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Persistent changes to ecosystems following winter road construction and abandonment in an area of discontinuous permafrost, Nahanni National Park Reserve, Northwest Territories, Canada

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Abstract

Subarctic ecosystems are experiencing rapid changes as a result of climate warming and more frequent and severe disturbances. There is considerable uncertainty regarding ecological trajectories following disturbance in forested ecosystems underlain by permafrost because their structure and function is controlled by feedbacks among soil conditions, vegetation, and ground thermal regime. In this paper, we studied post-disturbance ecosystem recovery in an area of discontinuous permafrost 32 years after construction and abandonment of a winter access road in Nahanni National Park Reserve (NNPR). Ecosystem recovery was examined by comparing disturbed (road) and undisturbed (adjacent to the road) sites in the following terrain types: spruce peatland, black spruce parkland, deciduous forest, and alpine treeline terrain. Our field data show that disturbances to discontinuous permafrost terrain can lead to large and persistent changes to ecosystem composition and structure. Our findings indicate that the ecological response of discontinuous permafrost to disturbance and climate warming will depend on interactions between soil conditions and vegetation communities. In instances where disturbance to discontinuous permafrost fundamentally disrupts stabilizing interactions between soil conditions and vegetation communities, we should expect lasting changes to ecosystem structure and function.

INTRODUCTION

Recent temperature increases at high latitudes have been double the global average, and Canada's western Arctic has experienced disproportionately more warming than other northern regions (Arctic Climate Impact Assessment, 2005; IPCC, 2007; Serreze et al., 2000). Across the Arctic and subarctic, warming air temperatures have been accompanied by increases in permafrost temperatures (Kokelj and Jorgenson, 2013; Romanovsky et al., 2010; Smith et al., 2010b; Throop et al., 2012). Permafrost degradation and range retractions are predicted to be most severe at the southern margin of discontinuous permafrost, where perennially frozen ground is maintained by surface conditions that insulate frozen ground from warmer air temperatures (Camill and Clark, 1998, 2000; Halsey et al., 1995; Jorgenson et al., 2010; Romanovsky et al., 2010; Shur and Jorgenson, 2007; Throop et al., 2012). In these environments, it is unclear how resilient permafrost will be to disturbance or increases in air temperatures.

Holling (1973) described resilience as the capacity of an ecosystem to absorb disturbance and sustain function, structure, identity, and feedbacks. Disturbances are discrete events like fires, floods, and landslides that impact ecosystem structure, resource accessibility, and the physical environment (Chapin et al., 2009). Resilience theory predicts that changes to parameters with strong feedbacks to ecosystem function are particularly likely to drive persistent state changes in which recovering ecosystems exhibit significantly different structure and feedbacks (Chapin et al., 2009; Folke et al., 2004; Gunderson, 2000; Holling, 1973; Thrush et al., 2009). Recent field studies suggest that ecosystem resilience in discontinuous permafrost is controlled by the strength of the feedbacks among several factors: (1) organic layer depth, (2) soil moisture, (3) vegetation structure, and (4) snow cover (Harper and Kershaw, 1996, 1997; Jorgenson et al., 2001; Smith et al., 2008). Ecological responses to disturbance also depend on the nature and rate of post-disturbance vegetation succession, which varies with terrain type (Sannel and Kuhry, 2008; Calmels et al., 2012).

Factors that control ecosystem resilience are likely to be impacted by both disturbances and increased temperatures. Disturbances that affect ecosystem function in the subarctic include infrastructure development, fires, resource extraction, landslides, and thermokarst. At Scotty Creek, Northwest Territories (NWT), Canada, Williams et al. (2013) showed that discontinuous permafrost thaw associated with linear disturbances initiated hydrological changes that affected land cover types. In an area of continuous permafrost, Lantz et al. (2009) showed that disturbances associated with thawing permafrost created feedbacks among snow pack and soil conditions that facilitated persistent changes in vegetation community structure. In some areas of discontinuous permafrost, recent observations suggest that increasing air temperatures are exceeding ecosystem thresholds and causing permafrost degradation (Chasmer et al., 2011; Grosse et al., 2011; Schuur et al., 2008). Shifting permafrost boundaries will have strong impacts on terrestrial and aquatic ecosystems because hydrology, nutrient availability, and carbon dynamics are strongly affected by permafrost thaw (Connon et al., 2014; Jorgenson et al., 2001; Lantz et al., 2009; Natali et al., 2011; Quinton et al., 2011). Additional case studies examining variation among post-disturbance ecological recovery trajectories will increase our understanding of factors that influence ecosystem resilience in discontinuous permafrost terrain.

The Prairie Creek winter access road was built by a mining company during the winter of 1981 and abandoned the following year. Although not originally situated within Nahanni National Park Reserve (NNPR), a portion of the road is now located within NNPR after a park boundary expansion in 2009. This road was built using a bulldozer to level the surface of the ground, clear trees and brush, and pack snow so that ground freezing was enhanced and the surface could support large vehicles. The Prairie Creek road is located in an area of discontinuous permafrost, which spans alpine treeline, black spruce parkland, spruce peatland, and deciduous forest. Portions of the road have naturally revegetated in the years since it was abandoned. The impacts of road construction include changes to ground thermal regime, disruption and removal of surface vegetation and organic materials, changes to drainage patterns, compaction of soils, and changes to vegetation communities. As such, the road provides an excellent opportunity to explore the effect of disturbance on vegetation, soils, and near-surface ground temperature across different terrain types. Although climate change and road construction are fundamentally different disturbances, they may have comparable impacts on ecosystem structure and function if they affect the same feedbacks to ecosystem resilience. In this paper we assess ecological responses to disturbance in four terrain types by comparing vegetation, soil, and permafrost conditions along the abandoned roadbed with nearby undisturbed terrain.

METHODS

Study Area

This study was conducted in NNPR in the southwestern corner of the NWT (Fig. 1). With an area of over 30,000 km^2 NNPR is one of the largest national parks in Canada. It is situated in the boreal forest within the taiga plains ecozone and is underlain by extensive discontinuous permafrost (Smith et al., 2010a; Johnson et al., 1995). The climate in this region is continental and is characterized by short warm summers and long cold winters. Mean annual temperature and precipitation (2001–2014) at a meteorological station approximately 35 km away from our study site were –1.25 °C and 146 mm, respectively (Environment Canada, 2012). The western part of our study area lies in the carbonate and siliciclastic Neoproterozoic–Cambrian rocks of the Mackenzie Mountains (Narbonne and Aitken, 1995). Further east, our study area is situated in the geologically unique North Karst area, which is comprised of Middle Devonian limestone overlain with Upper Devonian shale and glaciolacustrine deposits (Ford 2010, 1976). Though evidence of historical glaciation is present, highly developed karst features imply that large parts of NNPR remained unglaciated during the past 300, 000 years (Ford, 2010, 1976).

In 1981, an 8-m-wide winter road was built in the region to access a silver and base metal mine near Prairie Creek (Fig. 1). The road was not used extensively and was abandoned the following year. Although a mining company obtained permits to build and operate a winter road in 2014, as of 2016 it remained unused. Approximately 84 km of the 180 km Prairie Creek Access Road passes through the eastern portion of NNPR. The road spans numerous terrain types, ranging from high-elevation alpine tundra to low-lying peatlands. The research described in this paper focused on four of the dominant terrain types in this part of NNPR (Fig. 2).

Black spruce parkland is prevalent at mid-elevations (696–1005 m) and is characterized by a moderately dense canopy of *Betula glandulosa* Michx. and *Picea mariana* Mill., and an understory dominated by lichens and moss. Spruce-dominated peatlands at lower elevations (271–224 m) are distinguished by abundant mosses and sedges, ericaceous shrubs, *B. glandulosa*, *P. mariana*, and *Larix laricina* (DuRoi) Koch. Deciduous forest is common at elevations ranging from 463 to 221 m and is typically dominated by a closed canopy of *Populus tremuloides* Michx. and *Populus balsamifera* L. interspersed with *Picea glauca* Moench and an understory of *Cornus canadensis* L., *Linnea borealis* Forbes, *Rosa acicularis* Lindl. S. lat, and *Vibernum edule* Michx. Alpine treeline terrain is found at high elevations (1101–1115 m) in the Mackenzie Mountains and is characterized by open stands of *P. glauca* and a dense cover of *Ledum groenlandicum* Oeder, *Vaccinium vitis-idaea* L., *Vaccinium uliginosum* L., *B. glandulosa*, mosses, and lichens. Nomenclature used throughout this paper follows Cody (2000).

Response Variables

To investigate how disturbance affects ecosystems in different terrain types, we compared a suite of biotic and abiotic response variables in terrain types impacted by the Prairie Creek access road and adjacent control sites not impacted by the road. To select sites in alpine treeline, spruce peatland, deciduous forest, and black spruce parkland, we used a land-cover classification (Stow and Wilson, 2006) and field reconnaissance. During the summer of 2013, we established 10 sites in spruce peatland, 10 sites in black spruce parkland, 8 sites in deciduous forest terrain, and one site in the alpine treeline terrain (n = 29). Sites in each terrain type were separated by at least 500 m.

At each site, paired line transects were established down the center of the road corridor (disturbed) and in the undisturbed terrain adjacent to the road. Disturbed transects ran along the center of the road for 70 m. Undisturbed transects ran parallel to the disturbed transect for 70 m, but were located 10 m from the edge of the roadbed. Data from Smith et al. (2005, 2008) from a cleared right-of-way suggest that 10 m is far enough from the unused road bed that disturbance-related thermal effects are negligible.

Community composition at disturbed and undisturbed sites was described by visually estimating the percent cover of all plants within quadrats placed at 10 m intervals along each transect. Within a 1 m^2 quadrat, percent cover was evaluated for all species except sedges and grasses, which were grouped at a family level, and lichen and mosses, which were identified as functional groups. The cover of tall shrubs (woody species >0.4 m tall) was estimated inside a 5 m^2 quadrat centered on the 1 m^2 quadrat. The heights of the tallest shrub and understory plant were recorded within the 5 m^2 and the 1 m^2 quadrat, respectively. Canopy cover, stem density, and diameter at breast height (DBH) of trees were recorded within a 25 m^2 plot centered on each 1 m^2 plot. Trees that were less than 0.5 m tall were counted and assigned a DBH of less than 1 cm.

Within each 5 m^2 quadrat, five measurements of active layer thickness were obtained by pushing an active layer probe into the ground until depth of refusal. To control for variation associated with microtopography, active layer measurements were recorded on hummock tops. Active layer measurements from alpine treeline and deciduous forest terrain were discarded because talus and thick clays made it difficult to probe to the base of the active layer. Organic layer thickness (F and H horizons) and litter depth (L horizon) were recorded once in each 5 m^2 quadrat using a shovel and a small metal ruler up to a maximum depth of 30 cm. In spruce peatlands, where organic soils persisted beyond the top of the permafrost table, we measured (the L horizon) and recorded the depth of the organic layer up to a maximum of 30 cm. Volumetric soil moisture was determined by averaging five measurements recorded on the same day with a Theta moisture probe (Type ML2x, Delta-T Devices Ltd.) at multiple points in the 5 m^2 quadrat.

Near-surface ground temperature was recorded at disturbed and undisturbed sites in each terrain type using data loggers attached to two external temperature probes (HOBO Pro v2 2x External Temperature Data Logger, Onset Computing, Pocasset, Massachusetts, U.S.A.). These temperature probes were mounted on a PVC pipe that was inserted into a hole such that the probes recorded temperatures 10 cm and 100 cm below the ground surface. We set the loggers to record ground temperature every 2 h for a year. In August 2012, 11 thermistors were installed at disturbed and undisturbed areas in black spruce parkland (n = 4), alpine treeline (n = 3), deciduous forest (n = 2), and spruce peatland (n = 2). Despite equipment malfunctions and animal encounters, ground temperature data were recovered from thermistors in control and disturbed transects in black spruce parkland (n = 2), alpine treeline (n = 2), and deciduous forest terrain types (n = 2). Because of animal encounters in spruce peatland terrain, we only obtained ground temperature data from the disturbed transect (n = 1).

Statistical Analysis

To examine differences in community composition among control and disturbed sites in the four terrain types, a nonmetric multidimensional scaling (NMDS) ordination of a Bray-Curtis resemblance matrix based on percent cover data was performed with the PRIMER software program (Plymouth Marine Laboratories, Plymouth, U.K.) (Clarke and Gorley, 2001; Clarke and Warwick, 2001). Abundance data were log(x+1) transformed before NMDS ordination (Clarke, 1993). To minimize the influence of rare species, plants found in fewer than two subplots were excluded from the analysis. Two unvegetated plots in disturbed alpine treeline and black spruce parkland were also deleted from the analysis. To determine whether community composition was significantly different among control and disturbed areas in each terrain type, we used the ANOSIM (analysis of similarities) function in PRIMER. The two-way nested design option was used to account for the grouping of plots along transects. To test the significance of the R_{ANOSIM} statistic, we used PRIMER to conduct 999 permutations on the resemblance matrix. Terrain types with R_{ANOSIM} values below 0.25 were considered to be indistinguishable based on their species composition (Clarke and Gorley, 2001). To identify species that made the greatest contribution to pairwise differences among terrain types, we used PRIMER to perform a SIMPER analysis on the log(x+1) transformed percent cover data (Clarke and Gorley, 2001).

To compare the forest structure of disturbed and undisturbed sites and to determine if the size distributions of trees were significantly different, we plotted histograms of tree DBH and used a two-sample Kolmogorov-Smirnov test in R (R Core Team, Vienna, Austria). To explore the stand-scale impact of the road on forest structure, trees from all subplots and sites within a terrain type were combined. To constrain this analysis to dominant species, tree species were only included in analysis when there were more than 50 individuals within each terrain type.

To test whether biotic and abiotic variables were significantly altered by the construction of the road, and to assess whether these impacts varied by terrain type, we used linear mixed effects models. This analysis was conducted with the GLIMMIX procedure in SAS version 9.3 (SAS Institute, Cary, North Carolina, U.S.A.). Terrain type (black spruce parkland, spruce peatland, alpine treeline, and deciduous forest) and disturbance level (control and disturbed) were included in the models as fixed factors. Site and transect within site were included in the models as random factors to account for spatial nesting of the data. The Kenward-Roger method was used to estimate degrees of freedom, and the Bonferroni corrected LS MEANS procedure was used to perform pairwise comparisons among site types. Residuals were examined for homogeneity of variance and were plotted to observe deviations from normal and no transformations were necessary. Due to a lack of replication of sites in alpine treeline, data from this terrain type were excluded from statistical analysis.

Results

Plant community composition varied among all disturbed and undisturbed sites (Fig. 3; Table 1), but the magnitude of the difference depended on the terrain type. Spruce peatland sites exhibited large differences in community composition between control and disturbed sites (R_{ANOSIM} = 0.791, $P < 0.001$) that were driven primarily by increases in sedge and litter at disturbed sites. Tall shrubs, predominantly *Salix* spp. and *Betula glandulosa*, were also more abundant at disturbed spruce peatland sites. Undisturbed spruce peatland was characterized by *Picea mariana*, moss, and ericaceous shrubs. Distinct vegetation communities were also observed at control and disturbed sites in the deciduous forest (R_{ANOSIM} = 0.565, $p < 0.001$). In this terrain type, the abandoned roadbed was characterized by higher cover of *Picea glauca*, moss, and *Shepherdia canadensis*, and lower cover of *Populus tremuloides*, litter, *Vibernum edule*, and *Cornus canadensis* compared with undisturbed sites. Disturbance also impacted plant community composition in black spruce parkland (R_{ANOSIM} = 0.579, $p < 0.001$). Disturbed sites had greater cover of *Salix* spp. and reduced cover of *Picea mariana*, *Betula glandulosa*, *Cornus canadensis*, and lichen compared to undisturbed sites. Impacted alpine treeline sites exhibited no cover of *Betula glandulosa*, moss, lichen, ericaceous shrubs, and *Picea glauca*, which were common species at the control site in this terrain type (Table 1). *Dryas integrifolia* was the dominant vegetation cover on the mostly barren roadbed (Fig. 2), but *Salix* spp. were also present in some places.

Road construction significantly affected stand structure at forested sites, but the effects of disturbance also varied by terrain type (Figs. 4, 5, 6). Tree size distributions at disturbed sites were log-normal and were characterized by a large number of small individuals. At undisturbed sites tree size distributions depended on terrain type, but typically included a greater number of large individuals. In most terrain types, the dominant species along the road also differed from the nearby forest. Along the road in spruce peatland, a large cohort of *Larix laricina* replaced *Picea mariana* as the dominant tree, which displayed signs of recruitment failure following disturbance (Fig. 4). At disturbed deciduous forest sites, *Populus tremuloides* did not regenerate following road abandonment, but was replaced by *Picea glauca* and *Betula papyifera* (Fig. 5). In black spruce parkland, the same tree species were found on the road and adjacent to the road, but *Pinus contorta* was the dominant tree species on the road, and *Picea mariana* was the dominant tree species at undisturbed sites (Fig. 6).

The presence of the road also had significant effects on abiotic conditions at the road after construction (Table 2; Fig. 7). In spruce peatland, volumetric soil moisture at disturbed sites was approximately double undisturbed levels (Fig. 7, part A). Volumetric soil moisture was greater at disturbed sites in black spruce parkland and deciduous forest, but the differences were not significant. The disturbed site at alpine treeline had lower soil moisture. Average organic layer thickness was greater at undisturbed sites than on the roadbed in all terrain types. In black spruce parkland and deciduous forest, soil organic layers were five times thicker at undisturbed sites, and soil organic layers at alpine treeline were 116 times thicker off the road (Fig. 7, part B). At disturbed spruce peatland sites, there was a nonsignificant reduction in organic soil thickness. Litter depth in most terrain types was also impacted by road construction (Fig. 7, part C). At disturbed spruce peatland sites, the road was associated with a doubling of litter depth. Disturbed black spruce parkland and deciduous forest sites both showed nonsignificant decreases in litter depth compared to undisturbed sites. Average active layer thickness was greater at disturbed spruce peatland sites than at undisturbed sites, but this difference was only marginally significant (Fig. 7, part D; Table 2). Active layer thickness did not differ between control and disturbed sites in black spruce parkland. Vegetation structure was also strongly impacted by the road. Maximum understory height was significantly greater in all disturbed terrain types except disturbed deciduous forest (Fig. 7, part E). Maximum shrub height was lower at disturbed sites at alpine treeline (Fig. 7, part F). Maximum shrub height was higher at disturbed black spruce parkland, spruce peatland, and deciduous forest, but differences between control and disturbed sites were not significant.

The impact of the road on near-surface ground temperatures varied among terrain types (Fig. 8). In black spruce parkland, temperatures beneath the abandoned roadbed were elevated at both 10 and 100 cm below ground surface when compared with undisturbed temperatures. Ground temperatures at 100 cm beneath the abandoned roadbed in spruce peatland remained close to zero for the entire winter. Near-surface temperatures at 10 cm beneath the roadbed in spruce peatland indicate that the ground cooled relatively slowly, and was at its coldest, –3.4 °C, in late March. Temperature data for undisturbed peatland is missing because the thermistor was damaged by an animal. However, permafrost was encountered in this terrain during active layer probing and drilling during thermistor installation. The presence of hummocks, thick layers of peat, and an open black spruce forest also suggest that conditions are suitable for the persistence of permafrost in undisturbed spruce peatland terrain (Bauer and Vitt, 2011; Shur and Jorgenson, 2007; Williams and Burn, 1996). Temperature profiles in deciduous forest did not show appreciable differences between control and disturbed sites. At alpine treeline, temperatures along the road at both 10 cm and 100 cm below ground surface were warmer than undisturbed sites during the summer and colder than controls during the winter.

DISCUSSION

Effects of the Prairie Creek Road

Our field data show that disturbances to discontinuous permafrost terrain can lead to persistent changes in ecosystems. More than three decades after road abandonment, community composition along the road remained distinct from undisturbed locations in all terrain types in NNPR. In spruce peatland, road construction likely triggered permafrost thaw, which significantly increased soil moisture and facilitated a transition from spruce peatland to sedge wetland. Permafrost thaw in this terrain type was evidenced by warm ground temperatures, thicker active layers, and increased soil moisture at disturbed sites. It is likely that permafrost degradation at spruce peatland sites was caused by the removal and compaction of organic material, which decreased the insulative capacity of soils and promoted the development of a thicker active layer (Chapin and Shaver, 1981; Mackay, 1970). Permafrost degradation and subsequent ground subsidence likely increased soil moisture by bringing the surface of the ground closer to the water table. This is consistent with observations made by Williams et al. (2013) and McClymont et al. (2013) of permafrost degradation, ground subsidence, and increases in soil moisture following linear disturbance in discontinuous permafrost at Scotty Creek, NWT (2013). Work by Kopp et al. (2014) and Zhang et al. (2001) also suggests that decreased evapotranspiration associated with the removal of large trees and other vegetation during road construction may have also contributed to increased soil moisture along the road. Increases in soil moisture in this terrain type may limit permafrost recovery because the latent heat effects of water delay ground freeze, and may persist over the course of the winter (Jorgenson et al., 2010; Romanovsky and Osterkamp, 2000). Increased soil moisture and thicker active layers along the road likely promoted the growth of hydrophilic vegetation. This sedge-dominated community was completely dissimilar to the surrounding black spruce forest and unless soil moisture levels change, it is unlikely that black spruce forest will regenerate along the road (Berg et al., 2009; Lloyd et al., 2003).

Ecosystem recovery at alpine treeline was also strongly influenced by the impacts of the road on soil conditions. Road construction through alpine treeline completely removed organic material and increased seasonal maximum and minimum ground temperatures. These harsh environmental conditions almost completely limited revegetation along the road (Fig. 2). The removal of stabilizing vegetation and organic soil layers during construction at alpine treeline may have also slowed subsequent vegetation recovery. The very sparse cover of pioneer species we observed is consistent with work by Harper and Kershaw (1996) and by Bell and Bliss (1973) showing that succession can be limited in extreme environments. Thicker organic soil layers provide protection against harsh environmental conditions, reduce water loss, and stabilize the surface of the ground, all of which enhance natural recovery of vegetation in alpine terrain (Brink, 1964; Chambers et al., 1990; Tscherko et al., 2003). Existing vegetation may facilitate subsequent vegetation recovery by improving microsite conditions (Callaway et al., 2002; Rawls et al., 2003). A large body of literature on severe disturbance to alpine tundra also indicates that ecosystem recovery times may vary anywhere from several centuries to millennia (Bell and Bliss, 1973; Harper and Kershaw, 1996; Haugland and Beatty, 2005; Hodkinson et al., 2003; Scalenghe et al., 2002; Whinam and Chilcott, 1999; Willard and Marr, 1971).

In black spruce parkland, vegetation composition 32 years after road abandonment also suggests that the impacts of the road are likely to persist until the next disturbance. It is probable that reduced organic layer thickness, and warmer ground temperatures following disturbance at these sites led to the establishment of a lodgepole pine sere after road abandonment (Brown, 1975; Johnstone and Chapin, 2006; Viereck, 1983; Ronco, 1967; Sheppard and Noble, 1976). The relative dominance of lodgepole pine recruits over spruce seedlings suggests that pine is likely to persist in the canopy of the disturbed area (Gutsell and Johnson, 2002; Johnstone and Chapin, 2003).

In deciduous forest, road construction transformed an aspen stand to white spruce forest. Although the transition from trembling aspen to a conifer stand is a well-documented successional pattern (Mueggler, 1988; Shepperd et al., 2001), the occurrence of this transition following disturbance is unusual. Other than a reduction in organic layer thickness, environmental conditions in this terrain type were comparable between control and disturbed sites. We believe that, by clearing the dense understory vegetation, litter, and organic soils along the road bed, road construction created favorable microsites for the establishment white spruce (Carlson and Groot, 1997; Constabel and

Lieffers, 1996; DeLong et al., 1997; Greene et al., 2007; Messier et al., 1998; Parker et al., 1997; Simard et al., 1998).

Resilience of Ecosystems Underlain by Discontinuous Permafrost

Sampling along the Prairie Creek road suggests that ecosystems in discontinuous permafrost are susceptible to long-term ecological change when disturbances fundamentally alter soil conditions. Our data show that large structural and compositional dissimilarities between disturbed and undisturbed ecosystems were associated with large differences in soil conditions at disturbed and undisturbed sites. This may be because severe disturbances to soils fundamentally alter stabilizing feedbacks. Increases in soil moisture caused by permafrost degradation in spruce peatland transformed this ecosystem from an open woodland to a sedge-dominated wetland. It is likely that the associated changes in ground temperature and vegetation, and increased soil moisture will prevent permafrost re-aggradation in this terrain type. In alpine treeline, ecological recovery was impaired when road construction removed organic soil layers and surface vegetation that had previously moderated harsh environmental conditions (Chambers et al., 1990). Previous research also suggests that extreme environmental conditions at alpine sites may limit the colonization of pioneer species, preventing ecosystem recovery for centuries (Haugland and Beatty, 2005; Svoboda and Henry, 1987; Willard and Marr, 1971). In black spruce parkland and deciduous forest terrain, changes to soil conditions also led to unexpected vegetation recovery patterns.

Our observations of ecosystem change are consistent with resilience theory, which predicts that changes to key environmental factors increase the likelihood of regime shifts, where an abrupt transition leads to ecosystems with fundamentally different structure and feedbacks (Chapin et al., 2009; Folke et al., 2004; Gunderson, 2000; Thrush et al., 2009). Several previous studies in the subarctic have also described ecosystem change following disturbance. Bauer and Vitt (2011) observed how a peat plateau transitioned into a continental bog-type ecosystem when permafrost thaw occurred following a forest fire. Intense subarctic fires can also lead to a persistent transition from white spruce to lodgepole pine as the dominant, long-term canopy cover (Johnstone and Chapin, 2003). Other research in high-latitude environments has shown that when disturbance alters the environmental factors that helped shape undisturbed vegetation communities, changes to vegetation are likely to persist for centuries (Gill et al., 2014; Harper and Kershaw, 1996; Johnstone and Kokelj, 2008; Lantz et al., 2009; Williams et al., 2013).

Implications

Understanding the long-term impacts of winter road construction and the ecological trajectories of varying terrain types after disturbance can help to inform environmental impact assessments for future road construction proposals in this and other discontinuous permafrost environments.

Our field data suggest that ecosystem recovery and the potential to restore sites to antecedent conditions depend on the magnitude of the impacts to soil conditions and abiotic and biotic processes. Where disturbance promoted permafrost thaw in spruce peatland, alterations to ecosystem configurations are likely to persist for centuries. Horizontal heat flows in wet soils may also drive additional permafrost degradation (Quinton et al., 2011; Romanovsky and Osterkamp, 2000; Jorgenson et al., 2013). The transformations we observed at alpine treeline, black spruce parkland, and in deciduous forest are also likely to persist for decades to centuries as abiotic conditions remain distinct from the predisturbance state.

Variation in the effects of road construction among terrain types also suggests that efforts to predict ecological responses to warming in discontinuous permafrost will be complicated by the potential for multiple successional trajectories. Along the Prairie Creek winter access road, none of the terrain types we assessed returned to predisturbance plant communities and are unlikely to do so. Divergent postdisturbance recovery following road construction emphasizes that ecosystem recovery is not necessarily bound to historical successional trajectories. As air temperatures and disturbance rates continue to increase, we should anticipate persistent changes in ecosystem function in discontinuous permafrost terrain when feedbacks between vegetation communities and soil conditions are disrupted.

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Figure Captions

FIGURE 1. Map of the study area showing field sites in each terrain type along the Prairie Creek access road. Green shading indicates vegetated areas, and white indicates unvegetated areas. Inset map at the bottom left shows the position of the study area in northwestern Canada. The black outline indicates the boundaries of Nahanni National Park Reserve, and the box with the red outline shows the extent of the upper map.

FIGURE 2. Photos of characteristic vegetation communities of each terrain type: (A–C) black spruce parkland, (D–F) spruce peatland, (G–I) deciduous forest, and (J–L) alpine treeline. Aerial views of the terrain types are in the left column, photos of the control transects are in the middle column, and photos of disturbed transects are in the right column.

FIGURE 3. Nonmetric multidimensional scaling ordination of plant community composition based on a Bray-Curtis similarity matrix. Symbols represent control and disturbed plots in the four terrain types.

FIGURE 4. Size class distribution of trees in spruce peatland terrain. Bars show the mean number of trees in a given size class, and error bars represent the standard error of the mean (by site). Control and disturbed sites that have significantly different tree size distributions at a terrain level are marked with three asterisks ($\alpha = 0.05$).

FIGURE 5. Size class distribution of trees in deciduous forest terrain. Bars show the mean number of trees in a given size class, and error bars represent the standard error of the mean (by site). Control and disturbed sites that have significantly different tree size distributions at a terrain level are marked with three asterisks ($\alpha = 0.05$).

FIGURE 6. Size class distribution of trees in black spruce parkland terrain. Bars show the mean number of trees in a given size class, and error bars represent the standard error of the mean (by site). Control and disturbed sites that have significantly different tree size distributions at a terrain level are marked with three asterisks ($\alpha = 0.05$).

FIGURE 7. Abiotic and biotic response variables measured in control and disturbed transects in black spruce parkland, spruce peatland, deciduous forest, and alpine terrain types: (A) volumetric soil moisture (%), (B) organic soil thickness (cm), (C) litter depth (cm), (D) active layer thickness (cm), (E) maximum understory height, and (F) maximum shrub height (cm). Bars and error bars show least square means and standard error for each site type. Significant differences in biotic and abiotic factors between control and disturbed terrain types are indicated with three asterisks ($\alpha = 0.05$, LS Means procedure). Although alpine treeline sites were excluded from statistical analysis, for the purposes of comparison we included the differences between road and control sites in this terrain type. Alpine treeline sites show means, and error bars show ± one standard deviation.

FIGURE 8. Ground temperatures recorded at 10 cm and 100 cm below the ground surface from August 2012 to August 2013 at disturbed (dashed line) and undisturbed (solid line) sites in black spruce parkland, spruce peatland, deciduous forest, and alpine treeline terrain types. Lines show the daily mean temperatures (°C). The dashed reference line shows 0 °C. Each temperature profile is from a single thermistor.

TABLE 1

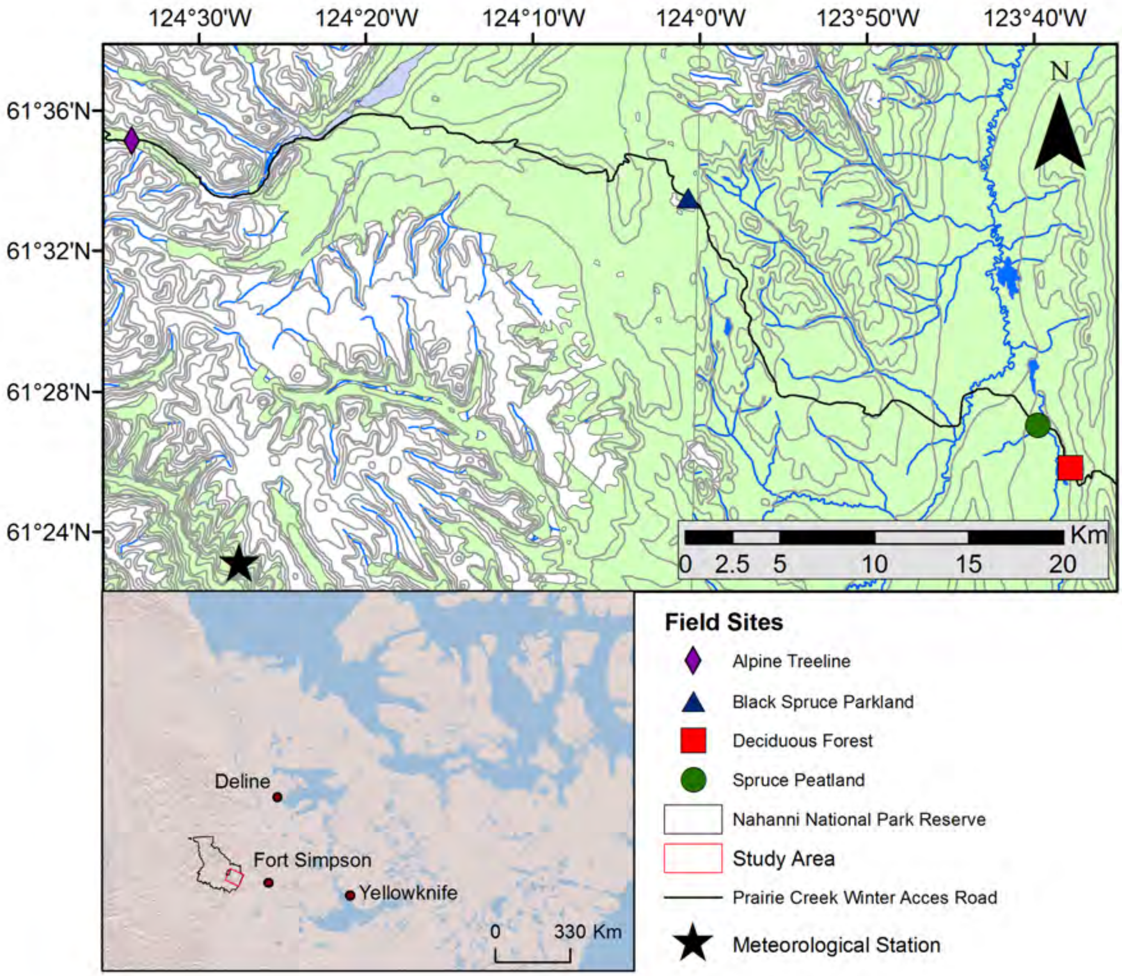
Results from the SIMPER analysis of community composition at disturbed and undisturbed sites in the four terrain types. The top seven species or species groups that contributed to between-group dissimilarity for comparisons of control and disturbed terrain types are shown. Mean cover is expressed as a percentage value.

Terrain Type	Species or Species Group	Mean Cover Control (%)	Mean Cover Disturbed (%)	Cumulative % Dissimilarity
Black Spruce Parkland				
	Mosses	71.65	18.94	7.20
	Betula glandulosa Michx.	13.74	2.73	13.23
	Salix spp.	7.33	16.94	19.01
	Cornus canadensis L.	9.41	4.82	24.68
	Pinus contorta Loud.	4.53	14.88	30.34
	Picea mariana Mill.	17.65	4.20	35.95
	Lichens	8.28	3.09	40.38
Spruce Peatland				
	Sedges	4.44	27.71	7.77
	Mosses	61.38	21.78	15.35
	Litter	10.74	36.09	22.59
	Ledum palustre L.	10.48	0.28	29.47
	Picea mariana Mill.	12.59	2.69	36.06
	Salix spp.	1.79	10.45	41.58
	Betula glandulosa Michx.	5.20	8.05	46.76
Deciduous Forest				
	Populus tremuloides Michx.	28.32	1.46	7.04
	Mosses	21.05	13.30	12.33
	Picea glauca Moench			17.22
	Litter	62.95	32.90	21.17
	Cornus canadensis L.	7.88	2.89	25.01
	Sheperdia canadensis (L.) Nutt.	3.32	8.89	28.73
	Vibernum edule Michx.	6.71	0.13	32.37
Alpine Treeline				
	Betula glandulosa Michx.	32.70	0.00	13.54
	Mosses	46.00	0.00	25.81
	Lichens	34.80	0.00	37.58
	Dryas integrifolia (M.) Vahl	0.00	15.33	48.45
	Vaccinium vitis-idaea L.	10.10	0.00	57.08
	Ledum groenlandicum Oeder	9.40	0.00	65.38
	Picea glauca Moench	15.90	0.00	71.28

TABLE 2

Mixed model results for biotic and abiotic response variables (α = 0.05, LS Means procedure). Terrain Type has four levels: black spruce parkland, spruce peatland, deciduous forest, and alpine treeline. Disturbance has two levels: control and disturbed.

Response Variable	Effect	*F* Value	*P* Value	Degrees of Freedom
Soil Moisture	Terrain Type	30.41	<0.0001	2, 50.1
	Disturbance Level	26.82	<0.0001	2, 50.1
	Terrain Type * Disturbance Level	13.86	<0.0001	2, 50.1
Organic Soil Thickness	Terrain Type	178.11	<0.0001	2, 50.27
	Disturbance Level	54.12	<0.0001	1, 50.27
	Terrain Type * Disturbance Level	14.31	<0.0001	2, 50.27
Litter Depth	Terrain Type	12.53	<0.0001	2, 50.04
	Disturbance Level	2.73	0.1048	1, 50.05
	Terrain Type * Disturbance Level	11.91	<0.0001	2, 50.04
Active Layer Thickness	Terrain Type	0.02	0.9002	1,34.25
	Disturbance Level	2.20	0.1471	1,34.25
	Terrain Type * Disturbance Level	2.49	0.1241	1,34.25
Understory Height	Terrain Type	20.86	<0.0001	2, 50.07
	Disturbance Level	10.19	0.0024	1, 50.08
	Terrain Type * Disturbance Level	4.49	0.0161	2, 50.07
Shrub Height	Terrain Type	13.13	<0.0001	2, 50.14
	Disturbance Level	0.04	0.8376	1, 50.15
	Terrain Type * Disturbance Level	1.24	0.2992	2, 50.14



124°30'W
124°20'W
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0 2.5 5 10 15 20
Deline
Fort Simpson
Yellowknife
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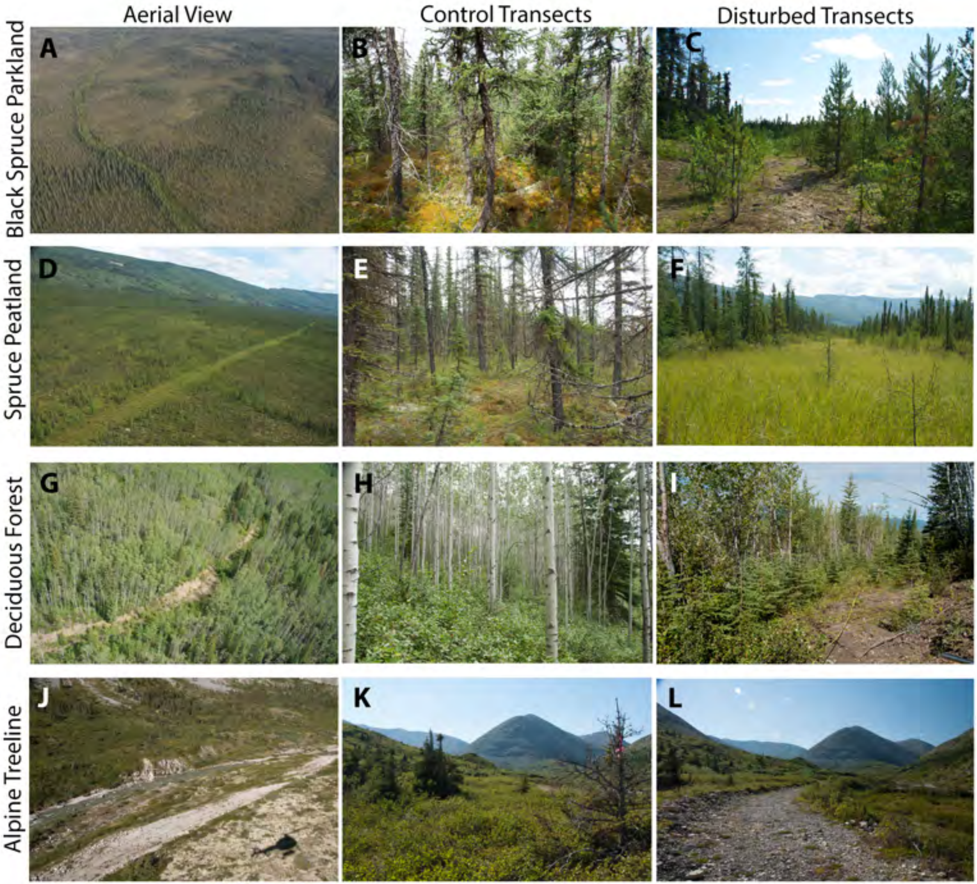
Field Sites
Alpine Treeline
Black Spruce Parkland
Deciduous Forest
Spruce Peatland
Nahanni National Park Reserve
Study Area
Prairie Creek Winter Acces Road
Meteorological Station


Aerial View
Control Transects
Disturbed Transects
Black Spruce Parkland
Spruce Peatland
Deciduous Forest
Alpine Treeline
A
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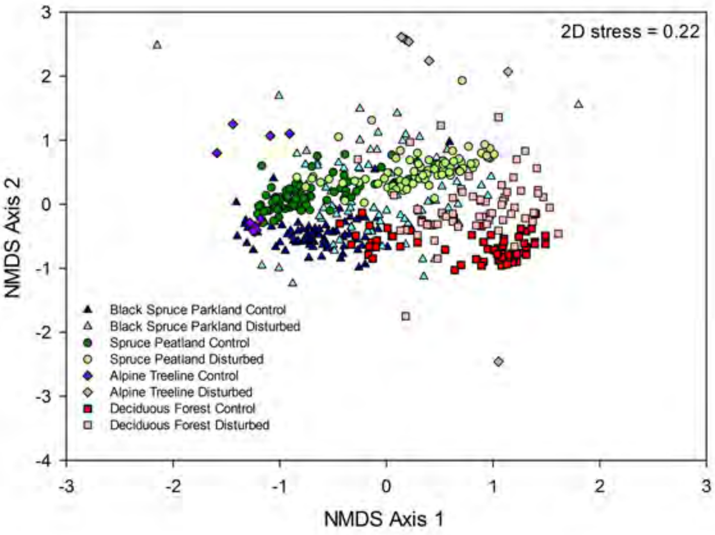
2D stress = 0.22
NMDS Axis 2
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3
2
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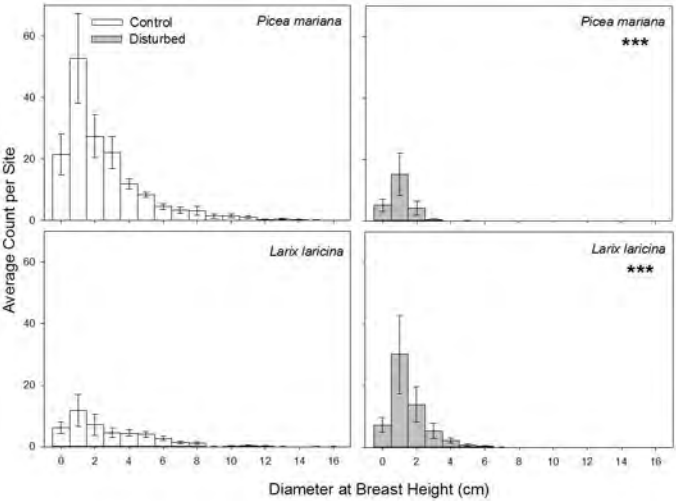
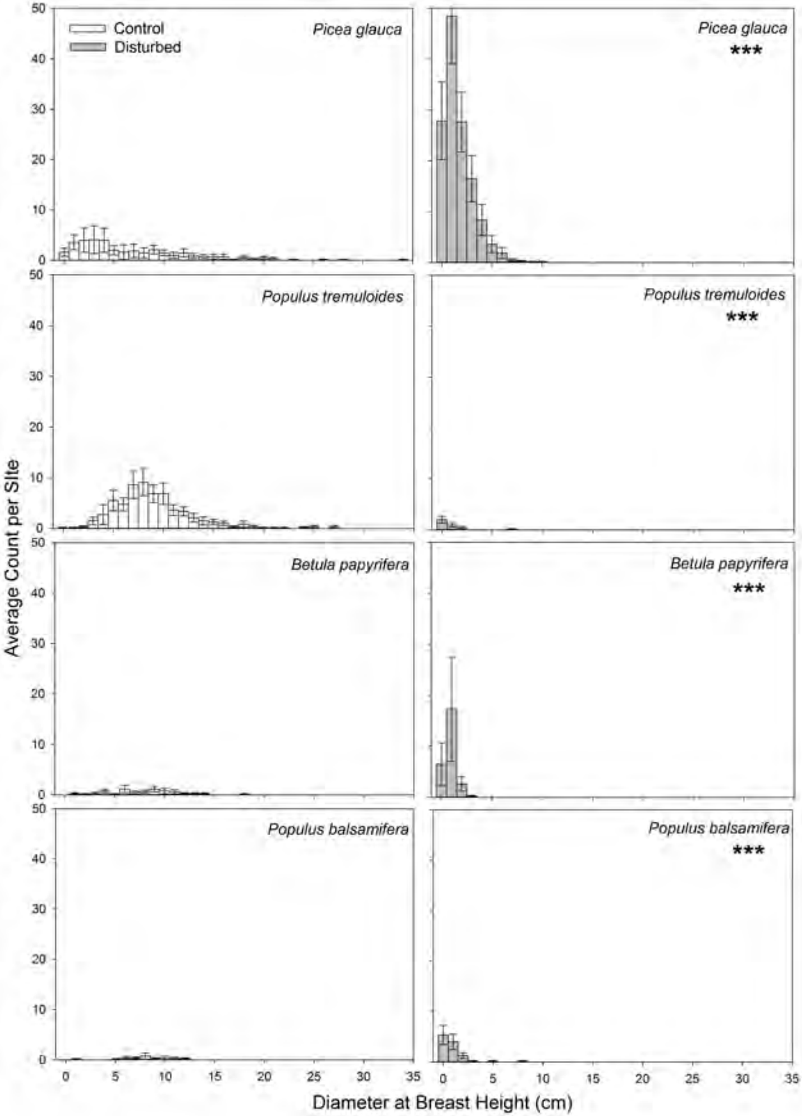
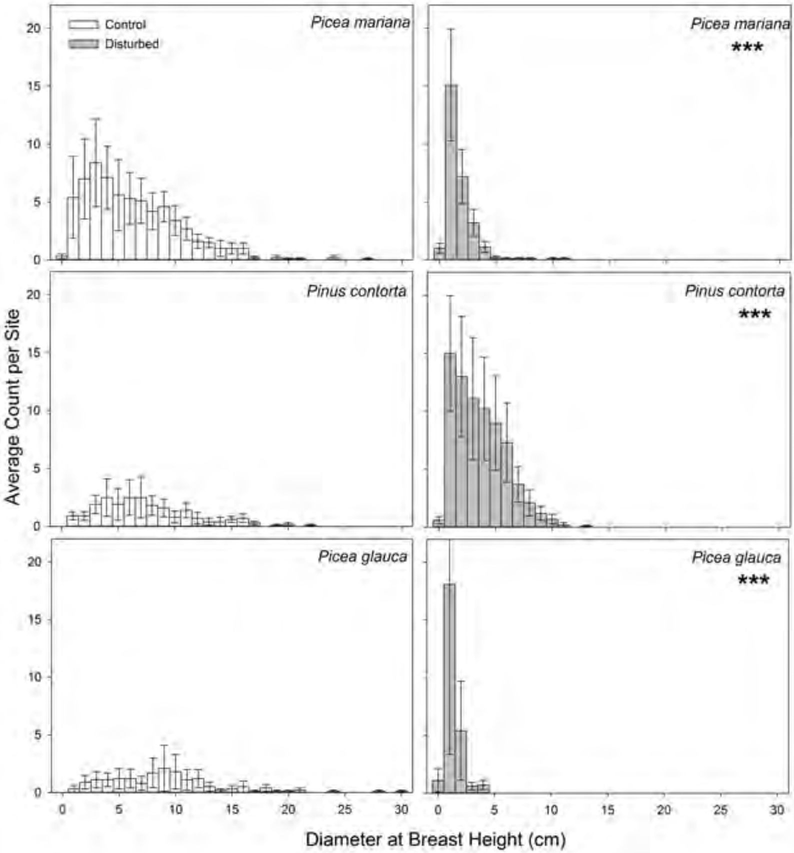
Black Spruce Parkland Control
Black Spruce Parkland Disturbed
Spruce Peatland Control
Spruce Peatland Disturbed
Alpine Treeline Control
Alpine Treeline Disturbed
Deciduous Forest Control
Deciduous Forest Disturbed

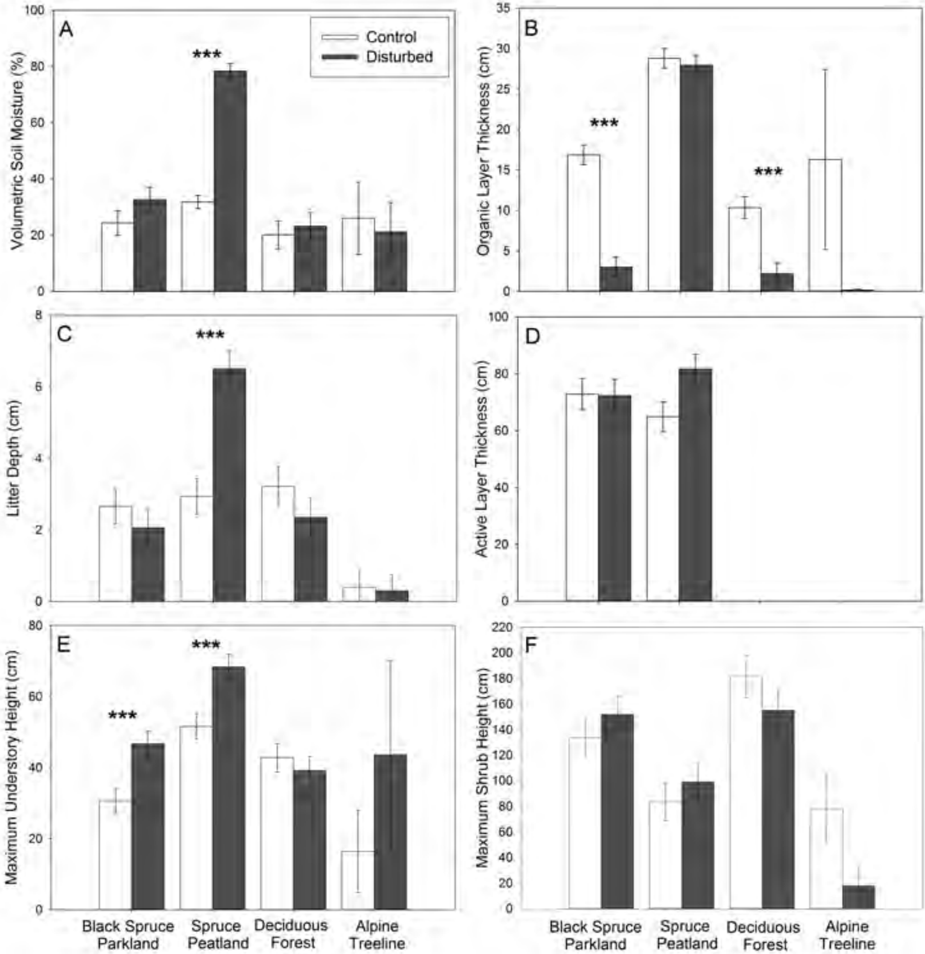


Control
Disturbed
Picea mariana
Picea mariana
***
Larix laricina
Larix laricina
***
Average Count per Site
Diameter at Breast Height (cm)

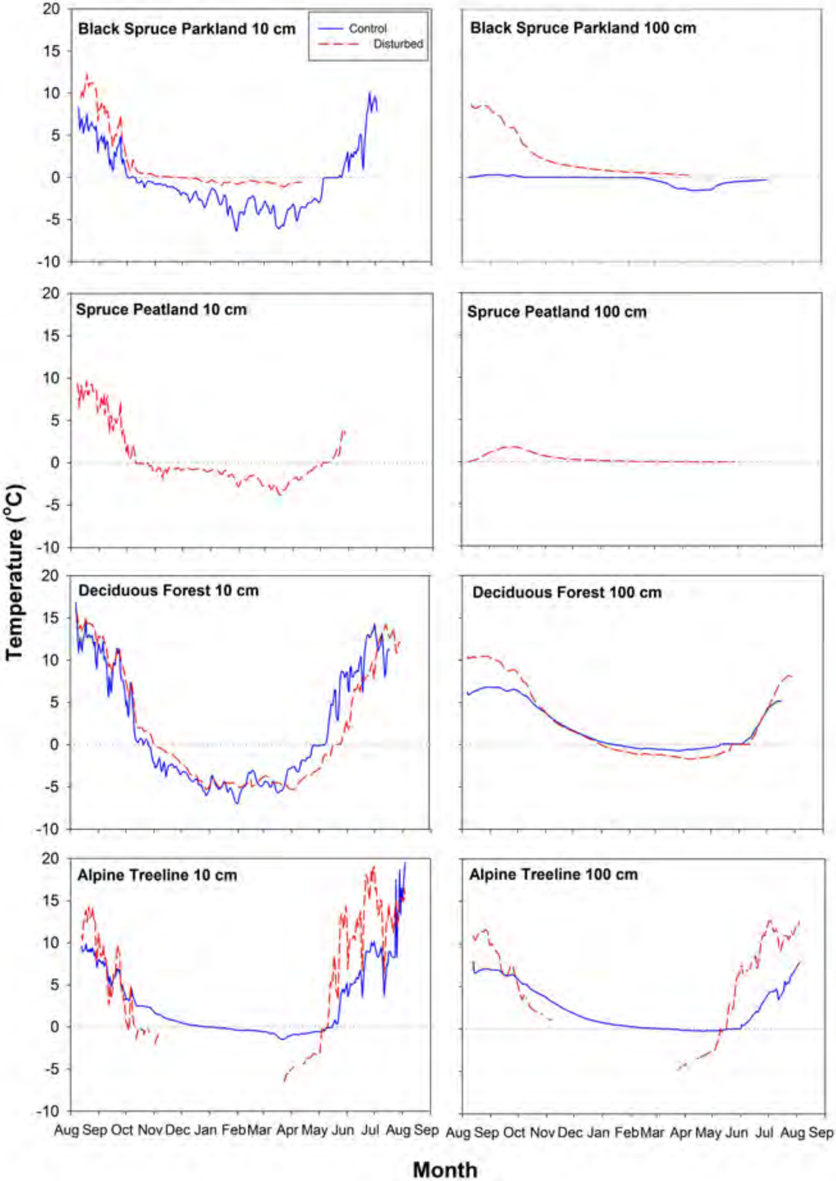


Control
Disturbed
Picea glauca
Picea glauca
***
Populus tremuloides
Populus tremuloides
***
Betula papyrifera
Betula papyrifera
***
Populus balsamifera
Populus balsamifera
***
Average Count per Site
Diameter at Breast Height (cm)
0
5
10
15
20
25
30
35
10
20
30
40
50


Control
Disturbed
Picea mariana
Picea mariana
***
Pinus contorta
Pinus contorta
***
Picea glauca
Picea glauca
***
Average Count per Site
Diameter at Breast Height (cm)
0
5
10
15
20
25
30



A
Control
Disturbed
***
Volumetric Soil Moisture (%)
B
***
***
Organic Layer Thickness (cm)
C
***
Litter Depth (cm)
D
Active Layer Thickness (cm)
E
***
***
Maximum Understory Height (cm)
F
Maximum Shrub Height (cm)
Black Spruce Parkland
Spruce Peatland
Deciduous Forest
Alpine Treeline



Black Spruce Parkland 10 cm
Control
Disturbed
Black Spruce Parkland 100 cm
Spruce Peatland 10 cm
Spruce Peatland 100 cm
Deciduous Forest 10 cm
Deciduous Forest 100 cm
Alpine Treeline 10 cm
Alpine Treeline 100 cm
Temperature (°C)
20
15
10
5
0
-5
-10
Aug Sep Oct Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep
Month