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Fuel-reduction management alters plant composition, carbon and nitrogen pools, and soil thaw in Alaskan boreal forest

April M. Melvin,[1,2,8] Gerardo Celis,[3] Jill F. Johnstone,[4] A. David McGuire,[5] Helene Genet,[6] Edward A. G. Schuur,[3] T. Scott Rupp,[7] and Michelle C. Mack[3]

[1]*Independent Researcher, Washington, D.C. 20001 USA*
[2]*Department of Biology, University of Florida, Gainesville, Florida 32611 USA*
[3]*Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona 86011 USA*
[4]*Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2 Canada*
[5]*U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA*
[6]*Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska 99775 USA*
[7]*Scenarios Network for Alaska & Arctic Planning, University of Alaska, Fairbanks, Alaska 99775 USA*

Abstract. Increasing wildfire activity in Alaska's boreal forests has led to greater fuel-reduction management. Management has been implemented to reduce wildfire spread, but the ecological impacts of these practices are poorly known. We quantified the effects of hand-thinning and shearblading on above- and belowground stand characteristics, plant species composition, carbon (C) and nitrogen (N) pools, and soil thaw across 19 sites dominated by black spruce (*Picea mariana*) in interior Alaska treated 2–12 years prior to sampling. The density of deciduous tree seedlings was significantly higher in shearbladed areas compared to unmanaged forest (6.4 vs. 0.1 stems/m^2), and unmanaged stands exhibited the highest mean density of conifer seedlings and layers (1.4 stems/m^2). Understory plant community composition was most similar between unmanaged and thinned stands. Shearblading resulted in a near complete loss of aboveground tree biomass C pools while thinning approximately halved the C pool size (1.2 kg C/m^2 compared to 3.1 kg C/m^2 in unmanaged forest). Significantly smaller soil organic layer (SOL) C and N pools were observed in shearbladed stands (3.2 kg C/m^2 and 116.8 g N/m^2) relative to thinned (6.0 kg C/m^2 and 192.2 g N/m^2) and unmanaged (5.9 kg C/m^2 and 178.7 g N/m^2) stands. No difference in C and N pool sizes in the uppermost 10 cm of mineral soil was observed among stand types. Total C stocks for measured pools was 2.6 kg C/m^2 smaller in thinned stands and 5.8 kg C/m^2 smaller in shearbladed stands when compared to unmanaged forest. Soil thaw depth averaged 13 cm deeper in thinned areas and 46 cm deeper in shearbladed areas relative to adjacent unmanaged stands, although variability was high across sites. Deeper soil thaw was linked to shallower SOL depth for unmanaged stands and both management types, however for any given SOL depth, thaw tended to be deeper in shearbladed areas compared to unmanaged forest. These findings indicate that fuel-reduction management alters plant community composition, C and N pools, and soil thaw depth, with consequences for ecosystem structure and function beyond those intended for fire management.

Key words: Alaska; black spruce; Boreal forest; carbon; deciduous; fuel reduction; nitrogen; permafrost thaw; Picea mariana; *soil; wildfire.*

Introduction

Across interior Alaska, climate change-driven warming and drying has been linked to an increase in the frequency, extent, and severity of wildfires (Flannigan et al. 2009, Kasischke et al. 2010, Kelly et al. 2013, Calef et al. 2015). Concurrently, there has been an increase in human settlement within the wildland–urban interface, heightening the potential for direct human exposure to wildland fires and property loss (Berman et al. 1999, Cohen 2000). In response to these changes, fire fighting agencies have increased the use of fuel-reduction treatments in inhabited areas. These treatments are designed to lessen the severity of wildfires, reduce the likelihood of fire spread, and make areas more defensible if fire occurs (Ott and Jandt 2005). Presently, it is estimated that about 40–80 ha have been thinned and 800–2,000 ha have been shearbladed in the Interior (unpublished values based on expert knowledge of authors and other wildfire management colleagues). While this forest management approach is an important tool for lessening wildland fire risks, it introduces a novel disturbance to Alaska's boreal forests that may facilitate changes in ecosystem structure, carbon (C) and nutrient dynamics, and permafrost stability.

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[8] E-mail: aprilmmelvin@gmail.com

Fuel-reduction management techniques currently used in interior Alaska are generally known to be effective in the western contiguous United States (Agee and Skinner 2005, Ager et al. 2007, Stephens et al. 2009) and include manual forest thinning and mechanical harvesting known as shearblading (Butler et al. 2013). These practices are intended to remove aboveground tree biomass. Manual thinning reduces stem density and often includes the removal of ladder fuels (lower limbs) on the remaining trees, to reduce the likelihood of fire spread from the forest floor into the canopy (Graham et al. 1999). Shearblading involves using heavy equipment to remove all aboveground tree biomass, but can also disturb soils, including the removal of a portion or all of the soil organic layer (SOL). These techniques are commonly used in stands of black spruce (*Picea mariana* [Mill.] B. S. P.), a highly flammable tree species that dominates Alaska's boreal forests and is underlain by permafrost in many areas (Van Cleve et al. 1983*a*). Black spruce has low net primary productivity (Yarie and Billings 2002) and is not commercially harvested. Therefore, harvested trees and any disturbed SOL are typically piled on site, given time to dry, and then burned.

The biogeochemical and ecological implications of fuel-reduction treatments in black spruce forest remain largely undocumented. We are aware of only one peer-reviewed publication that evaluated how shearblading and thinning may alter fire behavior in Alaska (Butler et al. 2013) and no studies that have quantified how fuel-reduction affects C and nutrient pools, permafrost thaw, and ecosystem processes. In addition to C and nutrients lost from the physical removal of biomass and SOL material, harvest disturbances could influence permafrost thaw and plant succession. Aboveground biomass removal in managed areas has been shown to increase radiation at the soil surface (Yarie 1993) and soil warming in floodplain white spruce (*Picea glauca* [Moench]) in interior Alaska (Viereck et al. 1993), in harvested black spruce in Québec, Canada (Smith et al. 2000), and in other forest types within the boreal region (Kreutzweiser et al. 2008, Kulmala et al. 2014). Removal of the SOL could further warm soils. Thick, moss-dominated SOLs commonly found in black spruce forest have low bulk density and thermal conductivity, and high water-holding capacity that keeps soils cool (O'Donnell et al. 2009, Turetsky et al. 2012) and protects permafrost from thaw (Van Cleve et al. 1983*a*, Jorgenson et al. 2010). Loss of the SOL from fire disturbances (Yoshikawa et al. 2002, Viereck et al. 2008, Nossov et al. 2013, Brown et al. 2015) and bulldozed firebreaks (Viereck 1982, Mackay 1995, Nicholas and Hinkel 1996) has led to soil warming and permafrost degradation in black spruce stands. Collectively, these findings suggest that fuel-reduction treatments in black spruce stands are likely to increase soil temperatures, thereby increasing the likelihood of permafrost thaw.

Fuel-reduction treatment in black spruce forest may also affect establishment of understory plants and trees. In interior Alaska, shearblading was noted to cause declines in moss and increases in grasses and sedges, while thinning had little impact on understory species composition (Butler et al. 2013). Clearcutting and logging in mixed species and conifer-dominated stands in other parts of the boreal region have also resulted in an increase in abundance of deciduous broadleaf trees (Carleton and MacLellan 1994, McRae et al. 2001, Taylor et al. 2013). Similarly, increased fire severity that reduces residual SOLs or exposes mineral soil have been associated with increased establishment of broad-leaf deciduous trees (Johnstone et al. 2010*a*, *b*, Gibson et al. 2016).

We quantified the effects of thinning and shearblading on C and nitrogen (N) pools, soil thaw, and vegetation composition across 19 black spruce-dominated areas in interior Alaska. Fuel-reduction management was conducted between 2 and 12 years prior to our sampling. In addition to sampling treated areas, we sampled adjacent, unmanaged stands at each location to serve as a reference. We expected managed areas to exhibit relatively smaller aboveground and SOL C and N pools, deeper soil thaw depth, and differences in understory vegetation, including higher deciduous tree seedling abundance. We anticipated that shearblading would have a larger effect than thinning on measured characteristics because of the mechanical harvesting process and greater biomass removal associated with this treatment type.

Methods

Sampled sites

We sampled seven hand-thinned and 12 shearbladed sites located in interior Alaska during summer 2012 and 2013 (Table 1, Fig. 1). These were all the treated sites in the Interior that we identified and were able to gain access. Adjacent, unmanaged stands dominated by black spruce were also sampled at each location. The year of fuel-reduction treatment varied across sites and ranged from approximately 2 to 12 years prior to our sampling. Harvested biomass was burned on site within a few years of treatment for all sites except Chena Hot Springs Road North, where very little tree biomass was present. At Chena Hot Springs Road South, and Harding Lake site 1, burned windrows did not combust fully and large quantities of woody debris were present at the time of sampling.

For most study sites, we established two transects 20 m in length and located approximately 20 m apart in each fuel-reduction treated area and adjacent unmanaged black spruce stand. When the location of burned windrows or piles were evident in treated stands, the transects were situated so that they crossed the burned area, to capture site heterogeneity in SOL characteristics and woody debris. The fuel-reduction treatment design for the Badger Road, Delta, and Toghotthele sites was considerably different from all other locations and required a modification to the site sampling methods outlined above. These

TABLE 1. Site name (and abbreviation), location in interior Alaska, and year of treatment and sampling for each site included in the study.

Site name	Latitude (N)	Longitude (W)	Cut year†	Sample year
Thinned				
Badger Road (BAD)	64°49′22.55″	−147°32′58.75″	2001	2013
Delta (DEL)	63°49′49.00″	−144°58′26.34″	2002	2013
Eielson Air Force Base (EAFBTH)	64°41′38.83″	−146°56′13.86″	2008	2012
Fort Greely thinned (FTGTH)	63°59′22.83″	−145°37′59.66″	2005	2013
Harding Lake site 3 (HDL3)	64°26′48.51″	−146°54′11.82″	2010	2012
Nenana Ridge‡ (NRTH)	64°37′41.01″	−148°43′18.85″	2006	2013
Toghotthele (TOG)	64°43′7.47″	−148°46′42.44″	2001	2013
Shearbladed				
Cache Creek Road (CCR)	64°52′42.39″	−148°19′2.27″	2007	2012
Chena Hot Springs Road North (CHSRN)	64°53′59.17″	−147°16′31.47″	2007	2012
Chena Hot Springs Road South (CHSRS)	64°52′46.42″	−147°13′7.26″	2010	2012
Eielson Air Force Base (EAFBS)	64°41′41.02″	−146°56′24.59″	2008	2012
Fort Greely site 1§ (FTG1)	63°59′18.25″	−145°37′48.29″	2007	2012
Fort Greely site 2 (FTG2)	63°58′21.09″	−145°36′50.20″	2005	2012
Fort Greely site 3 (FTG3)	63°59′10.31″	−145°38′14.99″	2005	2012
Harding Lake site 1 (HDL1)	64°26′33.37″	−146°49′57.09″	2009	2012
Harding Lake site 2 (HDL2)	64°26′42.74″	−146°47′20.21″	2009	2012
Harding Lake site 4 HDL4)	64°25′48.90″	−146°48′28.10″	2008	2012
Nenana Ridge‡ (NRS)	64°37′38.94″	−148°42′42.45″	2006	2012
Old Murphy Dome Road East (OMDE)	64°57′44.45″	−148°2′39.44″	2008	2012
Old Murphy Dome Road West (OMDW)	64°57′11.79″	−148°11′15.75″	2007	2012

†Many harvests were conducted in winter months that spanned two calendar years. The years listed here indicate when harvesting began.
‡Tree seedling data was also collected in 2011 in a separate experimental block at this site.
§Site was ripper-plowed, in addition to being shearbladed.

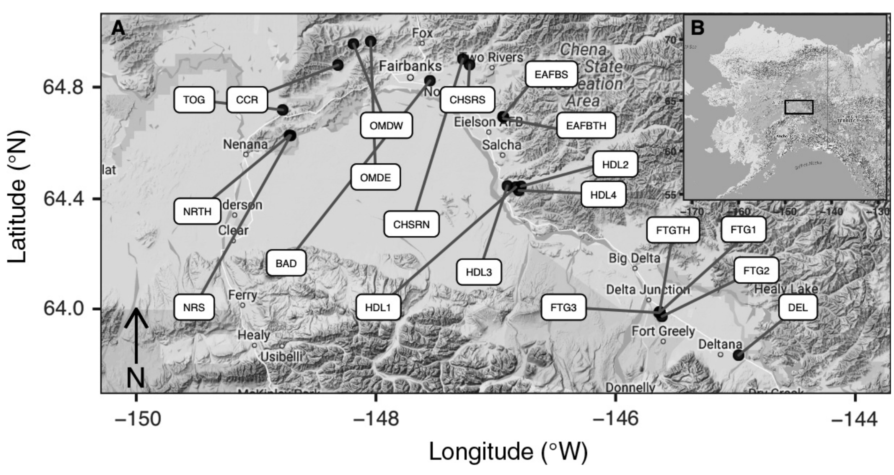

FIG. 1. Map showing (A) the location of sampled sites across (B) interior Alaska. Full site names, coordinates, and treatment information is in Table 1.

sites consisted of 9 × 9 m sampling plots that were unmanaged or thinned to multiple tree spacings situated within larger treated areas (see Ott and Jandt [2005] for details). We sampled plots in two treatments that were hand-thinned to specifications of 2.4 × 2.4 m and 3 × 3 m spacing of trees, in which ladder fuels had also been removed, and paired these with two unmanaged plots at each site. Unlike other sampled sites, harvested tree biomass was not burned on site, but instead was manually removed from the plots. Because of the small plot size, we shortened our sampling transects to 7 m length and positioned the two transects at least 1 m from the plot edge and 2 m from each other. We also included data on tree seedling establishment that we collected in 2011 along three 30-m transects sampled at 5-m intervals in shearbladed and thinned stands at the Nenana Ridge site. These samples were located in a separate experimental block than the areas sampled in 2013.

Vegetation and woody debris

All live and standing dead trees and tall shrubs ≥1.4 m tall (diameter at breast height, DBH) rooted within 1 m of either side of the transect line were identified by species and DBH was recorded. Fallen dead trees standing at an angle of >45 degrees were categorized as standing dead and DBH measurements were recorded. Dead trees lying at an angle <45 degrees were considered part of the downed woody debris pool. Biomass of woody species was estimated using allometric equations reported by Alexander et al. (2012) for trees and Berner et al. (2015) for tall shrubs. For dead trees, biomass values were multiplied by 0.5 to account for the observation that many dead trees had lost crown and upper stemwood biomass, which we did not quantify in this study. We assumed the C concentration of all live and dead wood to be 50% for estimation of aboveground C pool sizes.

The density of seedlings and trees ≤1.4 m in height was estimated using five 1 × 1 m quadrats placed at random locations (and five fixed locations for the 2011 Nenana Ridge sampling, using a 0.5 × 0.5 m quadrat) along each sampling transect. Within each quadrat, all seedlings and small trees were counted and species identification was recorded. Layering in black spruce was also included in the seedling counts for this species. Values were standardized to number of stems per square meter prior to statistical analysis. Abundance and composition of understory vegetation was assessed using the point intercept method (Goodall 1952). Every 1 m along the transect, a pin flag was dropped and the number of hits were recorded for some specific plant species and many plant functional types including *Betula nana*, *Salix* spp., other deciduous shrubs, evergreen shrubs, sedges, grasses, graminoids, *Equisitum* spp. and other forbs, and *Lycopodium* spp. For general types, the most abundant plant species was also recorded. The composition of the ground cover at the point location was also noted, with ground layer types including sphagnum moss, feather moss, lichen, litter, liverworts, burned and unburned coarse woody debris, burned and unburned SOL, and bare mineral soil. Values were standardized by dividing the total number of hits by the number of sampling points along each transect.

Downed woody debris was quantified using the line intercept method (Brown 1974) along each sampling transect. All dead woody material residing on the surface of the SOL or the mineral soil (if no SOL was present) was considered to be part of the downed woody debris pool, in addition to dead trees lying at an angle <45 degrees. Fine woody debris was categorized into five size classes and the number of intercepts of each size class was recorded and converted to wood mass using black spruce multiplier values reported in Nalder et al. (1997). Coarse woody debris with a diameter ≥7 cm was converted to area using methods described in Ter-Mikaelian et al. (2008). Similar to aboveground biomass, we assumed wood to be 50% C and multiplied the estimated biomass values by 0.5 to calculate woody debris C pool sizes.

Soils

The SOL was characterized in the same quadrats used to estimate seedling density. The depth of the SOL (extending from the SOL surface to the mineral soil) was estimated by removing an intact block of organic material with a surface area of approximately 10 × 10 cm using a knife, then recording the depth of each organic horizon using a ruler. At two of the five sampling locations along each transect, we collected the 10 × 10 cm SOL block and the top 10 cm of mineral soil (6.9 cm diameter core) immediately below the SOL for additional soil characterization. All collected samples were put on ice, then frozen until laboratory analysis. In some shearbladed locations, no SOL was present and only mineral soils were collected. At other locations, frozen mineral soil was encountered in the 10 cm increment and collected cores were shallower than 10 cm. This was taken into consideration when estimating soil C and N pools, as detailed later in this section. Soil thaw depth was estimated adjacent to each of the soil sampling locations using a 1.5–2 m steel probe that was inserted into the ground until ice was hit. These thaw depth measurements were taken at the time of soil sampling, in mid-summer (between 9 and 26 July for sites sampled in 2012 and 10 July and 9 August for 2013). The maximum thaw depth (or active layer depth) is reached in the fall season and was not measured in this study. At the Badger Road, Delta, and Toghotthele sites, where sampled areas were smaller, we measured SOL depth and thaw depth at two locations along each transect and collected soils at one location per transect. Values reported here for thaw depth have been normalized to account for differences in SOL depth and represent the thaw depth of only the mineral soil underlying the SOL.

In the laboratory, soil samples were removed from the freezer and allowed to thaw prior to processing. Because of the large volume of many SOL samples, the blocks were split in half vertically using an electric cutter and only one half the core was processed. Vascular plant material was removed from the surface of all SOL blocks and the SOL block was then weighed and dimensions (length, width, height) were recorded. Green moss was then clipped off the SOL surface while the block was still intact and dimensions without the moss were recorded. Next, the SOL block was pulled apart by hand and coarse roots (>2 mm in diameter) and large pieces of non-decayed wood that were embedded in the SOL block were removed. These components were weighed wet, dried at 60°C for at least 48 h, then re-weighed. The remaining SOL block was then thoroughly homogenized using pruners. A representative subsample was then weighed wet and dried at 60°C to estimate moisture content and for C and N analysis. Mineral soil cores were split into 0–5 cm and 5–10 cm increments for processing. Each 5-cm depth increment was pulled apart by hand and rocks and >2 mm roots were removed. Roots were weighed wet, dried at 60°C, then weighed dry. Rock volume was estimated by water displacement in a graduated cylinder.

Mineral soil samples were then homogenized using pruners to chop any fine roots, and a subsample was weighed and dried at 110°C to estimate moisture content. An additional subsample was dried at 60°C for C and N analysis.

Dried green moss and homogenized organic material were ground in a Wiley mill (model 3383-L10; Thomas Scientific, Swedesboro, New Jersey, USA) or coffee grinder and mineral soil was ground with a mortar and pestle. The ground samples were then analyzed for percent C and N using a Costech Analytical ECS 4010 Elemental Analyzer (Costech, Valencia, California, USA).

To estimate soil C and N pool sizes for the SOL, we combined information from field-collected samples processed in the laboratory with measurements taken only in the field to, increase our sampling size and ability to capture soil heterogeneity. First, we calculated sample-specific C and N pool sizes by multiplying the %C and %N values by the sample bulk density (where bulk density was determined to be the dry weight of the sample divided by the total sample volume), multiplied by the sample depth. We then multiplied site-level means of the %C, %N, and bulk density data from the field-collected samples with the field-only SOL depth measurements to estimate C and N pool sizes for field-only samples. The SOL results presented here are the combination of the laboratory-processed sample results and the field-only data. Mineral soil C and N pool sizes were calculated using only field-collected, laboratory-processed samples. For these samples, non-rock volume was used in estimating bulk density. Most samples were 5 cm in depth (0–5 cm and 5–10 cm increments were analyzed separately), however when samples were not 5 cm, the %C, %N, and bulk density data were multiplied by 5 to normalize all samples to the same metric. In the limited instances in which no sample within the 5–10 cm depth increment was collected, no sample for that increment was included in the analysis for that site. Ecosystem C stocks were calculated by summing the mean estimated C values at each site (on an area basis) for all measured pools.

Statistics

We utilized a variety of statistical approaches to evaluate the relationships among treatment types that account for small and uneven sample sizes, skewed data distributions, site variation, and differences in sampling date. For aboveground stand characteristics (including aboveground tree biomass, basal area, stem density, and woody debris), calculated values represent transect-level estimates, resulting in a small sample size for our statistical tests (n = 18 unmanaged, 7 thinned, and 12 shearbladed areas sampled). The distribution of these data sets was also often skewed and contained many low values and zeros for the shearbladed areas. To reduce the influence of inherent site variability on our evaluation of management effects, we performed our analyses on site-level mean differences between the treated and unmanaged areas (i.e., thinned minus unmanaged or shearbladed minus unmanaged for each site). For the Eielson Air Force Base site, the same unmanaged area was used as the reference for calculating differences for both thinned and shearbladed analyses because of limited unmanaged forest in close proximity to the treated areas. Using these relative differences as our inputs, we performed a Bayesian Bootstrap analysis in R (Bååth 2016). This method included 4,000 draws each for the site-level differences for each variable, followed by calculation of the posterior mean difference. This test does not make assumptions about data distribution and is appropriate for small sample sizes. We also used this bootstrapping approach to analyze our thaw depth measurements. We sampled thaw depth on only one date at each site during mid-summer (July–August) in either 2012 or 2013, so it is unlikely the soils had reached maximum thaw depth for the given year. Also, because we measured sites in one of two different years, interannual variability may have influenced our measured values. Therefore, we determined that evaluating the difference between the adjacent unmanaged and managed areas (that were measured on the same date at any given site) was most appropriate. For all analyses where we used the Bayesian Bootstrap approach, we present the absolute values based on field measurements in the main text (with no statistical analysis), as well as the site-level mean differences produced in the bootstrap analysis, with associated 2.5% and 97.5% quantiles. The statistical significance reported in the main text with the bootstrap values relate to the bootstrap-determined treatment differences (i.e., the difference between the thinned or shearbladed minus unmanaged) provided in Appendix S1: Table S1. Treatments were considered significantly different from each other if the established quantiles (95% probability) posterior mean difference distribution did not include zero.

Relationships between SOL depth and thaw depth were explored using a linear mixed effects model in R (nlme package; Pinheiro et al. 2016) with study site as a random effect and subsite (which influenced only the Nenana Ridge site experimental blocks) nested within site. Week of sampling was tested as a covariate to determine whether sampling date had a measureable influence on observed relationships for thaw depth. Patterns between year since treatment and thaw depth were also evaluated for treated areas using the same linear mixed effects model.

Our seedling data (standardized to number of stems/m^2), also exhibited a skewed distribution. To account for this, we used a generalized linear mixed model in R, with a zero-inflated Poisson distribution (glmmADMB package; Fournier et al. 2012, Skaug et al. 2016). This model included site as a random effect and subsite nested within site. A post-hoc Tukey's test was used to determine differences among stand types. To investigate possible relationships between seedling abundance and the SOL depth and time since treatment, we used a stepwise regression with forward selection that included these covariates. All models were then compared using likelihood ratio Chi-square test to determine whether the model improved with the addition of each new parameter.

To determine whether differences in plant composition and ground cover types were evident, we used the non-metric multidimensional scaling (NMDS) vegan package function metaNMDS in R (Oksanen et al. 2016). This is a rank-based ordination approach well suited for non-linear and non-normal distributions and allows for evaluation of community patterns across treatment types. The metaNMDS used a Bray-Curtis dissimilarity coefficient calculated from an initial matrix of 36 samples (one mean value per site, for each of the included treatment and unmanaged areas, with one site with zero vegetation excluded) and nine vegetation types (*Betula nana*, *Salix* spp., other deciduous shrubs, evergreen shrubs, sedges, grasses, graminoids, *Equisitum* spp. and other forbs, and *Lycopodium* spp.) for the plant composition analysis. An initial matrix of 36 samples and 10 ground cover types (sphagnum moss, feather moss, lichen, litter, liverworts, burned and unburned coarse woody debris, burned and unburned SOL, and bare mineral soil) was included for the ground cover analysis. In both analyses, the two-dimensional solutions were determined to be adequate based on the goodness of fit (stress lower than 0.2). We then tested differences among stand types using average projections for each level (unmanaged, thinned, and shearbladed) using the envfit function. To evaluate relationships between community composition and both SOL depth and years since treatment, we used the ordisurf function in the R vegan package, which relies on a Generalized Additive Model (GAM) to evaluate relationships and report the adjusted R^2 and approximate significance of smooth terms for the fitted response surface using Restricted Maximum Likelihood (REML) within this function.

Differences in the SOL, mineral soil, and coarse root pools, as well as bulk density, were evaluated using a linear mixed effects model in R (nlme package, Pinheiro et al. 2016) with the same nesting described for seedlings, and a post-hoc Tukey's test to determine differences among the stand types. Similarly, total measured ecosystem C stocks were evaluated using a mixed-effects model, with site as the random effect.

Results

Aboveground stand characteristics

Across study sites, unmanaged black spruce forest stored an average of 3.1 kg C/m^2 in aboveground biomass while thinned stands contained 1.2 kg C/m^2 and approximately zero biomass was observed in shearbladed areas (Table 2). The mean difference in aboveground live biomass C pools and live tree basal area between adjacent unmanaged and managed stands was about twice as large at shearbladed sites compared to thinned (Table 2), resulting in a statistically significant difference in the bootstrapping analysis (mean and quantile output included in Appendix S1: Table S1 for all aboveground analyses). Differences in standing dead tree biomass C were not significant between treatments

Table 2. Field-based estimates of aboveground stand characteristics (mean with standard error in parentheses) and mean differences between adjacent treated and unmanaged stands, with Bayesian bootstrap-calculated 2.5% and 97.5% quantiles.

	Site means			Site mean differences and bootstrapping results						
				(Thinned − Unmanaged)			(Shearbladed − Unmanaged)			
Parameter	Unmanaged	Thinned	Shearbladed	Mean difference	2.5%	97.5%	Mean difference	2.5%	97.5%	Significance
Live tree biomass (kg C/m^2)	3.1 (0.5)	1.2 (0.2)	0.0 (0.0)	−1.7 (0.5)	−2.5	−2.0	−3.3 (0.7)	−5.0	−2.3	*
Dead tree biomass (kg C/m^2)	0.2 (0.1)	0.02 (0.02)	0.0 (0.0)	−0.1 (0.1)	−0.2	−0.04	−0.2 (0.1)	−0.4	−0.1	ND
Basal area (m^2/ha)	21.2 (2.2)	9.6 (1.7)	0.0 (0.0)	−10.0 (2.5)	−14.0	−5.8	−21.9 (3.1)	−28.1	−16.9	*
Density (stems/ha)	9,370 (1,301)	1,700 (302)	21 (14)	−7,662 (2,216)	−12,200	−4,669	−10,229 (1,822)	−13,882	−7,215	ND
Woody debris (kg C/m^2	0.1 (0.02)	0.2 (0.05)	0.7 (0.1)	0.1 (0.1)	−0.02	0.2	0.6 (0.1)	0.5	0.8	*

Notes: Site means represent empirically determined site means, with $n = 18$ unmanaged, 7 thinned, and 12 shearbladed areas. Site mean differences are the values of the treatment minus the unmanaged stands at each site from the bootstrap analysis. The 2.5% and 97.5% quantiles were determined using the Bayesian bootstrap analysis.

*Significant difference determined by where quantiles (95% probability) posterior mean difference distribution did not include zero between the calculated relative difference (thinned minus unmanaged vs. shearbladed minus unmanaged) determined by the Bayesian bootstrap analysis; ND, no difference (see Appendix S1: Table S1 for additional values).

(Table 2). The difference in stem density tended to be larger in shearbladed sites, however stem density was highly variable across sites and no significant relationship between treatment and stem density was observed. Mean woody debris C pool sizes differed across stand types, with significantly larger changes resulting from shearblading than thinning (Table 2).

Seedling density and composition varied among stand types (Fig. 2). Conifer seedlings and layers were most abundant in unmanaged stands, followed by thinned, with statistically fewer conifer stems observed in shearbladed areas. In contrast, shearbladed areas exhibited a significantly higher mean deciduous seedling density (although density was variable) than unmanaged stands, with thinned stands not differing from either unmanaged or shearbladed areas. Thinned stands displayed a similar density of deciduous and conifer seedlings/layers. Alaska paper birch (*Betula neoalaskana*, Sarg.) was the most commonly observed deciduous tree across study sites and treatments, accounting for 85% of deciduous stems. Trembling aspen (*Populus tremuloides*, Michx.) comprised 14% of deciduous stems and larch (*Larix Laricina*, (Du Roi) Koch.) <1%. Statistical models were improved when SOL depth was included with total seedling abundance, while tree seedling species covaried with treatment type.

Stand type had a significant effect on observed vascular plant composition ($P = 0.001$). The vegetation types observed most frequently in the unmanaged and thinned stands were similar to one another and differed from those seen in shearbladed stands (Fig. 3A). Evergreen plants (commonly *Ledum palustre* [L. s.l.] and *Lycopodium*) showed a close association with unmanaged and thinned stands while deciduous plants (commonly *Vaccinium* spp. and *Rosa acicularis* [Lindl s.l.]), forbs, and grasses were more commonly associated with shearbladed areas. Sedges, *Betula nana*, *Salix* spp., and *Equisetum* were also more abundant in shearbladed areas than unmanaged and thinned stands. The depth of the SOL significantly influenced observed vegetation composition (Fig. 3B, $P < 0.001$, Appendix S1: Table S2) while years since treatment did not have an effect ($P = 0.274$, Appendix S1: Table S2). Ground cover also differed significantly among

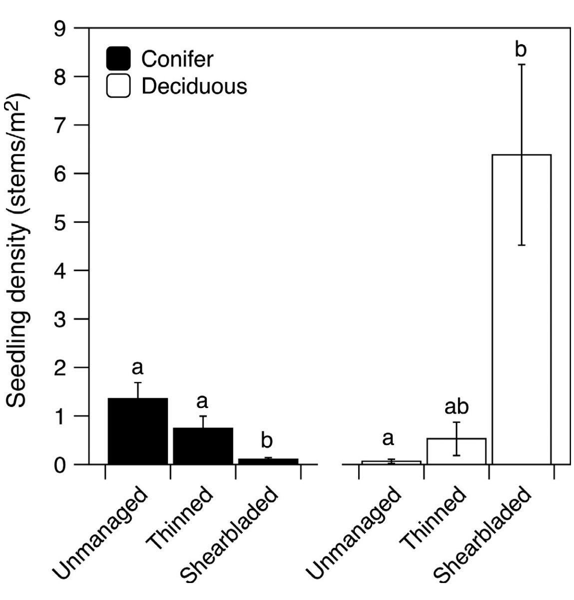

Fig. 2. Deciduous and conifer seedling density for unmanaged, thinned, and shearbladed study stands. Deciduous species include Alaska paper birch and aspen seedlings while conifer includes black spruce seedlings and layering. Values represent means and SE. Different lowercase letters indicate significant differences ($P < 0.001$) among treatments for each seedling type (n = 18 unmanaged, 7 thinned, and 12 shearbladed areas).

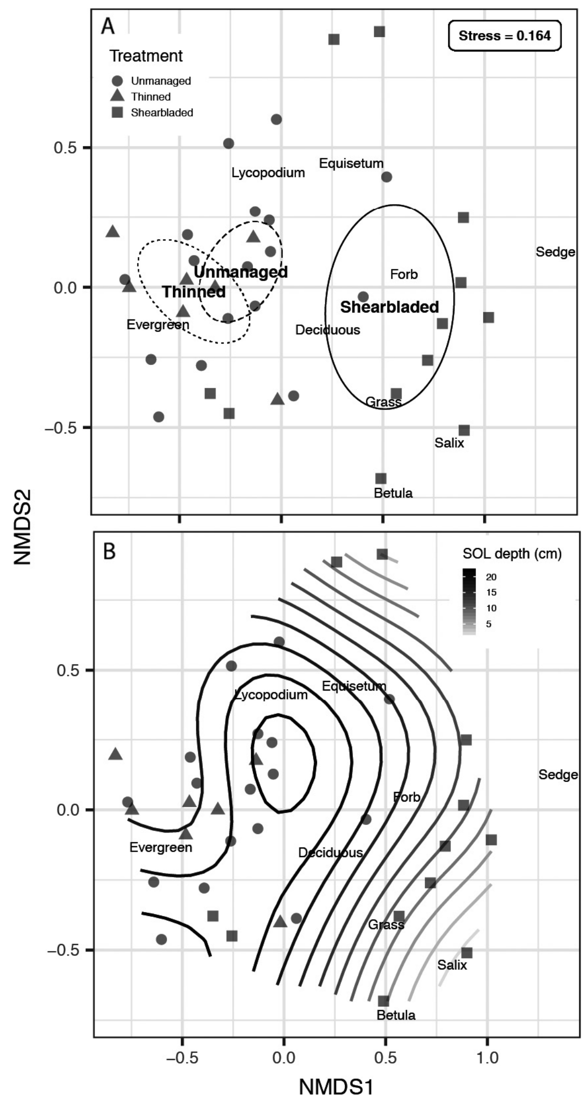

Fig. 3. Vascular plant types (measured as number of hits per sampling location) using nonmetric multidimensional scaling (NMDS). The location of the plant type name within the ordination space illustrates the mean while the points represent individual unmanaged and treated areas. (A) The relationship between plant composition and treatments, with circles indicating 95% confidence intervals for each treatment centroid type. (B) Differences in the soil organic layer (SOL) depth, represented by pictured contours.

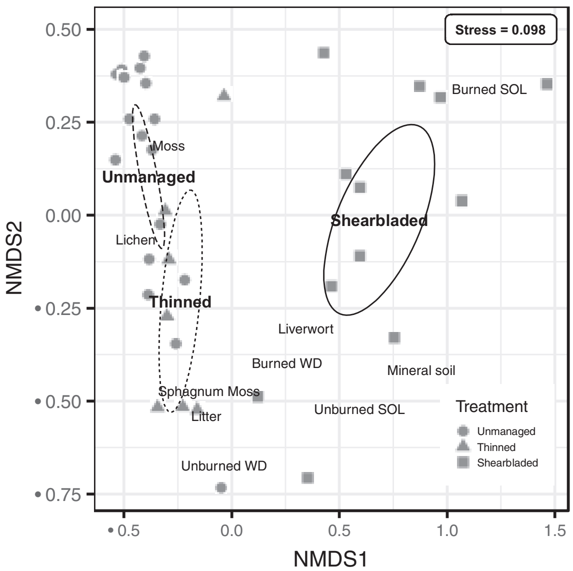

FIG. 4. Ground cover (measured as number of hits per sampling location) using nonmetric multidimensional scaling (NMDS). The location of the ground cover type name within the ordination space illustrates the mean while the points represent unmanaged and managed areas. The circles indicate 95% confidence intervals for each treatment centroid type. SOL represents the soil organic layer and WD is woody debris.

stands (P = 0.001, Fig. 4), with unmanaged stands linked closely to non-sphagnum mosses and lichen, while thinned stands were associated with lichen, leaf litter, and sphagnum mosses. For shearbladed stands, liverworts, bare mineral soil, and burned woody debris and SOL were commonly observed.

Soils

The SOL depth differed significantly among stand types, with the deepest SOL observed in unmanaged forest and the shallowest in shearbladed areas (Table 3). Bulk density of SOL also differed among all stand types, with shearbladed areas exhibiting the highest bulk density, and unmanaged forest the lowest. The SOL C pool size was comparable in unmanaged and thinned stands, while shearbladed areas exhibited about half the amount of C observed in the other stand types (Table 3). Similarly, shearbladed stands displayed a smaller mean SOL N pool size than both unmanaged forest and thinned stands (Table 3). Coarse root C in the SOL averaged 0.8 ± 0.2, 0.7 ± 0.1 and 0.3 ± 0.1 kg C/m^2 in unmanaged, thinned, and shearbladed stands, respectively, with significant differences between unmanaged and shearbladed (P = 0.0004) and between thinned and shearbladed stands (P = 0.0023).

No differences among stand types were observed in the mineral soils for bulk density or C and N pool sizes for either depth increment (Table 3). For all stand types, the within-stand bulk density was significantly higher in the 5–10 cm depth increment than the 0–5 cm (P < 0.0001). Within shearbladed areas, a significant difference in the C (P = 0.0012) and N (P = 0.02) pool size was observed between the two depth increments, while no difference between depths was observed in unmanaged or thinned stands.

Mean thaw depth was deepest in shearbladed areas and shallowest in unmanaged stands (Table 4). The mean relative difference in thaw depth between adjacent unmanaged and thinned stands was approximately 13 cm while the difference between unmanaged and shearbladed areas was 46 cm. Although this large difference in means was observed, thaw depth in treated areas relative to adjacent unmanaged stands was highly variable across study sites (Fig. 5), contributing to no statistically significant difference between treatments using our bootstrapping approach (Table 4, with bootstrapping values in Appendix S1: Table S1). A significant relationship between SOL depth and thaw depth was identified for all treatment types (P < 0.001, no interaction among treatments was present

TABLE 3. Soil organic layer and upper mineral soil characteristics for unmanaged, thinned, and shearbladed forest stands.

Parameter	Unmanaged	Thinned	Shearbladed
Soil organic layer (SOL)			
Depth (cm)	21.6^a (1.1)	16.1^b (1.9)	7.8^c (2.0)
Bulk density (g/cm^3)	0.08^a (0.00)	0.10^b (0.01)	0.14^c (0.01)
C (kg/m^2)	5.9^a (0.3)	6.0^a (1.0)	3.2^b (0.8)
N (g/m^2)	178.7^a (10.5)	192.2^a (40.9)	116.8^b (31.0)
0–5 cm mineral soil			
Bulk density (g/cm^3)	0.58 (0.04)	0.52 (0.05)	0.60 (0.04)
C (kg/m^2)	2.3 (0.2)	2.5 (0.3)	2.4 (0.1)
N (g/m^2)	120.6 (8.5)	129.7 (17.9)	122.6 (7.6)
5–10 cm mineral soil			
Bulk density (g/cm^3)	0.84 (0.04)	0.89 (0.11)	0.85 (0.07)
C (kg/m^2)	2.1 (0.1)	2.2 (0.3)	2.0 (0.2)
N (g/m^2)	109.1 (7.0)	112.9 (17.3)	109.2 (9.2)

Notes: Values are means with SE in parentheses. Different superscript letters within a given row indicate significant differences among treatments (P < 0.05). Reported values for SOL depth and C and N pools include field observations and laboratory-processed samples. For SOL bulk density and all mineral soil values, all data is from laboratory-processed samples. Green moss is not included.

Table 4. Field-determined mean normalized thaw depth and mean differences between adjacent treated and unmanaged stands, in addition to Bayesian Bootstrap-calculated 2.5% and 97.5% quantiles.

	Significance			Site mean differences and bootstrapping results						
				(Thinned − Unmanaged)			(Shearbladed − Unmanaged)			
Site means	Unmanaged	Thinned	Shearbladed	Mean difference	2.5%	97.5%	Mean difference	2.5%	97.5%	Significance
Thaw depth (cm)	40 (7)	53 (14)	86 (6)	13 (16)	−11	44	46 (8)	30	60	ND

Notes: Site means values are reported as mean, with SE in parentheses, and represent empirically determined site means. Site mean differences reflect the values of the treatment minus the unmanaged stands at each site, with n = 18 unmanaged, 7 thinned, and 12 shearbladed areas. The 2.5% and 97.5% quantiles were determined using the Bayesian bootstrap analysis. ND indicates no significant difference between the calculated difference (thinned minus unmanaged vs. shearbladed minus unmanaged) determined by the Bayesian bootstrap analysis (see Appendix S1: Table S1 for additional values).

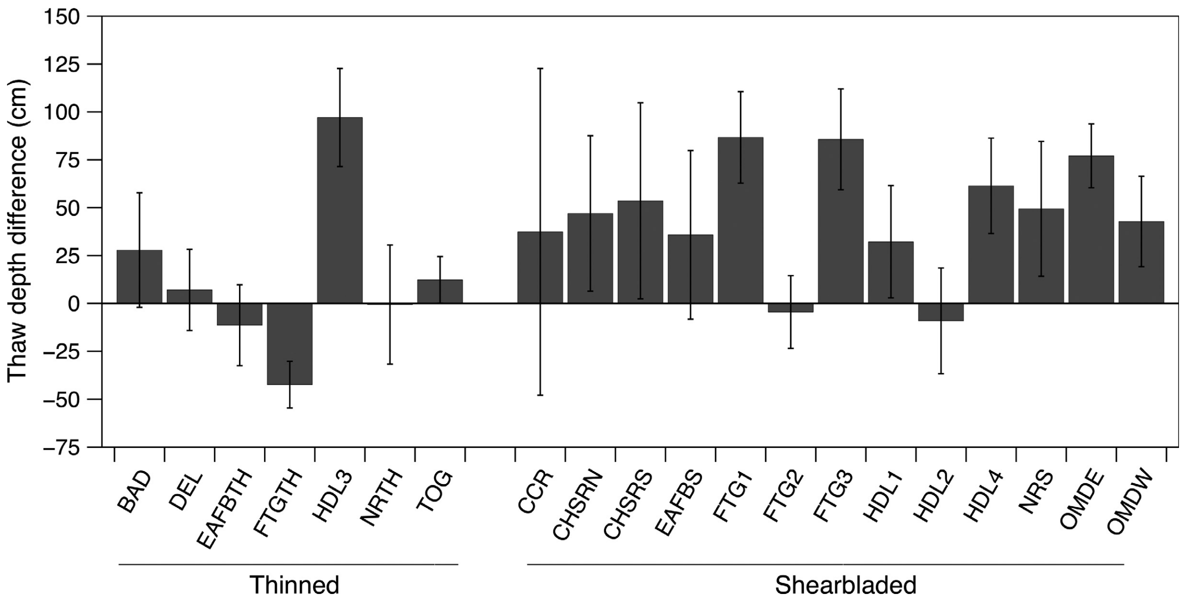

Fig. 5. Mean difference (± propagated error) in thaw depth between adjacent treated and unmanaged stands presented by study site. Positive values indicate sites where mean measured thaw depth was deeper in the treated area relative to the unmanaged stand. Site names are identified in Table 1.

in the model), where thaw depth decreased as SOL depth increased (slope = −1.43, Appendix S1: Fig. S1). Deeper thaw was observed in shearbladed areas for any given SOL depth when compared to unmanaged stands ($P < 0.01$). Week of the year sampled did not improve the model ($P = 0.62$), suggesting sampling date was not a driving factor of observed patterns. No significant relationship was found between years since treatment and measured thaw depth ($P = 0.12$).

Summed C stocks for all measured ecosystem pools were 14.1 ± 0.7, 11.4 ± 1.5, and 8.3 ± 1.1 kg C/m^2 for unmanaged, thinned, and shearbladed areas, respectively. These differences resulted in significantly larger total C stocks in the unmanaged stands relative to shearbladed areas (Fig. 6). Variation in stocks among stand types was driven primarily by differences in aboveground biomass, with additional influence of SOL and dead wood pool sizes.

Discussion

Our results indicate that thinning and shearblading practices used to reduce fuel hazards alter C and N pool sizes and plant species composition. As hypothesized, the impacts of shearblading were generally larger than those of thinning when compared to unmanaged forest. Differences in pool sizes tended to be largest aboveground and were presumably driven by the physical removal of tree biomass. The loss of SOL material also contributed to reduced SOL C and N pools in shearbladed stands and likely influenced observed differences in thaw depth, as well as plant species composition. These impacts of fuel-reduction treatments, especially the larger effects caused by shearblading, may have long-term implications for C and N dynamics, and other aspects of ecosystem structure and function.

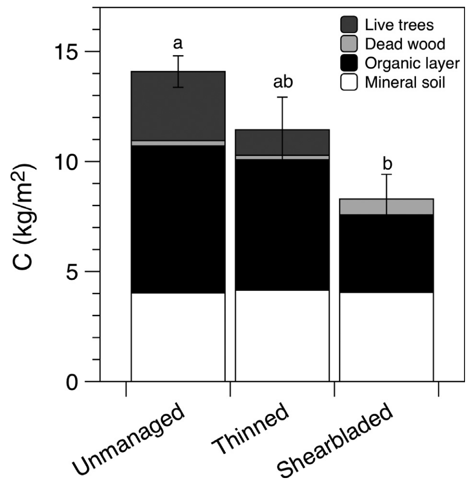

FIG. 6. Total ecosystem C stocks for pools measured in this study. Values reported for each component and treatment type are the mean of all sampled sites. Dead wood includes standing dead trees and woody debris. Error bars indicate standard error for the summed C stocks and different letters reflect significant differences among treatment types ($P < 0.001$).

Soils

The smaller SOL C and N pools in shearbladed areas compared to thinned and unmanaged stands suggests that at least a portion of the SOL was removed during aboveground biomass harvest. This treatment type also displayed the highest SOL bulk density, likely due to compression by the heavy equipment used during harvest at these sites. Thinned stands exhibited similar SOL C and N pools to unmanaged stands, suggesting that SOL material was not removed during manual thinning. However, higher SOL bulk density in thinned stands relative to unmanaged stands indicates that this management practice can compact the SOL. It is also possible that warmer SOL temperatures associated with tree removal could have increased decomposition, thereby contributing to the smaller SOL C and N pools observed in shearbladed areas (Yarie 1983). The absence of significant differences in bulk density and C and N pool sizes in the mineral soil suggests that at least within the early years post-treatment, fuel-reduction impacts are primarily found aboveground and in the SOL.

The trend towards deeper thaw depth in managed areas, especially those that were shearbladed, suggests that fuel-reduction management changed the soil thermal regime. The relationship between the SOL and thaw depth we found, where thinner SOLs were associated with deeper thaw depth, likely resulted from reduced insulating capacity caused by SOL removal and compaction. Increased radiation caused by tree removal may have also influenced this finding (Yarie 1993). These patterns are consistent with previous observations from fire disturbance (Yoshikawa et al. 2002, Brown et al. 2015) and bulldozer SOL removal in interior Alaska (Viereck 1982, Nicholas and Hinkel 1996, Viereck et al. 2008). Interestingly however, Viereck et al. (2008) observed differing patterns of permafrost recovery between a burned area and adjacent bulldozed site over a 36-year study, suggesting that these disturbance types may have differing long-term influences on permafrost dynamics. For the 2–12 years since treatment we evaluated in this study, no significant effect of years since treatment was found. Rapid permafrost degradation following disturbance has been observed by others (e.g., Mackay 1995, Viereck et al. 2008). This finding may be influenced by the high degree of variability in thaw depth we observed across and within sites. Similarly, we did not find a significant influence of the week of the year the sampling took place on thaw depth. Because soils thaw throughout the summer months, it is likely that the exact date of sampling had some influence on measured thaw, but any differences were too small to be detectable within the few week differences in sampling dates and variability among sites.

If treated areas regenerate along a deciduous-dominated successional trajectory as our shearbladed seedling data suggests may occur, then a moss-dominated SOL may not reestablish (Johnstone et al. 2010*a*), which could leave permafrost more vulnerable to further thaw as climate change continues. Although we did not observe differences in mineral soil C pools among treatment types, long-term, sustained, permafrost degradation could increase C loss from these pools and contribute to a positive feedback to climate warming (Schuur et al. 2008, O'Donnell et al. 2011).

Management-driven reductions in the SOL N pool and impacts of permafrost thaw on N availability could have long-term and varying impacts on ecosystem N dynamics. Nitrogen is a limiting nutrient in boreal ecosystems (Van Cleve et al. 1983*b*). If fuel-reduction management treatments in our study increased net N mineralization and nitrification, as has been observed following logging (Kreutzweiser et al. 2008) and clear-cutting (Lindo and Visser 2003, nitrification increase only), then inorganic N pools could allow for greater N uptake by vegetation as the ecosystem recovers from the treatment disturbance. Similarly, if permafrost thaw increases N mineralization, as has been shown in tundra (Salmon et al. 2016), more N may be available for the plant community. In contrast, the reduced total SOL N pool in treated areas, as well as potential leaching losses of nitrate driven by higher nitrification rates, could reduce N availability and constrain net primary productivity. Follow-up research that focuses on treatment impacts on N cycling at our study sites could provide important insights into likely impacts of thinning and shearblading on these processes.

Vegetation

The large difference in vegetation composition observed in shearbladed stands relative to thinned and unmanaged stands suggests that shearblading can alter understory vegetation and possibly forest successional trajectories. Our analysis suggests this is strongly influenced by loss of SOL material. Others have shown rapid colonization by herbaceous and shrub species following exposure of the mineral soil, likely due to seed dispersal and establishment on a high-quality seed bed (Viereck et al. 2008). A positive relationship between the fraction of SOL consumed during fire and both abundance of forbs and *Salix* spp. stem density have been observed (Gibson et al. 2016), both of which are consistent with our findings of these plant types being associated with the shearblading treatment, where the SOL was shallowest. The high abundance of deciduous tree seedlings in shearbladed areas is also consistent with studies in severely burned areas where the SOL has been partially or completely removed (Gibson et al. 2016), which results in a high-quality seedbed on which deciduous tree species are able to outcompete black spruce and establish at high rates (Greene et al. 2007, Johnstone et al. 2010*b*). A shift from black spruce to deciduous-dominated forests has been shown to increase N cycling rates, shift the dominant C and N pools from the SOL to aboveground biomass, and reduce moss accumulation within the forest floor (Johnstone et al. 2010*a*, Melvin et al. 2015, Alexander and Mack 2016), resulting in long-term changes to ecosystem structure and function. However, deciduous forests have higher leaf moisture and may reduce the likelihood of fire (Terrier et al. 2013), which could provide a long-term benefit of reducing fires risks.

Conclusions

Balancing the growing need to reduce wildland fire risk in the wildland–urban interface and the ecological impacts of those fuel-reduction treatments will remain a challenge for fire managers in Alaska. Managers seek to maximize the effective length of reduced risk while minimizing the treatment costs, and those trade-offs may produce unwanted ecosystem consequences. Our results illustrate that thinning causes relatively small near-term ecosystem changes while shearblading results in large impacts on C and N pools, as well as plant community composition. Yet these impacts, whereby deciduous vegetation gains dominance of the site (which may occur, as indicated by an increased abundance of deciduous seedlings) may also produce the greatest reductions in fire risk and maximize the return on investment with respect to treatment costs. Consideration of longer term consequences of fuel-reduction treatments are warranted given the divergence of impacts produced, e.g., shearblading greatly reduces ecosystem flammability but may also lead to unwanted longer term positive feedbacks to the climate system. Future research focused on improving understanding of the efficacy of these management techniques on fire behavior while also considering undesirable changes in ecosystem processes will allow managers to make more informed decisions that maximize community well-being and safety and minimize unwanted impacts on ecosystem processes.

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Literature Cited

Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211:83–96.

Ager, A. A., A. J. McMahan, J. J. Barrett, and C. W. McHugh. 2007. A simulation study of thinning and fuel treatments on a wildland-urban interface in eastern Oregon, USA. Landscape and Urban Planning 80:292–300.

Alexander, H. D., and M. C. Mack. 2016. A canopy shift in Interior Alaskan boreal forests: consequences of above- and belowground carbon and nitrogen pools during post-fire succession. Ecosystems 19:98–114.

Alexander, H. D., M. C. Mack, S. Goetz, P. S. A. Beck, and E. F. Belshe. 2012. Implications of increased deciduous cover on stand structure and aboveground carbon pools of Alaskan boreal forests. Ecosphere 3:1–21.

Bååth, R. 2016. Bayesboot: an implementation of Rubin's (1981) Bayesian Bootstrap. https://cran.r-project.org/web/packages/bayesboot/

Berman, M., G. P. Juday, and R. Burnside. 1999. Climate change and Alaska's forests: people, problems, and policies. Pages 21–42 *in* G. Weller and P. A. Anderson, editors. Assessing the consequences of climate change for Alaska and the Bering Sea region. Proceedings of a Workshop at the University of Alaska Fairbanks, 29–30 October 1998. Center for Global Change and Arctic System Research, University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Berner, L. T., H. D. Alexander, M. M. Loranty, P. Ganzlin, M. C. Mack, S. P. Davydov, and S. J. Goetz. 2015. Biomass allometry for alder, dwarf birch, and willow in boreal forest and tundra ecosystems of far northeastern Siberia and north-central Alaska. Forest Ecology and Management 337:110–118.

Brown, J. K. 1974. Handbook for inventorying downed woody material. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.

Brown, D. R. N., M. T. Jorgenson, T. A. Douglas, V. E. Romanovsky, K. Kielland, C. Hiemstra, E. S. Euskirchen, and R. W. Ruess. 2015. Interactive effects of wildfire and climate on permafrost degradation in Alaskan lowland forests. Journal of Geophysical Research: Biogeosciences 120: 1619–1637.

Butler, B. W., R. D. Ottmar, T. S. Rupp, R. Jandt, E. Miller, K. Howard, R. Schmoll, S. Theisen, R. E. Vihnanek, and D. Jimenez. 2013. Quantifying the effect of fuel reduction treatments on fire behavior in boreal forests. Canadian Journal of Forest Research 43:97–102.

Calef, M. P., A. Varvak, A. D. McGuire, F. S. Chapin, and K. B. Reinhold. 2015. Recent changes in annual area burned in interior Alaska: The impact of fire management. Earth Interactions 19:1–17.

Carleton, T. J., and P. MacLellan. 1994. Woody vegetation responses to fire versus clear-cutting logging: A comparative survey in the central Canadian boreal forest. Ecoscience 1: 141–152.

Cohen, J. D. 2000. Preventing disaster—home ignitability in the wildland-urban interface. Journal of Forestry 98:15–21.

Flannigan, M. D., M. A. Krawchuk, W. J. de Groot, B. M. Wotton, and L. M. Gowman. 2009. Implications of changing climate for global wildland fire. International Journal of Wildland Fire 18:483–507.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27:233–249.

Gibson, C. M., M. R. Turetsky, K. Cottenie, E. S. Kane, G. Houle, and E. S. Kasischke. 2016. Variation in plant community composition and vegetation carbon pools a decade following a severe fire season in interior Alaska. Journal of Vegetation Science 27:1187–1197.

Goodall, D. W. 1952. Some considerations in the use of point quadrats for the analysis of vegetation. Australian Journal of Scientific Research Series B: Biological Sciences 5:1–41.

Graham, R., A. Harvey, T. Jain, and J. Tonn. 1999. Effects of thinning and similar stand treatments on fire behavior in western forests. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Greene, D. F., et al. 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Canadian Journal of Forest Research 37:1012–1023.

Johnstone, J. F., F. S. Chapin, T. N. Hollingsworth, M. C. Mack, V. Romanovsky, and M. Turetsky. 2010*a*. Fire, climate change, and forest resilience in interior Alaska. Canadian Journal of Forest Research 40:1302–1312.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin III, and M. C. Mack. 2010*b*. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16:1281–1295.

Jorgenson, M. T., V. Romanovsky, J. Harden, Y. Shur, J. O'Donnell, E. A. G. Schuur, M. Kanevskiy, and S. Marchenko. 2010. Resilience and vulnerability of permafrost to climate change. Canadian Journal of Forest Research 40:1219–1236.

Kasischke, E., et al. 2010. Alaska's changing fire regime—implications for the vulnerability of its boreal forests. Canadian Journal of Forest Research 40:1313–1324.

Kelly, R., M. L. Chipman, P. E. Higuera, I. Stefanova, L. B. Brubaker, and F. S. Hu. 2013. Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. Proceedings of the National Academy of Sciences USA 110: 13055–13060.

Kreutzweiser, D. P., P. W. Hazlett, and J. M. Gunn. 2008. Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: A review. Environmental Reviews 16:157–179.

Kulmala, L., et al. 2014. Changes in biogeochemistry and carbon fluxes in a boreal forest after the clear-cutting and partial burning of slash. Agricultural and Forest Meteorology 188:33–44.

Lindo, Z., and S. Visser. 2003. Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting. Canadian Journal of Forest Research 33:1610–1620.

Mackay, J. R. 1995. Active layer changes (1968 to 1993) following the forest-tundra fire near Inuvik, NWT, Canada. Arctic and Alpine Research 27:323–336.

McRae, D. J., L. C. Duchesne, B. Freedman, T. J. Lynham, and S. Woodley. 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environmental Reviews 9:223–260.

Melvin, A. M., M. C. Mack, J. F. Johnstone, A. D. McGuire, H. Genet, and E. A. G. Schuur. 2015. Differences in ecosystem carbon distribution and nutrient cycling linked to forest tree species composition in a mid-successional boreal forest. Ecosystems 18:1472–1488.

Nalder, I. A., R. W. Wein, M. E. Alexander, and W. J. deGroot. 1997. Physical properties of dead and downed round-wood fuels in the boreal forests of Alberta and Northwest Territories. Canadian Journal of Forest Research 27:1513–1517.

Nicholas, J. R. J., and K. M. Hinkel. 1996. Concurrent permafrost aggradation and degradation induced by forest clearing, Central Alaska, U.S.A. Arctic and Alpine Research 28:294–299.

Nossov, D. R., M. T. Jorgenson, K. Kielland, and M. Z. Kanevskiy. 2013. Edaphic and microclimatic controls over permafrost response to fire in interior Alaska. Environmental Research Letters 8:035013.

O'Donnell, J. A., V. E. Romanovsky, J. W. Harden, and A. D. McGuire. 2009. The effect of moisture content on the thermal conductivity of moss and organic soil horizons from black spruce ecosystems in interior Alaska. Soil Science 174:646–651.

O'Donnell, J. A., J. W. Harden, A. D. McGuire, M. Z. Kanevskiy, M. T. Jorgenson, and X. M. Xu. 2011. The effect of fire and permafrost interactions on soil carbon accumulation in an upland black spruce ecosystem of interior Alaska: implications for post-thaw carbon loss. Global Change Biology 17:1461–1474.

Oksanen, J., et al. 2016. vegan: community ecology package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan

Ott, R. A., and R. Jandt. 2005. Fuels treatment demonstration sites in the boreal forests of interior Alaska.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. Team. 2016. nlme: linear and nonlinear mixed effects models. R package version 3.1-128. http://CRAN.R-project.org/package=nlme

Salmon, V. G., P. Soucy, M. Mauritz, G. Celis, S. M. Natali, M. C. Mack, and E. A. G. Schuur. 2016. Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw. Global Change Biology 22:1927–1941.

Schuur, E. A. G., et al. 2008. Vulnerability of permafrost carbon to climate change: implications for the global carbon cycle. BioScience 58:701–714.

Skaug, H., D. Fournier, B. Bolker, A. Magnusson, and A. Nielsen. 2016. Generalized linear mixed models using 'AD Model Builder'. R package version 0.8.3.3. http://glmmadmb.r-forge.r-project.org

Smith, C. K., M. R. Coyea, and A. D. Munson. 2000. Soil carbon, nitrogen, and phosphorus stocks and dynamics under disturbed black spruce forests. Ecological Applications 10:775–788.

Stephens, S. L., et al. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. Ecological Applications 19:305–320.

Taylor, A. R., T. Hart, and H. Y. H. Chen. 2013. Tree community structural development in young boreal forests: A comparison of fire and harvesting disturbance. Forest Ecology and Management 310:19–26.

Ter-Mikaelian, M. T., S. J. Colombo, and J. X. Chen. 2008. Amount of downed woody debris and its prediction using stand characteristics in boreal and mixedwood forests of Ontario, Canada. Canadian Journal of Forest Research 38: 2189–2197.

Terrier, A., M. P. Girardin, C. Périé, P. Legendre, and Y. Bergeron. 2013. Potential changes in forest composition could reduce impacts of climate change on boreal wildfires. Ecological Applications 23:21–35.

Turetsky, M. R., B. Bond-Lamberty, E. Euskirchen, J. Talbot, S. Frolking, A. D. McGuire, and E. S. Tuittila. 2012. The resilience and functional role of moss in boreal and arctic ecosystems. New Phytologist 196:49–67.

Van Cleve, K., C. T. Dyrness, L. A. Viereck, J. Fox, F. S. Chapin, and W. Oechel. 1983*a*. Taiga ecosystems in interior Alaska. BioScience 33:39–44.

Van Cleve, K., L. Oliver, R. Schlentner, L. A. Viereck, and C. T. Dyrness. 1983*b*. Productivity and nutrient cycling in taiga forest ecosystems. Canadian Journal of Forest Research 13: 747–766.

Viereck, L. A. 1982. Effects of fire and firelines on active layer thickness and soil temperatures in interior Alaska. *In* 4th Canadian Permafrost Conference. National Academy Press, Washington, DC, USA.

Viereck, L. A., K. Vancleve, P. C. Adams, and R. E. Schlentner. 1993. Climate of the Tanana River floodplain near Fairbanks, Alaska. Canadian Journal of Forest Research 23:899–913.

Viereck, L. A., N. R. Werdin-Pfisterer, P. C. Adams, and K. Yoshikawa. 2008. Effect of wildfire and fireline construction on the annual depth of thaw in a black spruce permafrost forest in interior Alaska: a 36-year record of recovery. *In* Ninth International Conference on Permafrost. Institute of Northern Engineering, University of Alaska Fairbanks, USA.

Yarie, J. 1983. Environmental and successional relationships of the forest communities of the Porcupine River drainage, interior Alaska. Canadian Journal of Forest Research 13: 721–728.

Yarie, J. 1993. Effects of selected forest management practices on environmental parameters related to successional development on the Tanana River floodplain, interior Alaska. Canadian Journal of Forest Research 23:1001–1014.

Yarie, J., and S. Billings. 2002. Carbon balance of the taiga forest within Alaska: present and future. Canadian Journal of Forest Research 32:757–767.

Yoshikawa, K., W. R. Bolton, V. E. Romanovsky, M. Fukuda, and L. D. Hinzman. 2002. Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. Journal of Geophysical Research: Atmospheres 108:1–14.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1636/full

Data Availability

Data available from the LTER Network Data Portal:
https://doi.org/10.6073/pasta/001c6a367666a831e259826c0ca1d87c.
https://doi.org/10.6073/pasta/77836c63a314214755662e4c517c040d.
https://doi.org/10.6073/pasta/83520d21766657a7b6d3c600836e958c.
https://doi.org/10.6073/pasta/0ea09774a8e7d4c78fcc49f8505182d3.
https://doi.org/10.6073/pasta/ff93dca5559162842d4aa77d41f55502.
https://doi.org/10.6073/pasta/1019c036d3f02e32ae880605b2f11853.