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Effects of wildfire and soil compaction on recovery of narrow linear disturbances in upland mesic boreal forests

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ABSTRACT

Energy exploration has led to fragmentation of habitats worldwide. In boreal forests of Alberta, Canada narrow clear-cut linear disturbances (3–14 m wide) called seismic lines are often the largest local source of forest fragmentation. Many lines have failed to recover decades after their creation leading to changes in forest dynamics and biodiversity. In some cases, these linear features function as habitat and/or corridors for species, while being detrimental in other species, most notably the threatened woodland caribou (*Rangifer tarandus caribou*). Recently, industry and government have focused on reforestation of these lines using silvicultural treatments and tree planting. However, these applications are expensive (> $12,500/km) and do not account for wildfires that can destroy restoration investments (planted trees), yet also initiate early seral conditions that favor natural recovery. Here, we examined soil compaction (bulk density) and tree regeneration density in burnt and unburnt seismic lines within mesic upland forest types and compared these to adjacent (paired) forest controls. Bulk density on seismic lines increased by 34% compared to undisturbed adjacent forests, but was not severe enough to impede regeneration. Despite increases in compaction, regeneration density was 19% higher on lines than in adjacent forests. Specifically, regeneration density averaged 19,622 stems/ha in burnt lines, 11,870 stems/ha in unburnt lines, 16,739 stems/ha in adjacent burnt forest, and 6,934 stems/ha in adjacent unburnt forest where regeneration rates are expected to be lower. We suggest that leave-for-natural recovery (passive restoration) of seismic lines can be expected post-fire in mesic upland forests with even the majority of unburnt seismic lines recovering to densities above the 5,000 stems/ha guidelines. Active restoration treatments using intensive silviculture treatments should therefore only be considered where recovery is not observed or wildfire likely.

1. Introduction

Seismic lines, clear-cut linear disturbances (~3–14 m wide), are created for the purpose of generating and measuring seismic waves/vibrations to map underground petroleum reserves. Individually, seismic lines can run for many kilometers and are typically in a grid-like pattern with densities reaching up to 40 km/km^2 (Filicetti et al. 2019; Riva and Nielsen, 2020). When petroleum exploration occurs in a forest, seismic lines are often the largest anthropogenic disturbance (Lee and Boutin 2006; Pattison et al. 2016). Many seismic lines have not reforested many decades post-disturbance (MacFarlane 2003; Lee and Boutin 2006; van Rensen et al. 2015). Recent studies demonstrate simplified microtopography and local topographic depression of seismic lines affect reforestation patterns (Lovitt et al. 2018; Filicetti et al. 2019; Stevenson et al. 2019; Filicetti and Nielsen 2020). Changes in microtopography are often associated with compaction which can lead to poor regeneration due to root damage, reduced soil aeration, and poorer root penetration (Revel et al. 1984; MacFarlane 2003; Lee and Boutin 2006) and biotic shifts from trees to graminoids and shrubs (Revel et al. 1984; MacFarlane 2003; Lee and Boutin 2006; Dawe et al. 2017; Filicetti et al. 2019; Stevenson et al. 2019; Filicetti and Nielsen 2020). Most soil compaction studies focus on forest clear-cuts with responses being complex and dependent on the soils and trees present, the degree of compaction, and the timing of compaction (Greene and Johnson 1999; Frey et al. 2003). Compared to other boreal forests, mesic upland forests have soil characteristics where compaction is more likely to occur. In mesic upland forests dominated by trembling aspen (*Populus tremuloides* Michx.) the amount of compaction required to adversely affect tree establishment, growth, and survival is ~1.55–1.65 g/cm^3 (Daddow and Warrington 1983; Sealey and Van Rees 2019). Soil compaction and reforestation differ substantially between clear-cuts that are well-studied and

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seismic lines owing to the machinery and protocols that operators use. Seismic line clearing usually occurs in winter with light machinery producing a narrow forest gap (3–14 m wide), while clear-cuts use heavy machinery, result in many passes, and produce large forest gaps (>50 m wide). The narrow forest gap size and orientation of lines has been shown to influence sunlight transmission, seed dispersal, and tree regeneration (Roberts et al. 2018; Stern et al. 2018; Franklin et al. 2021). On one hand, tall and dense adjacent stands can provide more seeds and suckers which foster better conditions for regeneration density (Greene et al. 1999, 2004; Filicetti and Nielsen 2018, 2020), but on the other hand it can limit sunlight transmission in the narrow forest gap sizes of seismic lines (Stern et al. 2018; Franklin et al. 2021). As well as abiotic changes, the disturbance favors early seral vegetation with bare ground, graminoids, dwarf shrubs, non-vascular plants (bryophytes and lichens), and even small swales of open water. This can lead to competitive effects on trees that limit their establishment. In particular, graminoid cover has been shown to limit forest regeneration in boreal forests in general (Hogg and Lieffers 1991; Landhäusser and Lieffers 1998; Bockstette et al. 2017) and within seismic lines specifically (Filicetti et al. 2019; Filicetti and Nielsen 2020).

In most cases wildfires initiate and accelerate reforestation on seismic lines in both treed peatlands and xeric jack pine forests (Filicetti and Nielsen 2018, 2020), but little is known about responses to wildfires on seismic lines in mesic forests that are dominated in western Canada by aspen. Aspen suckers post-fire (Greene and Johnson 1999; Frey et al. 2003; Jean et al. 2020) and therefore expected to recover on lines like that of other fire-dependent systems if left alone (i.e., restricting recreational use of lines or line reuse by industry). However, wildfires can also increase soil compaction (Kozlowski 1999; Snyman 2005), which may further compound initial compaction of seismic lines during their creation and thus further limit tree regeneration.

Seismic lines have been a conservation concern in western Canadian boreal forests due to their effects on biodiversity (Riva et al. 2018; Roberts et al. 2018; Shonfield and Bayne 2019; Riva and Nielsen, 2020). Perhaps the most notable species of concern are woodland caribou, a high-profile species-at-risk in Canada's boreal forest (Hebblewhite 2017). Seismic lines function as movement corridors for many animals, allowing movements of species into preferred woodland caribou habitat that were not previously as accessible (Rettie and Messier 2000; Dickie et al. 2017). These access routes have increased opportunities of predation by wolves and bears resulting in declining caribou populations (James and Stuart-Smith 2000; Latham et al. 2011a). Increasing the resistance to movement along seismic lines is therefore a priority to restore woodland caribou habitat; and the most effective way to increase resistance on seismic lines is tree establishment (van Rensen et al. 2015; Filicetti and Nielsen 2018, 2020; Filicetti et al. 2019).

Efforts to actively restore seismic lines often involve silvicultural treatments (Filicetti et al. 2019), however, restoration treatments in these remote areas can exceed $12,500 (CAD) per km (Filicetti et al. 2019; Johnson et al. 2019). Since costs are high, understanding where treatments are most needed compared to where regeneration is already occurring, or likely to occur, and a no-cost leave-for-natural reforestation (passive restoration) strategy can be used is needed to efficiently plan restoration efforts (Johnson et al. 2020). Wildfires are the most common disturbance in the boreal forest and pose both a potential benefit and detriment to seismic line recovery. On the one hand, wildfires provide an ideal leave-for-natural passive form of restoration for seismic lines as they promote early seral conditions by exposing preferential seedbed conditions and seed rain from fire serotinous and semi-serotinous species (Filicetti and Nielsen 2018). On the other hand, wildfires can destroy investments in active restoration treatments

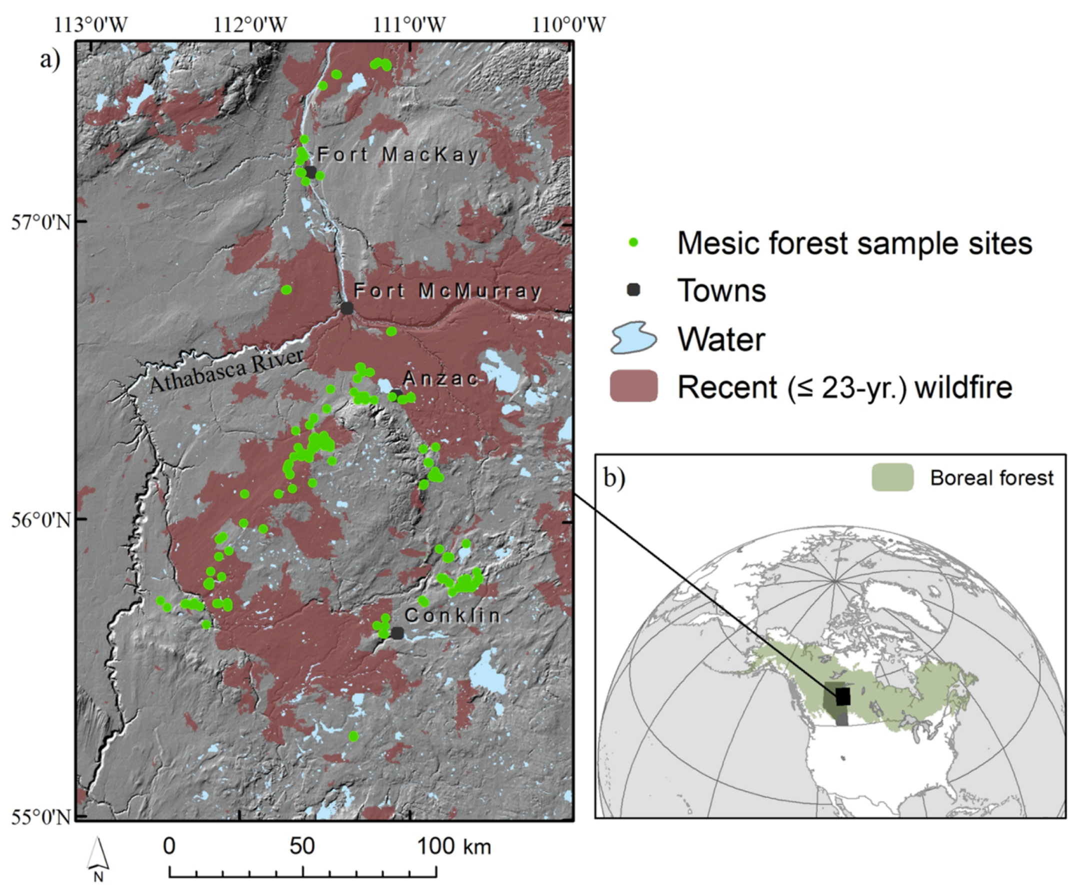

Fig. 1. Location of the study area: a) sample sites (green circles) within northeast Alberta, Canada and the extent of recent (≤23-years) wildfires in red with notable population centers in dark gray ovals; b) outline of the province of Alberta, Canada (grey) within North America and the region of boreal forests in North America.

associated with tree planting.

Here we compare soil compaction and tree regeneration density on seismic lines to paired adjacent forests for unburnt forests to that of burnt forests in mesic upland stands dominated by aspen for six recent (≤23-yrs) wildfires in northeast Alberta, Canada. Specifically, we predict that: (1) seismic lines will be compacted compared to adjacent forest controls, as anecdotal evidence suggests; (2) seismic lines will reduce regeneration density compared to adjacent forests, while recent wildfires (≤23-yrs) will increase regeneration density; and (3) local factors (compaction, wildfire severity, adjacent stand conditions, seismic line characteristics, and ground cover) will further influence these relationships. Specifically, we expect regeneration density to increase with: (a) lower compaction; (b) higher fire severities; (c) more productive stands; (d) seismic line width and orientation that increases sunlight transmission; and (e) lower amounts of ground cover, particularly graminoids.

2. Methods

2.1. Study area

The study area is centered around Fort McMurray in northeast Alberta, Canada, laying within the boundaries of McClelland Lake in the north, Conklin in the southeast, and Wandering River in the southwest (Fig. 1). The area encompasses ~25,000 km^2 of boreal forest in both upland and peatland environments and is represented as being in the Athabasca Oil Sands region. The focus of this study is mesic upland forests where the most common tree species from most to least common from field plots are: aspen (63%); white spruce (*Picea glauca* Moench. Voss) (17%); jack pine (*Pinus banksiana* Lamb.) (7%); Alaska birch (*Betula neoalaskana* Sarg.) (5%); balsam poplar (*Populus balsamifera* L.) (5%); and balsam fir (*Abies balsamea* L. P. Mill.) (2%). Similarly the most common shrubs were: prickly rose (*Rosa acicularis* Lindl.), squashberry (*Viburnum edule* Michx.), and green alder (*Alnus crispa* (Ait.) Pursh). Mesic upland forests can be further subcategorized into four forest types (ecosites) which is reported further in Appendix A. Here we focus on the broader forest type.

2.2. Site selection and field methods

Sample sites on seismic lines were a minimum of 400 m apart unless on a separate seismic line with a different orientation (more than a 45° difference) and/or if ecosite differed (see Appendix A). Six wildfires were sampled due to their large size (>40 km^2) that allowed at least 12 sites to be sampled, had upland mesic forests present, and a variety of post-fire ages (2, 7, 9, 16, 19, and 23 years prior to sample collection). The threshold of ≤ 23 year old wildfires was chosen for three reasons: (1) fire severity in much older wildfires are difficult to quantify in the field; (2) wildfires needed to occur after seismic line creation; wildfires ages were dated using spatial wildfire databases (Alberta Agriculture and Forestry 2017) and seismic line ages were dated using satellite imagery (Google Earth Pro 2018), permit tags (Government of Alberta: Alberta Environment and Parks 2021), or if required approximated by using the oldest tree observed on the line; and (3) the study area lacked large wildfires between 23 and 30 years old, providing a natural threshold. Locations were selected from a random set of available possible locations within 4 km ($\bar{x}$ = 610 m) of roads (including off-road trails) with final sites requiring consistent forest stand conditions (i.e., height, density, age) across an area > 0.8 ha surrounding sample sites. None of the seismic lines in this study were replanted or treated with any silvicultural treatment or mechanical site preparation, nor had evidence of extensive or recent all-terrain vehicle (ATV) use. Thus, this study does not represent intensively disturbed and re-used lines, but rather the condition where human activity is low and natural recovery is allowed to happen (Fig. 2). Selection of where to start a plot at a site was determined by a random toss of a metal stake in the middle of the seismic line.

All field work occurred in the summer of 2018 with 146 sites sampled with each site being represented by a pair of plots. One plot was on the seismic line and the other 25 m into the adjacent forest (n = 292 plots). A coin toss was used to randomly assign which side of the seismic line the adjacent forest plot was located. Out of the 146 sites, 68 sites (47%) did not experience a wildfire in the past 65 years (defined as 'unburnt'), while 78 sites (53%) had a wildfire in the last 23 years (defined as 'burnt'). Each plot represented paired 30-m belt transects with the seismic line transect located along the center of the seismic line and the adjacent forest transect located 25 m into the forest running parallel to the seismic line (see Filicetti and Nielsen 2018, 2020 for more details). Seismic line width was measured using a tape measure to the nearest 0.1 m at the 15 m center distance of each transect.

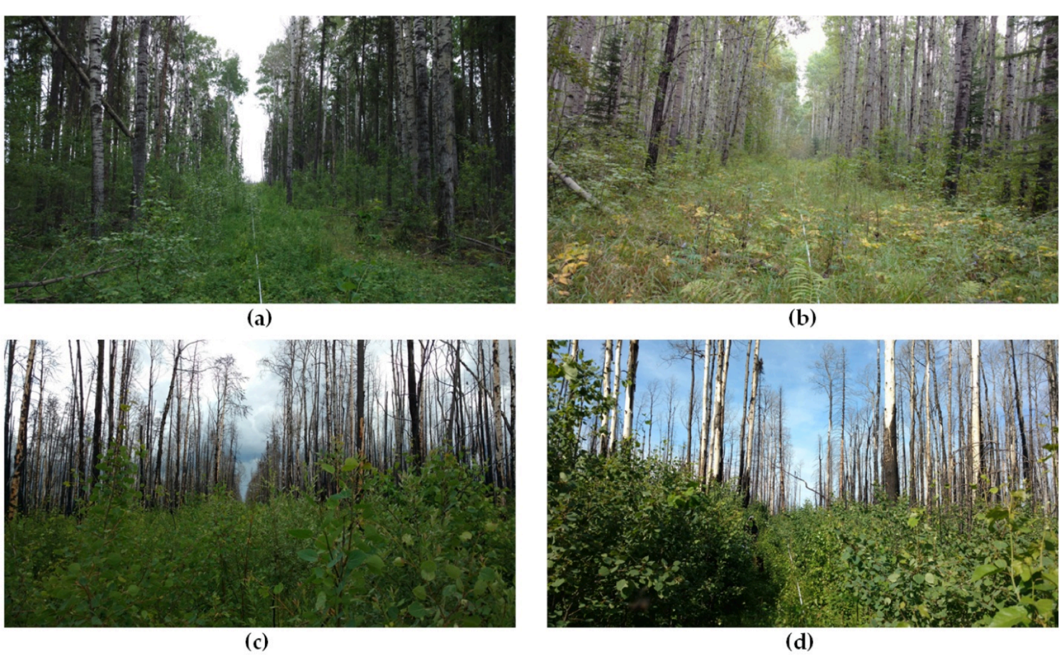

Fig. 2. Example seismic lines in mesic upland forests of northeast Alberta, Canada for: unburnt lines in mature forests (a & b) and burnt lines (c & d) from recent (≤23-yr old) high-severity fires.

Line orientation represented the compass bearing of seismic lines transformed to an index between 0 (east–west orientation) and 1 (north–south orientation) following the methods of van Rensen et al. (2015). Most lines in the area were on north–south and east–west axes (80%). Stand information was collected in the adjacent forest plot, including fire severity (defined as percent overstory tree mortality), stand basal area by species using a 2-factor metric prism (m^2/ha) at the midpoint of the adjacent forest transect (15 m line distance), stand age of representative mature trees in the same plot using dendrochronological aging via tree cores at DBH, and representative tree height using a Haglof Vertex IV (Sweden) hypsometer. Percent ground cover information was collected by averaging six sequential quadrats (2 × 5 m) along each transect for: graminoids, dwarf shrubs, woody debris, lichen, bare ground, bryophyte, and open water.

We measured soil compaction by taking bulk density measurements at the 10, 15, and 20 m distances of each transect (i.e., 3 samples per plot and 6 per site for a total of 876 samples). The 3 bulk density samples in a plot were averaged for a single plot value to match the scale of measures for tree regeneration. Because many seismic lines were created decades earlier and had only one pass of machinery and/or created in winter when soils were frozen, we focused on the upper soil depths (<20.1 cm) since deeper soils were unlikely to experience compression. The upper organic layers, Litter and Fermented, were always removed prior to sampling, while the deeper Humic layers were only removed if shallower than 15 cm from the surface. A cylinder with 5.1 cm height and 10.8 cm diameter (467 cm^3) was used to sample bulk density. Samples were oven dried at 110 °C for 24 h, then all coarse material (rocks, roots, etc.) greater than 2 mm were sieved with all masses and volumes recorded.

Since we were interested in large woody trees/shrubs that will initially reforest seismic lines and slow animal movements by increasing in horizontal and vertical structure, we combined green alder, a tall shrub (up to 6-m), with other trees and define this here forth as simply 'trees' or 'regeneration density' (green alder accounted for 14% of all tree stems). Regeneration densities were measured within belt-plots along each 30 m transect. Regeneration densities (<5 cm DBH) were counted in 1 × 30 m belt quadrats (30 m^2), while densities for larger trees (≥5 cm DBH) were counted in 2 × 30 m belt quadrats (60 m^2). The purpose of the two size categories (<5 cm DBH and ≥ 5 cm DBH) was to compare regeneration density on seismic lines to adjacent forests at a DBH size-class that emphasized recent regeneration, as the adjacent forest, by definition, had many mature trees. Therefore, when examining regeneration density for seismic line and adjacent forests, the < 5 cm DBH was used, while analysis of regeneration density on only seismic lines used all trees regardless of DBH as all trees on a seismic line were assumed to be regenerating post-disturbance (only 4.2% of all trees on seismic lines had a DBH ≥ 5 cm). All regeneration densities were calculated to a common scale of stems per 100 m^2 (0.01 ha) for analysis, but in some cases reported as stems per hectare for ease of comparison with the literature.

2.3. Effect of seismic lines on soil bulk density

We stratified bulk density measures into two categories, seismic lines (146 plots) and adjacent forests (146 plots). We then used a paired *t*-test to examine whether seismic lines differed from the paired adjacent forests. Additional analyses testing changes in bulk density post-fire can be found in Appendix B.

2.4. Effects of fire and seismic line on regeneration

First, we plotted the mean and standard errors of regeneration density (per ha) for trees < 5 cm DBH against the presence/absence of wildfire and seismic line presence (burnt line, unburnt line, burnt forest, unburnt forest) to visualize and test for differences in the main experimental effects using a pairwise test with a Bonferroni adjustment (*pwmean mcompare(bonferroni)*; STATA 15.1/SE StataCorp, 2017). We then used mixed-effects negative binomial models (*xtnbreg* command in STATA 15.1/SE; StataCorp, 2017) to model differences in regeneration density (trees per 100 m^2) of wildfire (burnt versus unburnt) and seismic line presence. We used site ID as a random effect to account for the paired nature of the seismic line and adjacent forest plots within a single site. We then created binary dummy variables to represent the presence (1) or absence (0) of a recent wildfire, and seismic line (1) or adjacent forest (0) plots. Control plots and reference conditions for categorical contrasts of variables in models were therefore sites in mature, undisturbed forests. We limited the predictor variables to the interaction of two main treatment variables (fire presence and seismic line presence versus adjacent forest), regardless of their significance. We report coefficients (β) for negative binomial models, but we also interpret them as percent change in regeneration per one unit change in the predictor variable by exponentiating them, subtracting one, and multiplying by 100% ([exp[β] -1]×100%).

2.5. Relationship between stand, fire severity, and seismic line characteristics on regeneration

For this section we restrict the analysis to only seismic lines, therefore, we define here regeneration density as any tree on the seismic line regardless of its size (DBH). This allows us to more directly test whether regeneration density on lines is affected by: (1) bulk density, as anthropogenic compaction of soils is not an issue in the adjacent forest; (2) fire (presence/absence, severity, and time since); and (3) seismic line characteristics, such as line orientation and width (forest gap size). Although models with more complicated interactions could combine adjacent forest and line data, some combinations are not possible (line width or orientation). We also considered the effect of the adjacent stand characteristics on regeneration density on seismic lines by including stand height, stand basal area (total and species specific), stand age, and their interaction with seismic line (forest gap) width, line orientation, and fire. Finally, we examined the effects of graminoid, dwarf shrubs, woody debris, lichen, bare ground, bryophyte, and open water ground cover on seismic line regeneration density.

We used Pearson correlations to assess initial collinearity among variables, with only two variables, stand height and stand age, being highly colinear ($|r| = > 0.7$) at $r = 0.74$. We therefore did not include stand height and stand age in the same model, but potentially one of the variables. Here we used standard negative binomial regression models (*nbreg* command in STATA 15.1/SE; StataCorp, 2017). We developed models from a list of candidate variables based on prior literature, our prior experience in other ecosites, and objectives of the paper. Specifically, we fit models with all *a priori* treatment and site variables, but only retained significant (at $\alpha = 0.05$) and uncorrelated ($r < |0.7|$) variables to reduce model complexity. We again analyzed regeneration density at a scale of stems per 100 m^2 and we report coefficients for negative binomial models, but we also interpret them as percent change in regeneration per one unit change in the predictor variable by exponentiating them, subtracting one, and multiplying by 100% ([exp[β] −1] × 100%).

Table 1
Stand characteristics and tree regeneration rates for 146 mesic upland forest sites sampled in northeast Alberta, Canada. This includes both recently burned and mature forests for paired plots in seismic lines and adjacent forests ($n = 292$ plots).

Stand variable	Minimum	Median	Maximum	Mean (S.E.)
Age (years)	2	57	138	51 (2.9)
Height (m)	0.2	17	36	16 (0.8)
Basal area (m^2/ha)	0	24	68	25 (1.1)
Tree stems per ha (DBH < 5 cm)				
Seismic line	0	12,250	69,333	16,197 (1060)
Adjacent stand	0	8,833	56,833	12,400 (858)
Tree stems per ha (DBH ≥ 5 cm)				
Seismic line	0	0	7,500	708 (119)
Adjacent stand	0	1,250	5,500	1,586 (100)

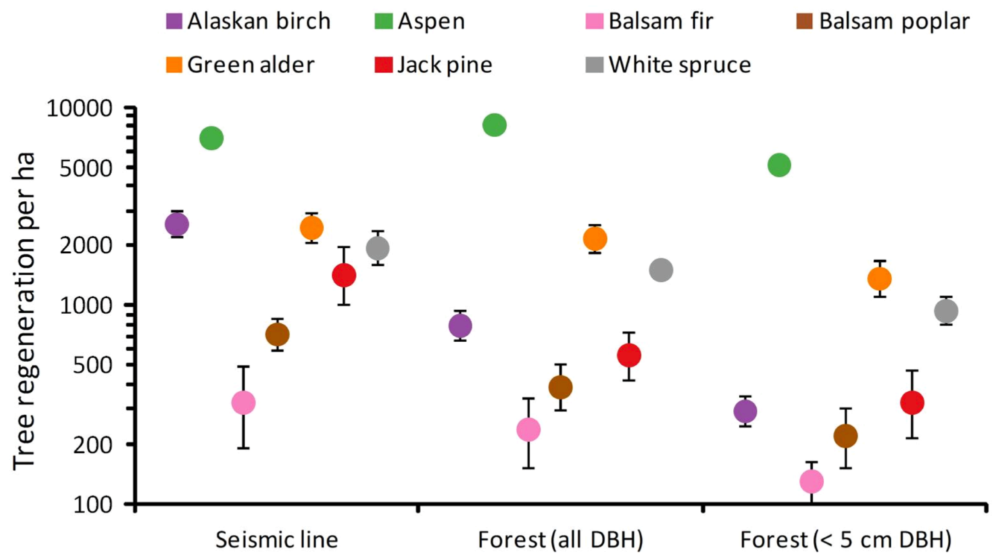

Fig. 3. Regeneration density on seismic lines [all diameter at breast height (DBH) classes] and adjacent forests (all DBH classes and < 5 cm DBH) for the seven most common tree species in upland mesic forests of northeastern Alberta, Canada. Error bars are represented by one standard error; error bars not visible have ranges smaller than the point. Note here that the y-axis is in $\log_{10}$ scale since abundances of species vary greatly, but mostly dominated by aspen.

3. Results

3.1. Stand characteristics and overall patterns in regeneration density

Age of stands sampled ranged from 2 to 138 years ($\bar{x} = 51$, SE = 2.9), stand height varied from 0.2 to 36 m ($\bar{x} = 16$, SE = 0.8), basal area in stands adjacent to seismic lines varied from 0 to 68 m^2/ha ($\bar{x} = 25$, SE = 1.1), while saplings and understory trees [< 5 cm diameter at breast height (DBH)] ranged from 0 to 56,883 ($\bar{x} = 12{,}400$, SE = 858) stems per hectare (Table 1). Widths of seismic lines ranged from 3 to 14.0 m ($\bar{x} = 6.5$, SE = 0.21) (see Fig. 2 for examples).

Species composition of regenerating trees was similar on the seismic line compared with the adjacent forest with perhaps the most notable exception being Alaskan birch which were much more abundant on seismic lines (Fig. 3; see Appendix A Fig. A1 for results by ecosite). Jack pine, in particular, was a good indicator of local moisture regimes, where high, medium, and low jack pine densities represented low, medium, and high site moisture, respectively.

3.2. Effect of seismic lines on soil bulk density

Soil bulk density ranged from 0.12 to 1.47 g/cm^3 ($\bar{x} = 0.59$, SE = 0.02) and was 34% higher on seismic lines than in adjacent forests ($p < 0.001$) (Table 2; see Appendix A Table A1 for results by ecosite and Appendix B Table B1 for how bulk density changes post-fire). The large range in bulk densities relates most to differences in ecosite and associated soils (e.g., grain size, organic matter, etc.).

Table 2
Mean, standard error, and results of a paired *t*-test comparing bulk densities (g/cm^3) for all lines with all forests in northeast Alberta, Canada.

Statistic	Line	Forest
Mean	0.67	0.50
Standard Error	0.03	0.02
n	146	146
t	5.59	
df	145	
p-value	<0.001	

3.3. Effects of fire and seismic line on regeneration

Analyses demonstrated increases in regeneration density after recent wildfires, including in the 2-year-old wildfire, as regeneration density for both burnt lines and forests were higher and statistically different from unburnt lines and forests. Moreover, the interaction between seismic line (vs. forest) and presence of wildfire within the last 23 years on regeneration density was significant and positive (Fig. 4 and Table 3; see Appendix A Fig. A2 and Table A2 for results by ecosite). On average, burnt lines had 19,622 regenerating stems/ha (SE = 1,626), unburnt lines had 11,870 regenerating stems/ha (SE = 1,130), the adjacent burnt forests had 16,739 regenerating stems/ha (SE = 1,253), and the adjacent unburnt forest had 6,934 regenerating stems/ha (SE = 740). Burnt lines, therefore, had 65% more regenerating stems per hectare than unburnt lines ($p < 0.001$), 17% more regenerating stems per hectare than burnt

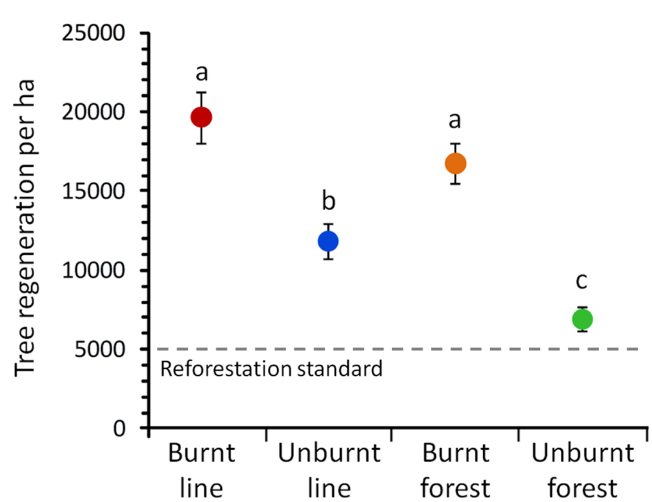

Fig. 4. Regeneration density (DBH < 5 cm) per hectare by seismic line or adjacent forest and presence/absence of recent (≤23-yrs.) wildfire. Different letters between treatments indicate significant ($p < 0.0125$) differences based on pairwise comparisons with Bonferroni adjustments. Note, dashed gray line represents 5,000 stems/ha which is the highest density class in Alberta's reforestation standards (Alberta Agriculture and Forestry 2018).

Table 3
Mixed-effects negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density per hectare (DBH < 5 cm) to presence of recent (≤23 yrs.) wildfire, seismic line (vs. adjacent forest), and their interaction in northeast Alberta, Canada. Note, the intercept is unburnt forest. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha)	β (SE)
Constant (intercept)	0.74 (0.14)***
Presence of recent (≤23 yrs.) wildfire	0.88 (0.12)***
Seismic line (vs. forest)	0.45 (0.10)***
Interaction	−0.35 (0.12)**
Model statistics	
n	292
Log likelihood	−1,672
Wald X^2	67.71
Prob > X^2	<0.001

Table 4
Negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density of all tree species on seismic lines to fire severity (% tree mortality), line characteristics, stand variables (BA represents basal area in m^2/ha), and percent ground cover in northeast Alberta, Canada. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha) on seismic lines		β (SE)
	Constant (intercept)	4.210 (0.212)***
Stand variables		
	Height (m)	0.024 (0.009)**
	Jack pine BA (m^2/ha)	0.086 (0.021)***
Fire variables		
	Severity (% tree mortality)	0.010 (0.001)***
	Jack pine BA × severity	−0.001 (0.0003)**
Ground cover (%)		
	Graminoid	−0.008 (0.003)*
Model statistics		
	n	146
	LR χ^2	57.13
	Prob > χ^2	< 0.001

forest, but was not significant ($p = 0.603$), and 183% more regenerating stems per hectare than unburnt forest ($p < 0.001$) (Fig. 4). Burnt forests had 140% more stems per hectare than unburnt forests ($p < 0.001$) and 41% more stems per hectare than unburnt lines ($p = 0.025$). Finally, unburnt lines had 71% more regenerating stems per hectare than unburnt forests ($p = 0.048$). There were, therefore, more regenerating tree stems on burnt seismic lines, compared to unburnt lines, adjacent burnt forest (although not a significant difference), and adjacent undisturbed forests illustrating that wildfires promote substantial natural regeneration (passive restoration) for most linear disturbances in mesic-upland boreal forests that lack extensive anthropogenic reuse of the lines. Overall, regeneration density was 141% higher in burnt versus unburnt sites, 57% higher on seismic lines versus adjacent forest, but 30% less for the interaction of burnt and seismic lines (see Fig. 4 and Table 3). Average regeneration rates were always above 5,000 stems/ha, the highest density class in Alberta's reforestation standards.

3.4. *Relationship between stand, fire severity, and seismic line characteristics on regeneration*

Model selection favored two stand variables (stand height and jack pine basal area), one wildfire variable (fire severity), the interaction between jack pine basal area and fire severity, and one ground cover variable (graminoid ground cover). Regeneration rates on lines increased by 1% per 1% increase in fire severity, increased by 9% per 1 m^2/ha increase in jack pine basal area, decreased by 0.1% for each one unit change in the interaction of fire severity and jack pine basal area, increased by 2% per 1-m increase of stand height, and decreased by 0.8% per 1% increase in graminoid ground cover (Table 4; see Appendix A Table A3 for results by ecosite). Note, the effect of bulk density on regeneration was non-significant when considering stand and site variables.

4. Discussion

Findings here illustrate that seismic lines had higher bulk densities than adjacent undisturbed forests, but this did not adversely affect tree regeneration. The presence of both recent wildfires and seismic lines increased regeneration density, but the effect of line presence was diminished when occurring with a recent wildfire. Overall, the effect of wildfires was larger than lines, and burnt lines were no different than burnt forests. Finally, stand and site variables affecting regeneration density included an interaction of fire severity and jack pine basal area (the effect of severity was moderated in the presence of jack pine), a positive effect with stand height, and a negative effect with graminoid ground cover.

4.1. *Effect of seismic lines on soil bulk density*

Bulk density was 34% higher on seismic lines supporting observations from industry, government, and researchers of increased compaction (Revel et al. 1984; MacFarlane 2003; Lee and Boutin 2006; Davidson et al. 2020). However, bulk density measures overall were low ($\bar{x} = 0.59$ g/cm^3) due to the high organic matter typical of boreal forests [ranges between 0 and 50% ($\bar{x} = \sim 15\%$) in the region (Grigal et al., 1989; Périé and Ouimet 2008; Hossain et al. 2015)]. Bulk density on seismic lines in nearby peatland forests were even lower averaging 0.3 g/cm^3 for wide seismic lines and 0.04 g/cm^3 for narrow lines, which was similar to undisturbed forests of 0.05 g/cm^3 (Davidson et al. 2020). Maximum bulk density in this study was 1.47 g/cm^3, with only 6 of the 146 sites being over 1.40 g/cm^3. This is below levels of bulk density where they begin to negatively affect tree establishment, growth, and survival in boreal aspen forests (1.55–1.65 g/cm^3) (Daddow and Warrington 1983; Sealey and Van Rees 2019). Other factors that may be affecting bulk density and thus compaction include: (1) lines that were most recently re-used or heavily re-used in the past should have higher levels of compaction; (2) ecosite, particularly sites with more organic matter should result in less compaction (see Appendix A); (3) wildfires may increase compaction under certain conditions (see Appendix B); and (4) animal trails are more common on seismic lines resulting in local compaction (Latham et al. 2011b; Tigner et al. 2014, 2015; Dickie et al. 2020).

4.2. *Effects of fire and seismic line on regeneration*

Both wildfires and seismic lines increased regeneration density in mesic-upland forests, with fires having a larger effect (141% increase) than seismic lines (57% increase) when compared to unburned sites and adjacent forests. Contrary to some reports pointing to arrested succession with little to no tree development on seismic lines in mesic-upland forests (MacFarlane 2003), unburnt seismic lines without extensive re-disturbance had higher regeneration rates than the adjacent forests illustrating an expected response to early seral conditions. Comparisons with unburnt lines to burnt forests show that seismic line disturbances are different from wildfires. Although seismic lines demonstrate early seral conditions, regeneration densities are still much lower than in wildfires. Clearly these forests are fire-adapted yet do not demonstrate the same level of resilience to seismic lines. A similar pattern was observed in peatland forests, although at much lower densities (Filicetti and Nielsen 2020). Seismic lines in mesic upland forests, either burnt or unburnt, have regeneration densities well over 5,000 stems/ha which is the highest density class in Alberta's reforestation standards (Alberta Agriculture and Forestry 2018).

Although comparing seismic lines to paired adjacent forests have limitations, they do provide for broad comparisons and control for local site conditions. Because mature forests are not expected to have substantial amounts of understory regeneration, the more meaningful comparisons are between unburned lines, burned lines, and burned adjacent forests where regeneration of the forest is comparable. In those cases, tree regeneration on lines was still as high, or higher, than naturally regenerating forests suggesting significant early seral forest recovery. As seismic lines represent narrow clear-cut openings, they have higher levels of sunlight and wind (Stern et al. 2018; Franklin et al. 2021), and are next to readily available seeds/suckers from the adjacent forest and thus are useful comparisons. Although reports for other ecosites show a near lack of regeneration (Lee and Boutin 2006; van Rensen et al. 2015; Filicetti et al. 2019; Filicetti and Nielsen 2020), the conditions of seismic lines in mesic upland forests respond more similarly to early seral conditions with higher regeneration rates. However, many seismic lines are still easy to traverse, particularly unburnt lines, and thus require time to fill in and mature. This may be a much longer process due to attrition rates not accounted for in clear-cut studies as the small gap size of seismic lines can be shaded if the overstory is dense. Furthermore, the repeated usage of lines by animals can result in high levels of both herbivory and trampling. This is similar to observations in wetter ecosites, where a high water table and a lack of microsites restrict tree regeneration and growth (Lee and Boutin 2006; van Rensen et al. 2015; Filicetti et al. 2019; Filicetti and Nielsen 2020). However, the dense patterns of regeneration post-fire suggest that seismic lines minimally damage roots/suckers from immediately adjacent trees and site availability.

4.3. Relationship between stand, fire severity, and seismic line characteristics on regeneration

Time since wildfire was related to tree regeneration on seismic lines, but was not always a better predictor than a simple binary variable of fire presence and always worse than fire severity. This is similar to responses in xeric jack pine stands (Filicetti and Nielsen 2018), and treed peatlands (Filicetti and Nielsen 2020), where most seed abscission occurs within the first few years post-fire (Greene et al. 2013) and points to a reoccurring observation that time since disturbance on lines for, at least the last few decades, is less important than the severity of the disturbance and site characteristics. Aspen, which accounts for 43% of the regeneration density observed in this study, regenerated at higher rates post-fire, mostly from suckering (Greene and Johnson 1999; Frey et al. 2003; Jean et al. 2020), where > 95% of recruitment occurs within the first 3 years post-fire (Greene et al. 2004). Aspen increases their abundance in a stand post-fire with thinning occurring in the following years (Greene and Johnson 1999). Other species, like balsam fir and white spruce that are less adapted to fires, are able to establish seedlings post-fire with aerial seeds banks (de Groot et al. 2013). Regardless, immediately after a wildfire competition to colonize and establish new sites is high and recruitment after the first couple of years is minimal.

Regeneration density of trees on seismic lines were also positively related to basal area of jack pine and the interaction with fire severity. This may relate to two factors: (1) drier sites, that are associated with jack pine, regenerate at higher rates because they have more jack pine and aspen, which both regenerate well post-fire compared to hygric and less fire-adapted species, such as balsam poplar and balsam fir; and (2) hygric sites that contain less jack pine tend to burn less often and at lower severity and therefore are less likely to initiate early seral conditions. This is similar to findings in treed peatlands where fens did not regenerate trees on seismic lines as well as bogs and poor mesic ecosites (Filicetti and Nielsen 2020).

The positive relationship with stand height possibly reflects that larger trees: (1) are a good indicator that the site is more suitable for trees (Mao et al. 2017) and is therefore likely to have more available microsites for regeneration; (2) tend to produce more seeds (Greene et al. 1999); and (3) have larger reserves of carbohydrates in the root system and thus higher sucker dispersal and density (Greene et al. 1999, 2004).

Graminoid ground cover was negatively related to tree regeneration density, like that of seismic lines in treed peatlands (Filicetti et al. 2019; Filicetti and Nielsen 2020). When dividing seismic lines into 3 categories of graminoid cover: < 10%, 10 – 20%, and > 20%; we find that they consist of 56%, 20%, and 24% of lines; and 18,800; 16,800; and 15,600 stems/ha on average, respectively. Graminoid cover did reduce regeneration density, but only in rare instances did graminoid cover become dominant. Several studies in central and northern Alberta show negative effects of graminoids on tree regeneration in aspen forests. For instance, belowground growth of aspen decreased with smooth brome (*Bromus inermis* Leyss.) competition as this species rapidly spreads to available rooting space inhibiting water and nutrient availability (Bockstette et al. 2017). Another grass common to boreal forests of Alberta, *Calamagrostis canadensis*, can compete and inhibit tree regeneration and growth in several ways. *C. canadensis* competes for sunlight and nutrients, while its thick growth and litter reduces soil temperatures resulting in reduced access to nutrients and water due to a shorter thaw period and growing season (Hogg and Lieffers 1991). Presence of *C. canadensis* can inhibit aspen sucker emergence by 30% and suckers that do emerge have 40% less leaf area and are smaller resulting in reduced aspen regeneration and growth (Landhäusser and Lieffers 1998).

Contrary to suggestions from others (Revel et al. 1984; MacFarlane 2003; Lee and Boutin 2006), seismic line compaction does not appear to affect regeneration, at least for mesic boreal forests where lines are not extensively disturbed by ATV use. Extensive ATV use or re-use of these lines by industry for repeated exploration may very well lead to compaction levels that reduce regeneration and need to be considered. Perhaps compaction is more detrimental in the first few years after disturbance, as our sampling occurred later when compaction may have been alleviated. However, given that most of these forests contain high organic matter and line clearing was often in winter when the ground was frozen, soil compaction may not be a common issue for this forest type. Indeed, our findings are similar to other studies examining the effects of soil bulk density on tree regeneration in aspen forests (Kabzems and Haeussler 2005; Sealey and Van Rees 2019). Possibly soil compaction does negatively affect tree density, but it may also relate to other limiting/competing factors such as microsites, graminoid cover, bryophyte cover, shrubs, or other factors resulting in a more neutral overall response. Regardless, it is apparent that the majority of seismic lines in the region that are not extensively re-disturbed by human activity are not likely to be limited by soil compaction.

5. Management implications

Seismic lines in mesic upland forests have moderately more compacted soils compared to adjacent undisturbed forest controls. Regardless, the compaction on seismic lines appear to have negligible effects on regeneration density and are below the levels typically considered to be problematic for tree regeneration. Any mitigation efforts to alleviate compaction will reset the regeneration already initiated suggesting that: (1) sites in need of restoration that are truly arrested need to be identified first before widely applying restoration treatments; and (2) perhaps the more effective strategy is restricting human access (ATV, snowmobile, bulldozer, mulcher, etc.) to seismic lines to allow for natural recovery. Restoration of seismic lines is considered to be a billion-dollar issue (Hebblewhite 2017) with triage needed for when and where to spend limited restoration dollars to being efficient and effective. Since seismic lines in upland mesic forests not constantly re-used by humans have such high regeneration densities, well above 5,000 stems/ha, they are likely sufficient to develop forest structure even when accounting for self-thinning which is consistent with natural and post-harvest stands and should not be prioritized for treatments. In this study, most unburnt lines were restoring well on their own, yet some sources have suggested otherwise, this may be due to regeneration having poor growth and survivability due to compaction and shading on some sites studied. Here, we excluded lines having evidence of extensive recent human re-use to focus on ecological limitations of recovery. Therefore, we caution readers not to extrapolate these results to all possible seismic lines, particularly where there is more human activity and re-disturbance. There is potential that re-use of lines is much higher than most people suspect and data on this type of information is required to make better management decisions. Wildfires bestow an increase in regeneration density in a much shorter time-frame and can provide a potential option for low cost passive restoration under certain circumstances. There are substantial variations in fire frequency within a landscape due to features such as dominant tree species (Larsen 1997), fuel loads (Johnston et al. 2015), natural landscape features (Nielsen et al. 2016), and time since last fire (Beverly 2017). This can affect recovery patterns on lines as pointed to in Filicetti and Nielsen (2020). Climate change is expected to bring more frequent, more intense, and larger wildfires to much of the world, including northeast Alberta (Flannigan et al. 2009a, 2009b). Therefore, we propose that sites that are recently burnt, and areas that have a high likelihood of experiencing a wildfire in the short-term, should not be actively restored as wildfires will be able to regenerate trees with the use of no restoration dollars (use of prescribed fire for restoration in this system is unlikely). Our results suggest that controlling recreational (ATV and snowmobile use) and industrial (ATV, bulldozer, mulcher, etc.) access on lines where these activities occur, or are likely, is crucial to allowing natural recovery and is much less expensive than site preparation, stem bending, and tree planting associated with current restoration practices. This would save restoration investments for other places that are in more need.

CRediT authorship contribution statement

Angelo T. Filicetti: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Scott E. Nielsen:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Four common forest types (ecosites) of mesic upland forests

The mesic upland forests in this region can be divided into four forest types (ecosites) which are: (1) medium xeric with an overstory dominated by jack pine and aspen with occasional white spruce and an understory containing bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), hairy wildrye (*Leymus innovatus* (Beal) Pilg.), and buffaloberry (*Shepherdia canadensis* (L.) Nutt.); (2) medium mesic with an overstory dominated by aspen and to a lesser extent white spruce and an understory containing squashberry (*Viburnum edule* (Michx.) Raf.), bunchberry (*Cornus canadensis* L.), and buffaloberry); (3) medium hygric with an overstory dominated by aspen, balsam poplar, and white spruce and an understory containing horsetail (*Equisetum* spp.), willows (*Salix* spp.), and currants (*Ribes* spp.); and (4) rich hygric with an overstory dominated by balsam fir and white spruce with occasional aspen and balsam poplar and an understory containing ferns, red osier dogwood (*Cornus sericea* L.), and thick feather mosses using definitions from the Alberta Biodiversity Monitoring Institute ecosite classification (Alberta Biodiversity Monitoring Institute 2018).

Distribution of sample sites by ecosite for mesic forest types included 18 medium-xeric (36 plots), 102 medium-mesic (204 plots), 12 medium-

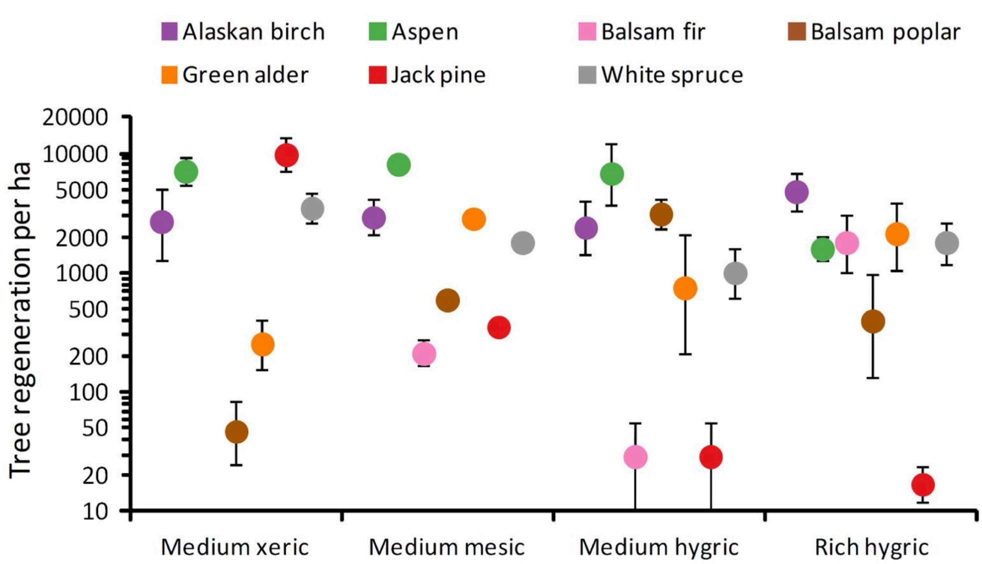

Fig. A1. Regeneration density for the seven most common species [all diameter at breast height (DBH) classes] found on seismic lines in four upland mesic ecosites of northeast Alberta, Canada. Error bars are represented by one standard error; error bars not visible have ranges smaller than the point. Note here that the y-axis is in $\log_{10}$ scale since abundances of species vary greatly.

hygric (24 plots), and 14 rich-hygric (28 plots) ecosites. Sites that experienced a wildfire in the last 23 years by ecosite were: medium-xeric at 13 (26 plots or 72%), medium-mesic at 53 (106 plots or 52%), medium-hygric at 8 (16 plots or 67%), and rich-hygric at 4 (8 plots or 29%). Sampling effort among ecosites was unequal with one ecosite (medium-mesic) accounting for 70% of sites since it was the most common in the region (sampling effort by ecosite was representative of the area of each ecosite thus rarer ecosites had fewer samples). Preliminary analyses demonstrated similarities among ecosites with only adjacent stand basal area of jack pine, which is less abundant in the ecosite, differing (Fig. A1, Fig. A2 and Tables A1–A3).

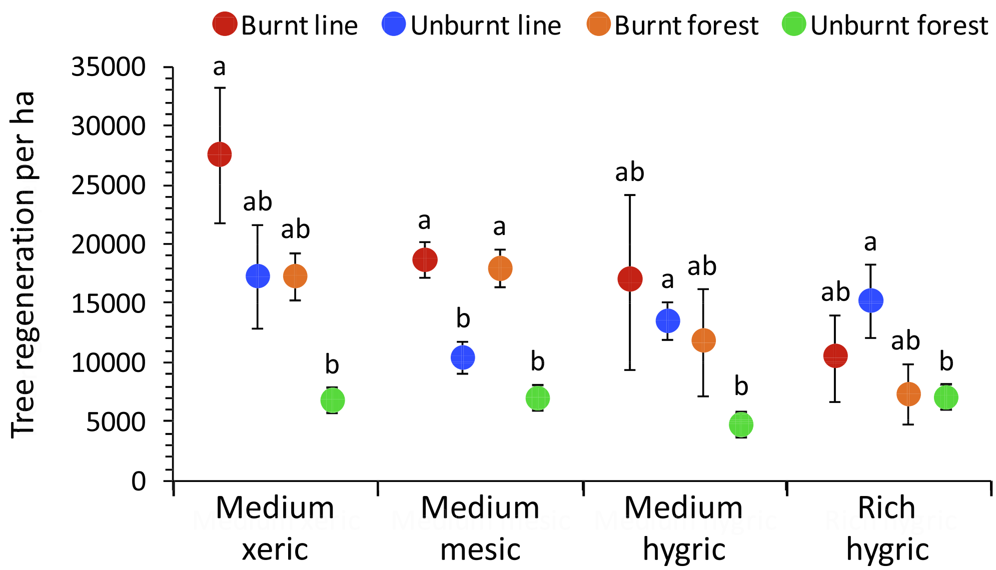

Fig. A2. Regeneration density [diameter at breast height (DBH) < 5 cm] (stems/ha), across four ecosites and wildfire presence in northeast Alberta, Canada. Significance of treatments within each ecosite was tested with a pairwise comparison (Bonferroni adjustment) with different letters indicating significant ($p < 0.0125$) differences within an ecosite.

Table A1
Mean, standard error, and results of a paired *t*-test comparing bulk densities (g/cm^3) for among four mesic ecosite on all lines and forests sampled in northeast Alberta, Canada.

Statistic	Medium xeric		Medium mesic		Medium hygric		Rich hygric	
	Line	Forest	Line	Forest	Line	Forest	Line	Forest
Mean	1.06	0.85	0.64	0.49	0.54	0.28	0.55	0.37
Standard Error	0.10	0.07	0.03	0.03	0.11	0.06	0.09	0.06
n	18	18	102	102	12	12	14	14
t	2.74		4.00		2.76		1.78	
df	17		101		11		13	
p-value	0.007		< 0.001		0.009		0.049	

Table A2
Mixed-effects negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density per hectare (DBH < 5 cm) of all tree species to presence of fire, seismic line location (vs. adjacent forest), and their interaction in northeast Alberta, Canada. Note, the intercept is unburnt forest. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha)		Medium xeric	Medium mesic	Medium hygric	Rich hygric
		β (SE)	β (SE)	β (SE)	β (SE)
	Constant (intercept)	0.58 (0.43)	0.77 (0.16)***	1.98 (0.78)*	1.1 (0.41)**
Fire variables					
	Presence of fire	0.8 (0.39)*	1.13 (0.14)***	−0.29 (0.54)	−0.05 (0.35)
	Fire × Seismic line	−0.05 (0.44)	−0.35 (0.14)*	−0.99 (0.32)**	−0.41 (0.43)
Seismic line location variable					
	Seismic line plot	0.35 (0.40)	0.4 (0.12)***	1.03 (0.23)***	0.6 (0.22)**
Model statistics					
	n	36	204	24	28
	Log likelihood	−217.37	−1147.04	−132.62	−150.31
	Wald χ^2	9.55	77.99	22.98	9.24
	Prob > χ^2	0.02	0.00	0.00	0.03

Table A3
Negative binomial regression model parameters (coefficient, β; and standard error, SE) relating regeneration density of all tree species on seismic lines to fire severity, line characteristics, stand variables (BA represents basal area in m^2/ha), and percent ground cover in northeast Alberta, Canada. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Tree density (stems/ha) seismic line only	Medium xeric	Medium mesic	Medium hygric	Rich hygric
	β (SE)	β (SE)	β (SE)	β (SE)
Constant (intercept)	5.14 (0.33)***	4.03 (0.27)***	3.86 (0.51)***	3.62 (0.38)***
Fire variables				
Severity (% tree mortality)		0.01 (0.002)***		
Jack pine BA × severity		−0.002 (0.001)*		
Line characteristics				
Line Width (m)	0.15 (0.05)**			0.15 (0.05)**
Bearing			−1.31 (0.49)**	
Stand variables				
Height (m)		0.026 (0.011)*		
Aspen BA (m^2/ha)	−0.11 (0.02)***			
Jack pine BA (m^2/ha)		0.27 (0.09)**		
Ground Cover (%)				
Graminoid		−0.01 (0.004)*		
Dwarf shrub			0.10 (0.03)***	0.04 (0.02)*
Model statistics				
n	18	102	12	14
LR χ^2	17.68	50.91	10.56	9.30
Prob > χ^2	< 0.001	< 0.001	0.005	0.010

Appendix B. Changes in bulk density due to wildfire

Four sub-categories were created to compare changes in bulk density post-fire: burnt lines (78 plots); unburnt lines (68 plots); burnt forests (78 plots); and unburnt forests (68 plots). Two-sample t-tests were used to test for differences on seismic lines (burnt lines vs unburnt lines) and in forests (burnt forests vs unburnt forests). Bulk density was 10% higher on burnt seismic line than on unburnt seismic lines, but not significant ($p = 0.122$), and 11% higher in burnt forests than in unburnt forests, but again not significant ($p = 0.144$). This suggests that wildfires can compact soils by approximately the same rate regardless of the initial level of compaction pre-fire, but that compaction levels vary substantially between sites and overall are not significant, but trend towards higher compaction following fire (see Table B1).

Table B1
Mean, standard error, and results of a two-sample *t*-test comparing bulk densities (g/cm^3) for burnt lines with unburnt lines and burnt forests with unburnt forests.

Statistic	Line only		Forest only	
	Burnt	Unburnt	Burnt	Unburnt
Mean	0.70	0.64	0.53	0.48
Standard Error	0.04	0.04	0.03	0.03
n	78	68	78	68
t	0.99		1.02	
df	144		144	
p-value	0.122		0.144	

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