived from Fort Simpson station data) between the same two dates to calculate rates of thaw (in cm/TDD) at each post within the westernmost 500 m of the plot. We then used multiple linear regression to model the relationship between rate of thaw and a selection of abiotic variables that had the strongest correlations with rates of thaw (soil moisture, organic

layer thickness and tree density within a 5 m radius of the post). We used this model ($R^2 = 0.31$, $p = 0.07$) to estimate rates of thaw (in cm/TDD) at the 105 posts in the easternmost portion of the plot for which we did not have known rates. Next, we calculated the difference in TDD between 27 August 2013 and 19 July 2012, as well as between 27 August 2013 and 5 August 2018. We then multiplied known and estimated rates of thaw at all 287 posts by differences in TDD between dates to make the 2012 and 2018 frost table depths comparable (in terms of TDD) to 27 August 2013 depths. Finally, we subtracted all adjusted 2012 values from adjusted 2018 values to estimate the amount of thaw (in cm) that occurred between 2012 and 2018 at each post.

We then assigned a score to each post (grid cell corner) based on the amount of (adjusted) thaw that occurred between years (0 = permafrost-free in both 2012 and 2018, 1 = 0–30 cm of thaw, 2 = >30 cm of thaw and 3 = permafrost present in 2012, but not in 2018). A categorical variable was necessary to differentiate between sites that had permafrost and had undergone no change in thaw depth versus those that had no permafrost in 2012 or 2018 and similarly had undergone no change. Next, we summed scores at the four corners of each grid cell to generate an aggregate thaw severity score that ranged from 0 (no change; all four corners were permafrost-free in 2012 and 2018) to a maximum of 12 (major change; all four corners had permafrost in 2012, but not in 2018).

2.4 | Data analysis

2.4.1 | Characterizing patterns in forest composition, structure, mortality and recruitment

To quantify forest compositional and structural attributes of the plot, we calculated stem density, basal area and species richness in each 20 m × 20 m grid cell. Hybridizing genera (*Betula* spp. and *Salix* spp.) were treated as single species, meaning species richness is somewhat underestimated. We also tallied the number of mortality and recruitment events for each species in each grid cell, and calculated overall rates of mortality and recruitment (as percentages of initial stem counts) across all grid cells. We included multiple stems produced by the same individual as separate stems in these calculations because each stem is functionally distinct. However, we also performed analyses at the genet level to ensure that our findings did not depend on treatment of multi-stemmed individuals (see Appendix 4). All data manipulation and analyses were performed in RStudio (R v. 4.0.2; RStudio v. 1.3.1056).

2.4.2 | Characterizing patterns in abiotic variables

Since the six measured abiotic variables (2012 soil moisture, 2018 frost table depth, 2018 organic layer thickness, 2018 fibric layer depth, 2018 soil humification and 2013 snow depth) covaried strongly, we sought to summarize major gradients using principal

components analysis (PCA). However, several of the abiotic variables we wished to include were categorical (ordinal). The von Post score is inherently categorical (ordinal), and we converted organic layer thickness and 2012 frost table measurements into categorical (ordinal) variables as well, since over 50% of the values of these two variables were censored beyond the limits of our equipment (i.e. beyond the length of the auger or frost probe). We therefore categorized 2012 frost table depth measurements into one of three categories (<50 cm, between 50 cm and 200 cm and >200 cm), and the organic layer thickness measurements into one of three categories (<60 cm, between 60 cm and 150 cm and >150 cm).

To incorporate a combination of continuous and categorical variables, we used mixed PCA (package PCAMIXDATA; Chavent et al., 2017), which performs a standard PCA on numeric variables, a multiple correspondence analysis (MCA) on categorical variables, and then combines the two into a single ordination. The three numeric variables were standardized to a mean of zero and standard deviation of one prior to analysis. We also performed a sensitivity analysis using higher numbers of categories for the categorical variables, but the results of the mixed PCA were not notably affected. Parallel analysis (via the PARAN package) indicated that the first two principal components (PC1 and PC2) should be retained (Appendix 5). We therefore extracted values of PC1 and PC2 for each 20 m post for all subsequent analyses. We averaged the values from the four corner posts of each grid cell together to generate mean values of PC1 and PC2 for each grid cell.

2.4.3 | Testing for associations between abiotic variables and forest attributes/dynamics

To test whether initial stems, deaths and recruits of each of the dominant taxa (*Picea mariana* (Mill.) Britton, Stems & Poggenburg, *L. laricina* (Du Roi) K. Koch, and *Betula* spp.) were significantly associated with the first or second principal components, we used an adjusted habitat association test developed for use with continuous environmental variables (Itoh et al., 2010). Specifically, we used a kernel density function to estimate the probability of initial stem, death and recruit occurrences of each of the dominant taxa across the full range of PC1 and PC2 values. Next, we used the same function to estimate the probability of occurrence of PC1 and PC2 values. We then divided the former by the latter to generate 'adjusted' probabilities of initial stem, death and recruit occurrence that took into account the frequency of PC1 and PC2 values (code provided by A. de Oliviera).

We extracted the mean PC1 and PC2 values from these adjusted distributions for use as test statistics. Other studies have used the standard deviation or the value at maximum probability as test statistics (Itoh et al., 2010), but we felt the mean would best capture the affinity of initial stems/deaths/recruits for particular values of PC1 or PC2. We then used torus translation to generate null distributions of PC1 and PC2 means. To do this, we held the positions

of initial stems/deaths/recruits constant and shifted the 20 m-resolution maps of PC1 and PC2 values in every combination of *x*- and *y*-directions (preserving all spatial autocorrelation in the values), then flipped the original maps vertically as well as horizontally and repeated each shift for a total of 960 shifts per PC (calculating the mean PC value each time). Finally, we extracted the 2.5 and 97.5 percentiles of the resulting distributions of means and compared observed means to these bounds.

2.4.4 | Testing for associations between permafrost thaw and forest dynamics

Because of the importance of permafrost thaw in peatland land cover changes (Baltzer et al., 2014), we sought to determine the extent to which thaw was driving forest dynamics. We evaluated associations between mortality and recruitment of the dominant taxa and thaw severity (represented by three categories of thaw severity scores: 0, 1–5 and >5) using a categorical torus translation test (Harms et al., 2001). We also evaluated associations between observed causes of *P. mariana* deaths (biological/unknown, falling/physical damage and waterlogging) and thaw severity using the same test. We restricted this last analysis to *P. mariana*, since we did not find obvious evidence of waterlogging-induced mortality in other taxa.

3 | RESULTS

3.1 | Spatial patterns in species composition, forest structure and edaphic conditions

The Scotty Creek ForestGEO plot is dominated in both stem density and basal area by three common boreal species. In the initial census, *P. mariana* comprised 80.1% of stems and was distributed throughout the plot, *L. laricina* made up 11.2% and occurred mainly in the eastern half of the plot, and *Betula* spp. comprised 7.3% with high-density patches in the eastern and western ends of the plot. The remaining 1.4% of stems was composed of *Salix* spp., *Alnus alnobetula* (Ehrh.) K. Koch, *Picea glauca* (Moench) Voss, and *Pinus banksiana* Lamb., all of which generally occurred in the eastern half of the plot (Figure 1). Botanical nomenclature follows Porsild and Cody (1990).

Salix spp. (likely composed of *Salix glauca* L., *Salix planifolia* Pursh, *Salix bebbiana* Sarg., *Salix pyrifolia* Andersson, *Salix serissima* (L.H. Bailey) Fernald and their hybrids) and *A. alnobetula* are shrub species, whereas *P. mariana*, *L. laricina*, *P. glauca* and *P. banksiana* are trees with very few records of multi-stemmed individuals. *Betula* spp. were predominantly shrub species (likely composed of *Betula occidentalis* Hook., *Betula glandulosa* Michx., *Betula pubescens* Ehrh., *Betula pumila* L. and their hybrids). The exception was *B. neoalaskana*, which is characterized by tree form, but hybridizes with *Betula* spp. shrubs as well. Tree and shrub stems were very small, with 73% of tree stems <5 cm DBH and 89% of shrub stems <2 cm DBH (Appendix 6).
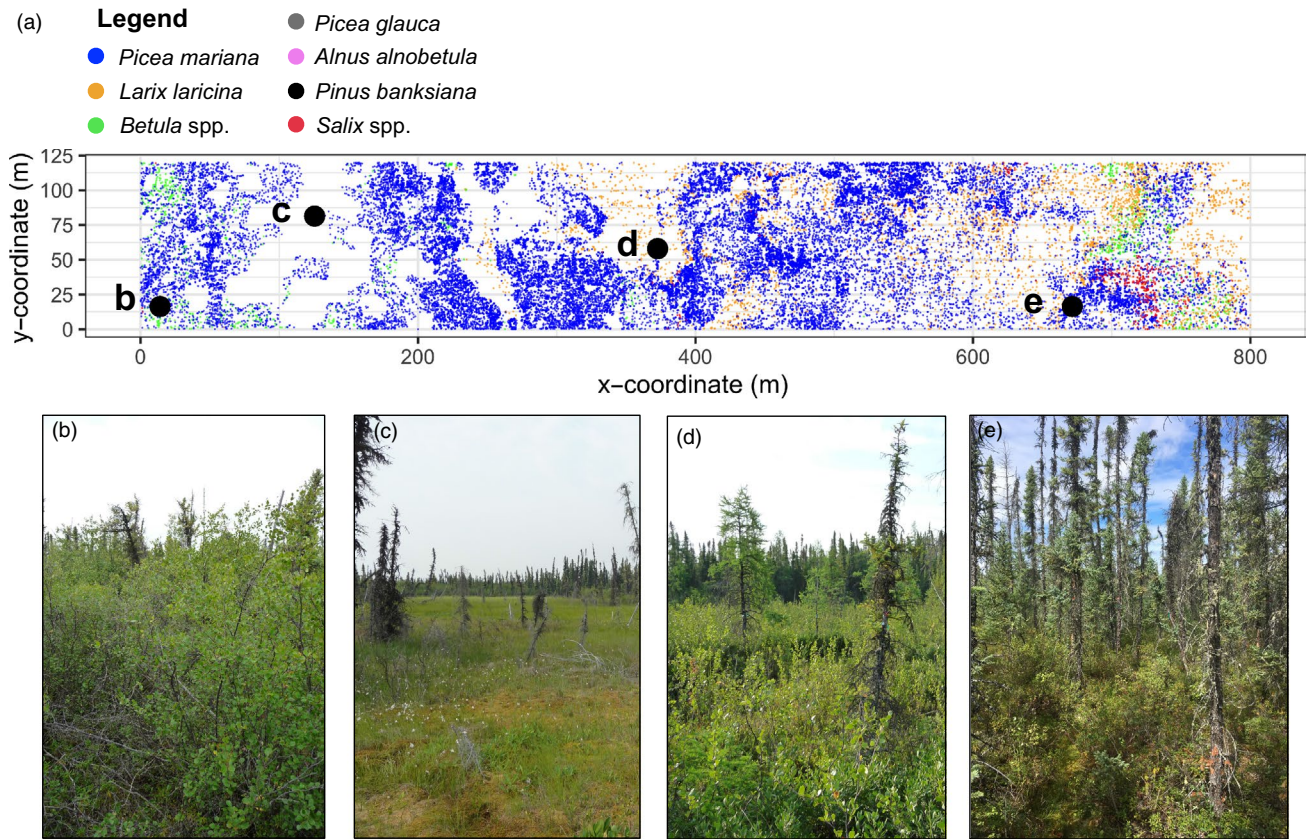
FIGURE 1 (a) Map of all stems in the Scotty Creek ForestGEO plot as of the initial census completed in 2014 (see Appendix 7 for separate maps of each species), with photos showing (b) a dense thicket of *Betula* spp. shrubs underlain by permafrost, (c) a permafrost-free bog with a few scattered *Picea mariana*, (d) a permafrost-free fen with a sparse canopy of *Larix laricina* and (e) a dense forest dominated by *P. mariana* and underlain by permafrost. Approximate locations of these pictures are denoted by the corresponding letters on the map

The first two axes in the mixed PCA captured 34.7% of variance in the six abiotic variables (Appendix 5). Note that while this is a relatively low amount of the variance, a standard PCA (with all variables included as continuous/numeric) resulted in a much higher explained variance (64.6% explained by the first two axes) with very similar axis loadings to the mixed PCA (see Appendix 5). The low explained variance in the mixed PCA is therefore due in large part to the inclusion of frost table and organic layer depth as ordinal (rather than continuous) variables, and we are confident that the first two axes are capturing the major gradients in the data. The first axis (PC1) explained 21.4% of variance and reflected a gradient in permafrost presence and soil moisture. High values represented dry soils atop permafrost plateaus, whereas low values represented permafrost-free wetlands. The second axis (PC2) explained an additional 13.3% of the variance and reflected a gradient in organic layer thickness, peat humification and maximum snow depth. Areas with high values tended to have mineral soil within 1.5 m of the surface, more highly humified peat and a deeper snowpack, whereas areas with low values had thick organic layers (>1.5 m), undecomposed peat and shallow snowpacks (Figure 2).

Patterns in species richness and basal area corresponded with gradients in both principal components while patterns in stem density were more erratic. Mean stem density at the grid cell scale was

4,227 $\pm$ 3,125 stems/ha and tended to be low in areas with low PC1 values (i.e. permafrost-free wetlands), but did not clearly correspond with patterns in PC2 (Figure 3a). Species richness of trees and tall shrubs was generally low (mean of 2.6 $\pm$ 1.2 species per grid cell), but increased with increasing values of PC1 and PC2, meaning it was highest in well-drained areas underlain by permafrost and mineral soil (Figure 3b). Mean basal area at the grid cell scale was 6.7 $\pm$ 5.1 m^2/ha and, like species richness, increased with increasing values of PC1 and PC2 to a maximum of 25.2 m^2/ha (Figure 3c).

3.2 | Spatial patterns of forest dynamics

Overall, the plot experienced a net loss of stems at a rate of 0.7% year^{-1} between censuses (calculated between 2013 when the initial census was completed and 2018), but mortality and recruitment varied spatially and among species. Mortality of *P. mariana* was more than double that of recruitment (2,586 deaths vs. 992 recruits), but because initial stem density was so high, they only experienced a 1.0% year^{-1} net loss of stems. In contrast, recruitment of *L. laricina* was more than four times that of mortality (128 deaths vs. 566 recruits), resulting in a 1.9% year^{-1} net gain in stems. Mortality of *Betula* spp. was only marginally greater than recruitment, but because rates were high, *Betula* spp. still

FIGURE 2 Mixed principal components analysis of abiotic variables measured at 20-m intervals throughout the Scotty Creek ForestGEO plot between 2012 and 2018. Panel (a) shows satellite imagery of the plot (Esri World Imagery; Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo and the GIS User Community). Panels (b and c) depict maps of the first and second principal components, respectively, for each of the 240 grid cells in the plot (i.e. each value is an average of the values at the four corners of a grid cell), and the scale bars are labelled with variables that had contributions of >20% to each axis. Panel (d) depicts the contributions of all six variables to axes 1 and 2 (expressed as percentages of total contributions and oriented in accordance with the direction they load onto each axis)
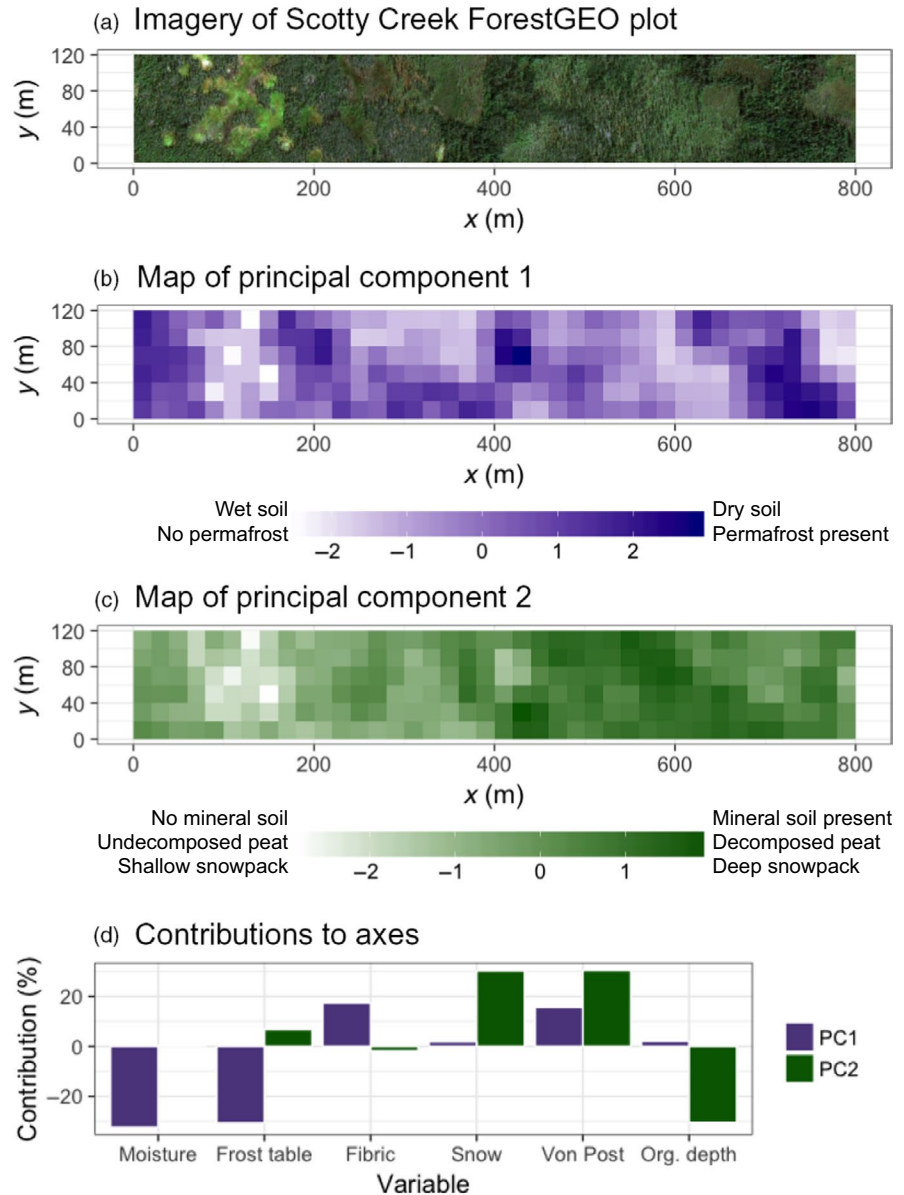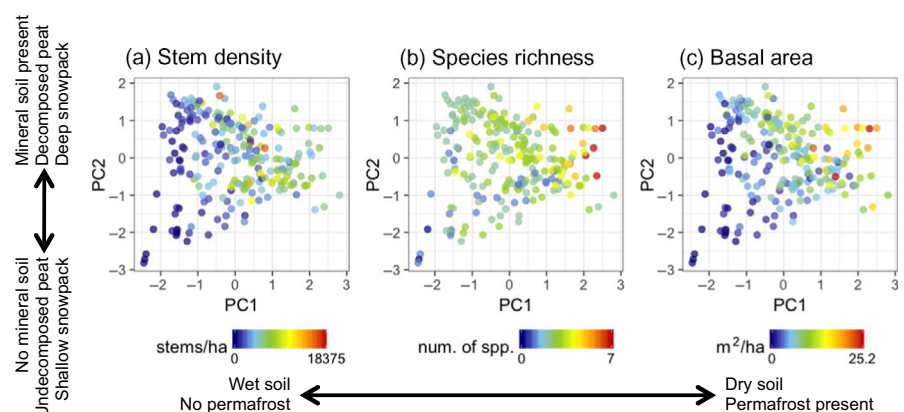

(a) Imagery of Scotty Creek ForestGEO plot

(b) Map of principal component 1

Wet soil / No permafrost — Dry soil / Permafrost present

(c) Map of principal component 2

No mineral soil / Undecomposed peat / Shallow snowpack — Mineral soil present / Decomposed peat / Deep snowpack

(d) Contributions to axes

FIGURE 3 Ordination plots showing each of the 240 20 m × 20 m grid cells in two-dimensional space defined by the first and second principal components depicted in Figure 2. Grid cells are colour-coded according to their (a) stem density, (b) species richness and (c) basal area

(a) Stem density (b) Species richness (c) Basal area

stems/ha 0 — 18375   num. of spp. 0 — 7   m²/ha 0 — 25.2

Wet soil / No permafrost ← → Dry soil / Permafrost present

experienced a 0.7% year^{-1} net loss of stems (Figure 4; see Appendix 8 for rates of *Betula* spp. genets). The remaining species (*Salix* spp., *A. alnobetula*, *P. glauca* and *P. banksiana*) experienced net losses as well,

although their initial densities were so low that these losses did not notably influence forest composition or structure. The net change in basal area was predominantly negative for all species due to the small
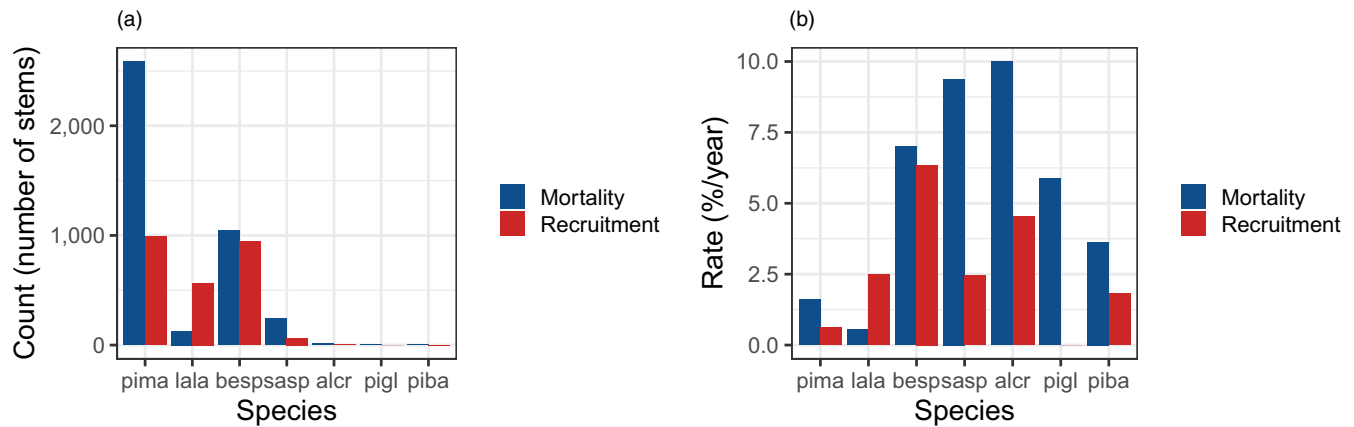
FIGURE 4 The (a) numbers of stem deaths and recruits and (b) rates of stem mortality and recruitment of each species in the Scotty Creek ForestGEO plot between the initial census completed in 2014 and the recensus in 2018. Species abbreviations are as follows: pima = *Picea mariana*, lala = *Larix laricina*, besp = *Betula* spp., sasp = *Salix* spp., alcr = *Alnus alnobetula* (formerly *Alnus crispa*), pigl = *Picea glauca*, piba = *Pinus banksiana*. See Appendix 9 for basal area losses and gains)

diameters of new recruits, although *L. laricina* showed net gains in basal area of between 1% and 77% in approximately half (51%) of the grid cells it occupied (Appendix 9).

The diameters of stems that died between 2013 and 2018 were very similar in distribution to the diameters of surviving stems, meaning mortality occurred more or less equally across size classes. A Kolmogorov–Smirnov test revealed that the diameter distributions of deaths and survivors were significantly different ($p < 0.05$ for all species), but unusually large sample sizes likely influenced the detection of small differences, and these differences are unlikely to be ecologically significant (see Appendix 6). In general, mortality and recruitment rates of shrub species were higher than those of tree species, mainly because clonal stems had high turnover rates (see Appendix 8).

Mortality and recruitment patterns varied spatially across the plot (Appendix 10). Specifically, eastern grid cells experienced net gains in stems and western grid cells experienced net losses (Appendix 10; Figure 1a). Net losses in the western half were attributable to a decline in *P. mariana* abundance (Appendix 10; Figure 1b), whereas net gains on the eastern side were driven by an increase in *L. laricina* abundance (Appendix 10; Figure 1c). *Betula* spp. dynamics were variable between adjacent grid cells, but there was no overall pattern in net gains or losses across the plot (Appendix 10; Figure 1d; see Appendix 8 for a map of net change in *Betula* spp. individuals).

3.3 | Abiotic drivers of forest dynamics

The abiotic variables governing the initial distributions of *P. mariana* and *Betula* spp. were different from those governing the distribution of *L. laricina*. The abundance of both *P. mariana* and *Betula* spp. stems was positively associated with PC1 (i.e. the presence of permafrost and correspondingly well-drained soils) according to habitat association tests. However, neither species was sensitive to

PC2 (i.e. organic layer thickness and snow depth). In contrast, *L. laricina* abundance was not significantly associated with PC1 (i.e. permafrost presence and soil moisture), but was positively associated with PC2 (i.e. thin organic layers and deep snowpacks; Figure 5; Tables 1 and 2).

Abiotic drivers of mortality often differed from those of recruitment, leading to spatial shifts in the distributions of stems, and the magnitude and direction of these shifts varied among species. *P. mariana* deaths and recruits were both associated with high values of PC1 (dry soils underlain by permafrost), like their initial stem densities. However, *P. mariana* recruits were also associated with high values of PC2 (thin organic soils and deep snowpacks), even though deaths and initial stems were not (Table 2; Figure 5), resulting in less severe net losses of *P. mariana* in the eastern half of the plot, and even a few grid cells with slight net gains (Appendix 10). *L. laricina* deaths occurred randomly in relation to environmental conditions (i.e. they were not significantly associated with PC1 or PC2). In contrast, recruits were significantly associated with low values of PC1 (wet, permafrost-free soils) and high values of PC2 (thin organic layers and deep snowpacks). As a result, net gains of *L. laricina* stems were highest in wet, permafrost-free areas with mineral soil near the surface (Figure 5; Tables 1 and 2; Appendix 10). Both deaths and recruits of *Betula* spp. were associated with high values of PC1 (dry soils underlain by permafrost), but were not sensitive to PC2 (organic layer thickness and snow depth), similar to their initial stem densities. As a result, there was no spatial shift in the abundance of *Betula* spp. stems within the plot. This was consistent when analysis was done at the genet level as well.

3.4 | Permafrost thaw and forest dynamics

The extent to which permafrost thaw drove mortality and recruitment varied notably among the three dominant species. *L. laricina* and *Betula* spp. deaths were not significantly associated with areas

FIGURE 5 Ordination plots showing each of the 240 20 m × 20 m grid cells in two-dimensional space defined by the first and second principal components depicted in Figure 2. Grid cells are sized according to the number of stems of each of the three most dominant species in the initial census (black, letters a–c), the number of deaths (blue, letters d–f) and the number of recruits that occurred between censuses (red, letters g–i). Note that scales differ between species, as well as between initial census values and deaths/recruits, and that circles are semi-transparent to show overlap
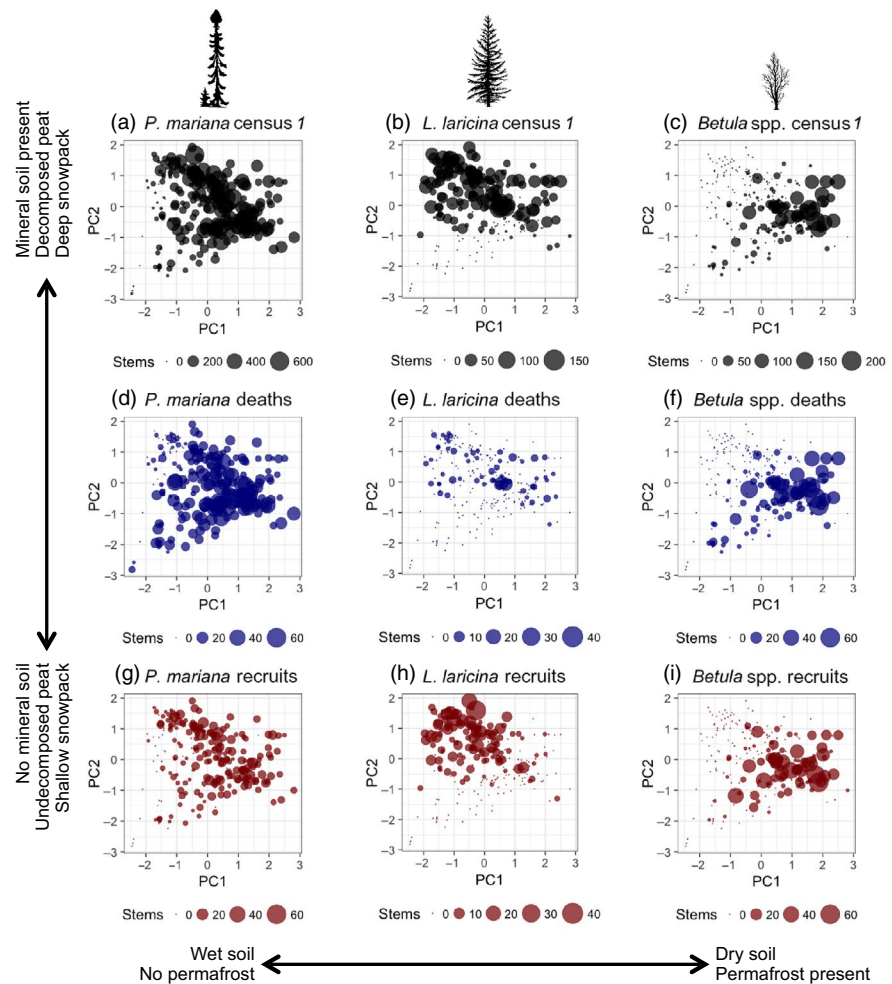

TABLE 1 Observed mean values of PC1 for each species (adjusted according to the probability of that species occurring at a given value of PC1, given the distribution of PC1 values) compared to 95% confidence intervals derived from 960 torus translations of the grid cells. Note that high values of PC1 correspond with low soil moisture content and shallow frost tables (Figure 2), and that bold type/asterisks indicate the observed mean is below (−) or above (+) the 2.5% or 97.5% bound, respectively, of the distribution of torus translated values

	Species	Torus mean lower bound	Torus mean upper bound	Observed mean (adj.)
Census 1	*P. mariana*	−0.18	0.51	**0.71***(+)
	L. laricina	−0.27	0.69	0.18
	Betula spp.	−0.63	1.11	**1.64***(+)
Deaths	*P. mariana*	−0.18	0.51	**0.76***(+)
	L. laricina	−0.79	1.30	0.56
	Betula spp.	−0.58	1.03	**1.48***(+)
Recruits	*P. mariana*	−0.15	0.48	**0.83***(+)
	L. laricina	−0.36	0.81	**−0.56***(−)
	Betula spp.	−0.54	0.93	**1.37***(+)

TABLE 2 Observed mean values of PC2 for each species (adjusted according to the probability of that species occurring at a given value of PC2, given the distribution of PC2 values) compared to 95% confidence intervals derived from 960 torus translations of the grid cells. Note that high values of PC2 correspond with thin organic layers, humified peat and deep snowpacks (Figure 2), and that bold type/asterisks indicate the observed mean is below (−) or above (+) the 2.5% or 97.5% bound, respectively, of the distribution of torus translated values

	Species	Torus mean lower bound	Torus mean upper bound	Observed mean (adj.)
Census 1	*P. mariana*	−0.97	0.12	0.02
	L. laricina	−1.23	0.61	**0.75***(+)
	Betula spp.	−1.67	0.94	−0.29
Deaths	*P. mariana*	−1.17	0.27	−0.55
	L. laricina	−1.73	0.79	0.35
	Betula spp.	−1.67	0.94	−0.46
Recruits	*P. mariana*	−0.82	−0.09	**−0.02***(+)
	L. laricina	−1.31	0.71	**0.99***(+)
	Betula spp.	−1.54	0.84	−0.39

TABLE 3 Results of categorical torus translation test of association between three categories of vertical permafrost thaw (no permafrost, minor thaw and major thaw; see methods for explanation of categories) and deaths/recruits of the three dominant species (*Picea mariana*, *Larix laricina* and *Betula* spp.) in the Scotty Creek Forest Dynamics Plot. Values indicate the number of torus-translated maps in which the true relative density of deaths in a given habitat is greater than, less than or equal to translated maps. Using a two-tailed test and alpha = 0.05, a relative density greater or less than 97.5% of the torus-translated maps (234 out of 240) indicates a positive or negative association, respectively (indicated by bold type and asterisk)

	No permafrost			Minor vertical thaw			Major vertical thaw		
	Greater	Less	Equal	Greater	Less	Equal	Greater	Less	Equal
Deaths									
P. mariana	0	**239***	1	**239***	0	1	**237***	2	1
L. laricina	97	131	12	187	44	9	73	160	7
Betula spp.	0	**239***	1	163	76	1	232	7	1
All spp.	0	**239***	1	**235***	4	1	**239***	0	1
Recruits									
P. mariana	1	**238***	1	161	73	6	**237***	2	1
L. laricina	224	14	2	91	147	2	2	**237***	1
Betula spp.	0	**239***	1	222	16	2	208	31	1
All spp.	4	**235***	1	208	31	1	215	23	2

TABLE 4 Results of categorical torus translation test of association between three categories of vertical permafrost thaw (no permafrost, minor thaw and major thaw; see methods for explanation of categories) and causes of *Picea mariana* mortality in the Scotty Creek Forest Dynamics Plot. Values indicate the number of torus-translated maps in which the true relative density of a given cause of mortality in a given habitat is greater than, less than or equal to translated maps. Using a two-tailed test and alpha = 0.05, a relative density greater or <97.5% of the torus-translated maps (234 out of 240) indicates a positive or negative association, respectively (indicated by bold type and asterisk)

	No permafrost			Minor vertical thaw			Major vertical thaw		
	Greater	Less	Equal	Greater	Less	Equal	Greater	Less	Equal
Causes of *P. mariana* mortality									
Biol./unk.	0	**239***	1	215	23	2	**239***	0	1
Waterlog.	0	**238***	2	**239***	0	1	2	**237***	1
Fall/damage	0	**239***	1	219	20	1	**239***	0	1

that experienced minor or major thaw (i.e. deaths were distributed randomly in relation to permafrost dynamics), but *P. mariana* deaths were positively associated with areas that experienced minor as well as major thaw (Table 3). Interestingly, *P. mariana* and *L. laricina* recruitment showed very different trends with respect to permafrost dynamics. *P. mariana* recruitment was negatively associated with permafrost-free areas and positively associated with areas that experienced major thaw, whereas *L. laricina* recruitment was positively associated with permafrost-free areas (though not significantly) and negatively associated with major thaw (Table 3). *Betula* spp. recruitment followed a similar pattern to that of *P. mariana*.

3.5 | Observed causes of mortality

Causes of mortality (identified for each individual death recorded during the 2018 recensus) varied among species, although biological/unknown causes were the most common. Biological/unknown causes accounted for 84% and 77% of *L. laricina* and *Betula* spp.

deaths, respectively, with the remainder due to stems falling over or physical damage. Most *P. mariana* mortality was also due to biological/unknown causes (59%), but the remainder was due to a combination of waterlogging (23%) and falling over or physical damage (18%; Appendix 11; Figure 1). Waterlogged *P. mariana* stems were positively and significantly associated with minor amounts of vertical thaw (thaw severity scores of 1–5) according to categorical torus translation tests of association while other causes (biological/unknown falling over, or physical damage) were positively and significantly associated with major thaw (scores of 6–12; Table 4). Most waterlogging occurred in the western half of the plot (i.e. areas with no underlying mineral soil), but there was no discernable east-west gradient in the magnitude of thaw (Appendix 11; Figure 1).

4 | DISCUSSION

We found that spatial patterns of forest composition, structure, mortality and recruitment in the Scotty Creek ForestGEO plot were

driven in part by gradients in soil moisture associated with permafrost conditions, but that they were also affected by soil organic layer thickness. Species richness, basal area and stem density were all higher atop well-drained plateaus than in surrounding permafrost-free wetlands, but basal area and species richness were also positively associated with thin organic layers (i.e. access to mineral soil). The plot experienced a net loss of stems at a rate of 0.7% year^{-1} between 2013 and 2018, which was partially driven by waterlogging of *P. mariana* associated with lateral permafrost thaw along permafrost plateau margins, and partially by indirect effects of vertical permafrost thaw within plateau interiors. Mortality occurred throughout the diameter range, meaning permafrost thaw was an agent of mortality for both smaller and larger trees. However, high recruitment of *L. laricina* and to a lesser extent *P. mariana* in areas with thin organic soils resulted in localized net gains of stems. Collectively, these results suggest that permafrost thaw is driving forest loss in the Scotty Creek basin, but that access to mineral soil and species-specific responses to thaw strongly mediate these dynamics. There is tremendous variation in organic soil layer thickness and surficial sediments across the boreal biome, implicating a need to better understand these interactions (Tarnocai et al., 2009).

Permafrost thaw is an ongoing and accelerating process in our study area and throughout the circumpolar north (Jorgenson et al., 2010; Lara et al., 2016; Quinton et al., 2011). Mean annual temperature in the boreal forest could increase by between 4 and 11°C by the end of the century (Gauthier et al., 2015). In our study area, it has already increased from −4.1°C (between 1896 and 1970) to −2.8°C (1981–2010; Quinton et al., 2009). Since permafrost in the northern boreal forest is often near 0°C and is maintained in large part by canopy shading, forest loss can greatly accelerate the rate of thaw (Baltzer et al., 2014; Lara et al., 2016). Temperatures are projected to continue increasing at northern latitudes over the coming decades (Hartmann et al., 2013) and, as a result, the rate of thaw will likely continue to accelerate. Thaw-driven shifts in forest composition or structure happening throughout the boreal (reviewed in Gauthier et al., 2015) are therefore unlikely to be ephemeral.

The overall mortality rate in the Scotty Creek ForestGEO plot was 2.0% year^{-1} across all species and diameter classes. In the Canadian boreal forest, permanent forest plots are primarily located in permafrost-free regions of the southern boreal forest, and exclude stems that are <5 cm DBH (Gillis et al., 2005), making direct comparisons with our results difficult. Mortality rates in these southern plots began to exceed 2.0% year^{-1} in western Canada after the early 2000s due in part to climate-induced drought stress (Birch et al., 2019; Peng et al., 2011). When we removed stems smaller than 5 cm DBH from our data, we found a mortality rate of 1.9% year^{-1} at Scotty Creek, suggesting that the direct and indirect effects of vertical and lateral permafrost thaw in northern portions of the boreal forest are resulting in comparable mortality rates to climate-induced drought stress in the southern portions.

Given the high latitude and extreme climate of the Scotty Creek plot, we expected stem mortality and recruitment rates to be lower than those in other ForestGEO plots (Stephenson & van Mantgem, 2005). However, the mortality rate we observed is comparable to those in other forest types, which tend to range between 1% and 5% year^{-1} for most species and diameter classes (Condit et al., 1995; Furniss et al., 2017; Gonzalez-Akre et al., 2016; Itoh et al., 2012). Furthermore, the large discrepancies between mortality and recruitment rates of the two dominant species in the Scotty Creek plot (net loss of *P. mariana* and net gain of *L. laricina*) are fairly unique among large forest plots. Other plots have observed discrepancies, but they tend to correspond with species-specific diseases, are found in less dominant species, or are related to known successional trends (Furniss et al., 2017; Gonzalez-Akre et al., 2016; Lutz et al., 2014). Given that the forest at Scotty Creek is not currently undergoing succession (i.e. *L. laricina* is not a late-successional species), permafrost thaw is almost certainly responsible for the discrepancies we observed, and may be initiating unprecedented shifts in boreal forest composition.

We found that organic layer thickness mediated forest response to permafrost thaw, particularly with respect to *L. laricina*. Despite the occurrence of thaw and associated flooding throughout the plot, substantial net gains of *L. laricina* stems frequently occurred in areas with thin organic layers. *L. laricina* can produce aerenchymatous tissue in the stem that facilitates root aeration, thereby maintaining higher root mass and root hydraulic conductivity than *P. mariana* in saturated soils (Islam et al., 2003). Partially because of the need to produce new foliage every spring, *L. laricina* is also notably more nutrient demanding than *P. mariana* (Islam & Macdonald, 2005), which explains why recruitment was so strongly associated with the presence of mineral soil near the surface.

Though we expected flood-tolerant *L. laricina* to fare better than *P. mariana* as soils became increasingly waterlogged, the fact that *L. laricina* recruitment was more than four times greater than mortality was surprising. It is likely that the loss of *P. mariana* from recently flooded sections of the plot provided new openings in the canopy for *L. laricina* to colonize. This is supported by the fact that *L. laricina* recruitment was strongly associated with high soil moisture even though initial stem distributions were not. Larch growth has responded positively to permafrost thaw in other regions as well, perhaps because it is capable of rapidly taking advantage of nutrients released at the thaw front (Islam & Macdonald, 2005; Keuper et al., 2012; Prokushkin et al., 2018; Zhang et al., 2019). *L. laricina* has also advanced northward in North America in response to climate warming over the past few decades (Mamet et al., 2019). The increase in *L. laricina* dominance at Scotty Creek has so far been restricted to areas with mineral soil near the surface, but it is possible that coalescing taliks (pockets of ground beneath the active layer that remain unfrozen year-round) and degrading permafrost 'dams' will facilitate the movement of nutrient-rich groundwater to formerly isolated bogs as thaw progresses (Connon et al., 2014, 2018). This could enable *L. laricina* to overtake *P. mariana* in other areas as well.

Despite our expectation that *P. mariana* mortality would be driven primarily by waterlogging associated with permafrost thaw, we found that most deaths were due to biological or unknown

causes, and that deaths due to stems falling over or incurring physical damage were almost as common as deaths due to waterlogging. Some deaths were likely the delayed result of damage incurred during a wet snowfall event in late spring 2012 (J. Baltzer, pers. obs.). Damage assessments done on large stems (those >10 cm DBH) in 2012 support this notion. Notably, 36% of live stems with snapped crowns in 2012 had died by 2018, which is a considerably higher mortality rate than we observed among stems with other types of damage (26% or less) or no damage (only 8%; Appendix 11; Figure 2). As climate warms, spring snowfall and frost events could become increasingly common sources of damage or mortality for boreal trees (Man et al., 2013). These events will likely affect *P. mariana* more severely than *L. laricina*, since the top-heavy crown architecture of the former makes it particularly susceptible to damage via snow loading, and because deciduous species are generally less susceptible to overwinter damage than evergreens due to reduced canopy snow capture (Man et al., 2013; Nykänen et al., 1997). Lastly, windthrow could become increasingly common in peatlands as stems are lost to waterlogging and damage, since trees at forest edges or in thinned stands are more susceptible to windthrow than those in dense stand interiors (Peltola et al., 1999). These penetrating edge effects have been documented in forests globally, most notably in response to forest harvesting and associated fragmentation (e.g. Laurance et al., 2002); there is evidence that such processes are also playing out in these landscapes that are becoming fragmented as a result of climate warming (Baltzer et al., 2014).

Causes of *P. mariana* deaths other than waterlogging (i.e. biological/unknown, falling over or physical damage) were positively and significantly associated with high rates of vertical permafrost thaw, supporting the mounting evidence that trees growing atop plateaus may be suffering from thaw-induced drought stress. The water table is perched atop the frost table at this site such that any deepening of the latter makes it difficult for shallow-rooted *P. mariana* to access adequate moisture (Sniderhan & Baltzer, 2016). Drought stress can cause reductions in physiological function and growth (Patankar et al., 2015; Sniderhan & Baltzer, 2016; Sniderhan et al., 2020) or outright mortality (Peng et al., 2011). It may also leave trees more vulnerable to insects or pathogens, thereby indirectly increasing mortality rates (Desprez-Loustau et al., 2006). Furthermore, the thinning of forest stands within plateau interiors feeds back positively on the rate of vertical thaw, since it increases the amount of incident radiation reaching the ground surface (Baltzer et al., 2014; Lara et al., 2016). As such, the rate of *P. mariana* loss we observed in the Scotty Creek plot is likely to accelerate in the future, a process is occurring in permafrost peatlands throughout North America (e.g. Camill et al., 2010; Lara et al., 2016). Compositional shifts away from *P. mariana* are also being observed in response to other warming-induced changes to the disturbance regime, most notably the intensification of the boreal wildfire regime (reviewed in Johnstone et al., 2010), highlighting the potential for widespread changes throughout the boreal forest.

In contrast to our expectations, *P. mariana* deaths due to waterlogging were associated with minor rates of permafrost thaw. This association could be due in part to the fact that surface subsidence can occur without any change in active layer thickness (i.e. the depth from the surface to permafrost can remain constant as the ground surface subsides due to the melting of ground ice). Additionally, waterlogging is a response to lateral thaw (i.e. disappearance of permafrost) along abrupt plateau margins, which our frost table measurements often failed to capture due to the gridded sampling effort. Measurements tended to fall within permafrost-free wetlands or plateau interiors, where vertical thaw was occurring, but permafrost persisted between years. Locations where we did capture lateral thaw were immediately adjacent to permafrost-free wetlands, which experienced no change in frost table depth between 2012 and 2018, and were thus assigned a zero in our thaw severity rating. These zeros lowered the aggregate thaw severity scores of grid cells in which lateral thaw was observed at one or two grid cell corners. In short, the coarseness of our thaw depth measurements masked dynamic processes at plateau margins but effectively, the minor thaw category often corresponded with degrading plateau margins.

We found that *Betula* spp. experienced a very high turnover of stems, but spatial patterns in abundance were stable between censuses. Areas dominated by *Betula spp.* also tended to have more highly humified peat (high von Post scores) and showed evidence of fire (surficial charcoal; K. Dearborn, pers. obs.). It is possible that *Betula* spp. rapidly colonized these areas following small, localized fires, and subsequently prevented conifers from colonizing. *Betula* spp. are competitive, fast-growing and produce high-quality litter compared to evergreen species (Aerts et al., 1999; Bret-Harte et al., 2002). These characteristics could maintain patches of high *Betula* spp. abundance for extended time periods following small burns, similar to the long-term replacement of conifer forests by shrub fields following severe burns in the Cascade Mountains (Lauvaux et al., 2016). Their ability for clonal reproduction also means that once they become dominant, they likely remain that way with limited opportunity for succession towards a forested state, since rates of individual or genet mortality are low (Appendix 8).

5 | CONCLUSIONS

Our results, combined with the ongoing and projected increases in annual and summer boreal temperatures, suggest that permafrost thaw will continue to elevate black spruce mortality in boreal peatlands. A corresponding increase in larch abundance might maintain sparse forest cover, but is also likely to alter a range of key ecosystem functions. For instance, an increase in soil nutrient content and corresponding shift towards more minerotrophic plant communities could occur, since larch needles fall every year and are higher quality and more readily decomposable than spruce needles (Aerts et al., 1999; Carlyle & Malcolm, 1986). The thinning of forest stands and increasing dominance of deciduous species could also increase surface albedo in the winter, with potential consequences for snow

cover duration (Lundquist et al., 2013). Finally, a loss of raised plateau habitat will likely be detrimental to boreal caribou (*Rangifer tarandus caribou*) whether a sparse canopy is maintained or not, since the lichens growing atop plateaus in open spruce woodlands form an important component of their diet (Joly et al., 2010). In any case, the high disparities between mortality and recruitment among the dominant tree species suggest high rates of community change within boreal peatlands, even higher than those reported for more southerly boreal forests (Birch et al., 2019).

In the longer term, it is possible that extensive permafrost thaw and increasing hydrological connectivity within the watershed will result in sufficient landscape drainage to cause widespread drying of the landscape (Connon et al., 2014; Haynes et al., 2018). If this occurs, successional processes will likely initiate an increase in black spruce cover over time (in the absence of fire; Préfontaine & Jutras, 2017; Zoltai, 1993). However, we did not find any indication that this is occurring yet. Instead, the evidence we found of positive feedbacks between spruce loss and vertical thaw atop plateaus, combined with previously uncovered evidence of positive feedbacks between plateau subsidence and lateral thaw (Baltzer et al., 2014) suggest that the conversion of plateau-wetland mosaics into more homogeneous, larch-dominated wetlands is likely to accelerate in the coming decades.

AUTHORS' CONTRIBUTIONS

J.L.B. conceived ideas, obtained funding and contributed substantially to data analysis and writing; K.D.D. led the plot recensus in 2018, conducted data analysis, designed figures and wrote the manuscript; R.P. and C.A.W. led plot establishment, collected abiotic data, and provided feedback on methodology, data analysis and writing. All authors gave final approval for publication.

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SUPPORTING INFORMATION

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