

Tree regeneration on industrial linear disturbances in treed peatlands is hastened by wildfire and delayed by loss of microtopography¹

Angelo T. Filicetti and Scott E. Nielsen

Abstract: The world's forests are highly fragmented by linear disturbances, and many forests have failed to recover decades after abandonment. Lack of recovery is common in unproductive forests, such as treed peatlands, because of conditions that limit tree growth, including simplification of microtopography (loss of microsites). The persistence of these features affects biodiversity, but of particular concern in Canada is the detrimental effects on threatened woodland caribou. Although natural regeneration of trees in peatlands occurs in some places, it is not an effective recovery strategy for restoring the habitat of woodland caribou. This has led to restoration activities with costs exceeding CAD\$12 500/km. However, current restoration does not consider wildfires, which can destroy planted trees but also initiate early seral conditions that favor natural regeneration. Here we compared tree regeneration on seismic lines and adjacent forest controls for burnt (75 sites) and unburnt (68 sites) treed peatlands in northeast Alberta, Canada. Tree regeneration (stems with a DBH < 1 cm/ha) varied from 28 500 in burnt lines, 11 440 in unburnt lines, and 18 210 in burnt forest, to 9520 in unburnt forest. Wildfires promoted denser regeneration in sites with a greater proportion of serotinous species and water table depth. Microtopography and terrain wetness explained regeneration on burnt lines, but not unburnt lines. In burnt and unburnt lines, sunlight, microtopography, and depth of water table most affected tree regeneration patterns.

Key words: seismic line, linear disturbance, boreal forest, wildfire, forest gap.

Résumé : Les forêts du monde sont très fragmentées par les perturbations linéaires et plusieurs de ces forêts n'ont pas encore réussi à récupérer même si elles sont abandonnées depuis des décennies. L'absence de récupération est fréquente dans les forêts improductives telles que les tourbières boisées à cause des conditions qui limitent la croissance des arbres, incluant l'uniformisation de la microtopographie (perte de microsites). La persistance de ces caractéristiques est néfaste pour la biodiversité et le Canada est particulièrement inquiet des effets préjudiciables pour le caribou des bois qui est menacé. Bien que les arbres se régénèrent naturellement dans certaines tourbières, ce n'est pas une stratégie efficace de récupération pour restaurer l'habitat du caribou des bois. Cela a entraîné des activités de restauration dont les coûts excèdent 12 500 \$CAN/km. Cependant, la restauration actuelle ne tient pas compte des feux de forêt qui peuvent détruire les plantations d'arbres, mais aussi instaurer des conditions de début de succession qui favorisent la régénération naturelle. Dans cet article, nous comparons la régénération arborescente dans les lignes sismiques et les forêts témoins adjacentes dans le cas de tourbières boisées qui ont brûlé (75 sites) ou non (68 sites) dans le nord-est de l'Alberta, au Canada. La régénération arborescente (tiges avec un DHP < 1 cm/ha) varie de 28 500 tiges dans les lignes qui ont brûlé, à 11 440 dans celles qui n'ont pas brûlé, à 18 210 dans les forêts qui ont brûlé et à 9520 dans celles qui n'ont pas brûlé. Les feux de forêt ont favorisé l'apparition d'une régénération plus dense dans les sites où la proportion d'espèces sérotineuses est plus élevée et la nappe phréatique plus basse. La microtopographie et l'humidité du terrain expliquent la régénération dans les lignes qui ont brûlé mais pas dans celles qui n'ont pas brûlé. Dans les lignes qui ont brûlé ou non, l'ensoleillement, la microtopographie et la profondeur de la nappe phréatique ont le plus d'impact sur les patrons de la régénération arborescente. [Traduit par la Rédaction]

Mots-clés : ligne sismique, perturbation linéaire, forêt boréale, feu de forêt, trouée forestière.

Introduction

The world's forests are being increasingly fragmented from anthropogenic disturbances, including linear disturbances associated with, among other things, roads, transmission lines, pipelines, and oil and gas exploration. Indeed, the majority (70%) of the world's forests are now within 1 km of a forest edge (Haddad et al. 2015). Even when linear disturbances are considered temporary (i.e., for mineral exploration), they can become permanent

through consistent human use and expanded development. For instance, many "soft" linear features (such as unpaved roads or skid trails) fail to become reforested even decades after they are abandoned (Mercier et al. 2019). This pattern is most common in unproductive forests, such as treed peatlands, because of their slow growth and the generally harsh environment for tree growth.

One such anthropogenic disturbance common in boreal forests of western Canada is seismic lines. Seismic lines are narrow (3–

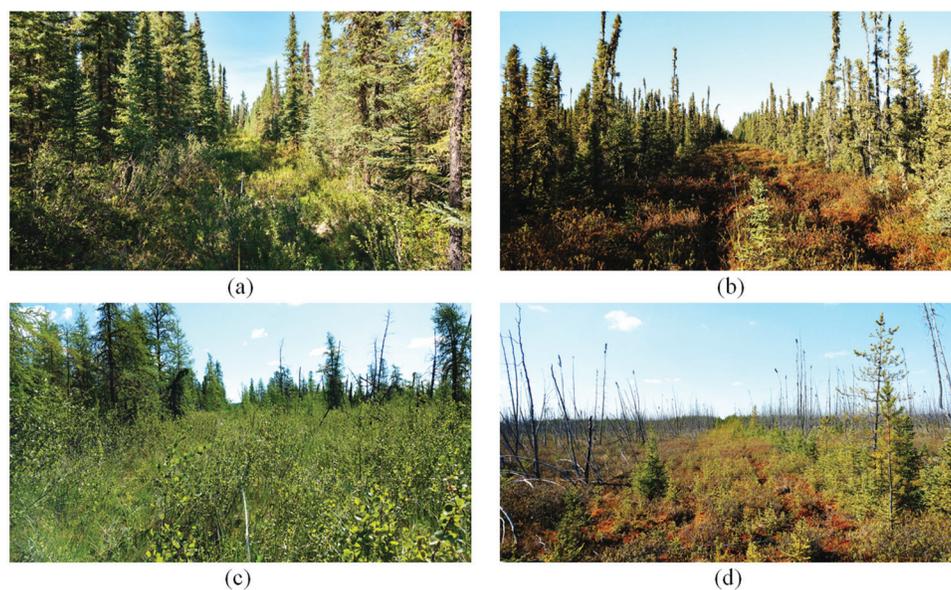
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Fig. 1. Examples of linear seismic disturbances in northern Alberta, Canada, boreal forest peatlands: (a) poor fen; (b) bog; (c) mid-severity burnt rich fen; and (d) high-severity burnt bog. All images courtesy of Angelo T. Filicetti.



12 m) linear openings (Fig. 1) created for mapping underground petroleum reserves through the use of seismic waves/vibrations. These lines can stretch for kilometers, are typically in a grid pattern, and can be as dense as 40 km/km² (50 m grid spacing) (Filicetti et al. 2019). Given their high density, seismic lines are the leading anthropogenic contributor to disturbance and fragmentation (dissection) of the boreal forests in Alberta, Canada (Arienti et al. 2009; Schneider et al. 2010).

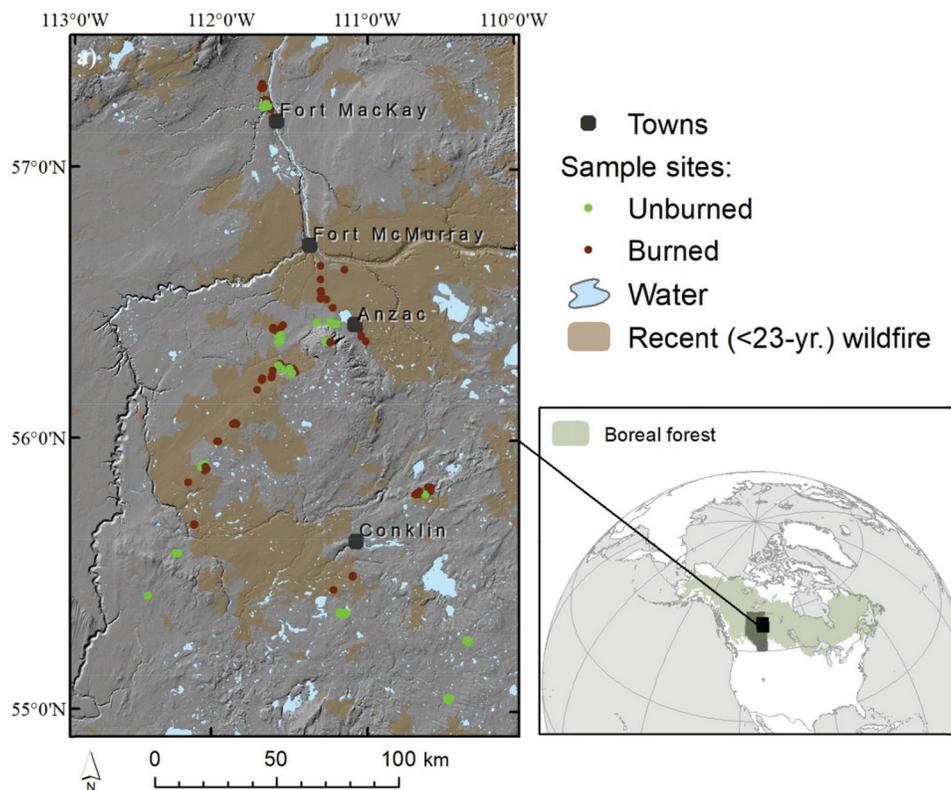
Many seismic lines in the boreal forest have not transitioned back to a forested state decades after their disturbance. In particular, treed peatlands have been shown to be the least likely to recover in Alberta (Lee and Boutin 2006; van Rensen et al. 2015; Filicetti et al. 2019). The exact reason for this delayed recovery is complex and not fully understood, but it is believed to be related to the characteristics of the initial disturbance. This includes the mechanized creation of seismic lines that simplifies the microtopography of peatlands (hummocks and hollows) and depresses its surface, resulting in a high water table (flooding) that leads to failures in tree recruitment and establishment (Liefvers et al. 2017). Seismic lines can also act as corridors for the movement of organisms that alter patterns of biodiversity and wildlife dynamics (Riva et al. 2018; Roberts et al. 2018). Of particular interest is the decline in woodland caribou (*Rangifer tarandus caribou*), one of the most high-profile species-at-risk in Canada's boreal forest (Dickie et al. 2017). These open corridors can function as "highways" for white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and wolves (*Canis lupus*), leading to increases in encounters with wolves and predation rates on woodland caribou via apparent competition with white-tailed deer and moose (Latham et al. 2011a, 2011b; James and Stuart-Smith 2000). The poor recovery rate for trees on seismic lines in treed peatlands (woodland caribou habitat) and major declines in woodland caribou populations (Dickie et al. 2017) have led to significant efforts to actively restore seismic lines (Filicetti et al. 2019). However, restoration treatments in northeast Alberta can exceed CAD\$12 500/km of seismic line (Filicetti et al. 2019) with hundreds of thousands of kilometers of seismic lines thought to need treatment, resulting in a billion-dollar conservation issue (Hebblewhite 2017). It may, therefore, be more economically feasible and efficient to first understand where treatments are most needed, where a no cost leave-for-natural reforestation (passive restoration) strategy could be

used, and how natural disturbances like wildfire can alter conditions that may benefit long-term tree recovery.

Wildfires are the most common natural disturbance in the boreal forest, having seemingly both positive and negative effects on seismic line tree recovery. On the one hand, wildfires provide the ideal leave-for-natural passive form of restoration for seismic lines by promoting the creation of microtopography (Benscoter et al. 2015), exposing preferential seedbeds (Sirois 1993), and increasing seed rain from fire serotinous and semi-serotinous species (Jayen et al. 2006). On the other hand, wildfires can eliminate gains from active restoration treatments, leading to a loss of restoration investments in tree planting (Pyper et al. 2014) and removal for up to 40 years of preferred winter forage (lichens) for woodland caribou (Skatter et al. 2017).

Here we examine reforestation dynamics on seismic lines in treed peatlands across six separate wildfires spanning a 22-year post-fire history in northeast Alberta. Our objectives were to assess: (i) whether wildfires promote the regeneration density of peatland forests on seismic lines compared with paired adjacent burnt forest and unburnt forests controls; (ii) which stand and line characteristics (stand age, height, basal area; line width and orientation) promote or impede the regeneration density of peatland forests on seismic lines; and (iii) whether changes in seismic line microtopography (complexity and depression), along with local terrain wetness, limit regeneration density in peatlands. Specifically, we hypothesize that: (i) sites will have higher regeneration density post-fire, in particular for sites with higher cover of semi-serotinous species (e.g., black spruce), as wildfires in the boreal forest initiate early seral conditions favorable for regeneration density; (ii) seismic lines will increase regeneration density at higher rates if: (a) they have experienced a wildfire, for the same reasons as above; and (b) are located on sites that have more productive adjacent stands (taller trees, higher basal area, etc.), because these sites will provide more seeds and microsites for tree establishment; and (iii) variables related to water table depth (lack of microtopographic complexity, line topographic depression, and terrain wetness) will be related to local regeneration failures on seismic lines because microsites available for tree establishment will be limited.

Fig. 2. Location of study sites (plots) within northeast Alberta, Canada, with respect to recent (1 to 22-year-old) wildfires, major water features, towns, and base terrain. Plots are labeled as either burnt within the past 22-years or unburnt recently. Inset map of North America illustrates extent of boreal forest in North America, location of Alberta, Canada (dark grey), and study area extent (black box). Base map of hillshade is based on Topographic Data of Canada (CanVec series) at 1:50 000 with hillshade derived from a digital elevation model (DEM) using ArcGIS 10.6.1. Recent fires based on Spatial Wildfire shapefile available from Alberta Agriculture and Forestry. Inset map base data from ESRI global boundary dataset and the boreal forest range based on Brandt (2009). Software used to create the map: ArcGIS 10.6.1. No permissions required. All geographic data of base layers are freely available (open).



Materials and methods

Study area

The study area of northeast Alberta, Canada, stretches from Wandering River and Conklin in the south, to McClelland Lake in the north, encompassing ~30 000 km² of the Athabasca Oil Sands (Fig. 2). Our sample plots were all within the Boreal Plains ecozone (at the Canadian national scale) overlapping with the Boreal Forest Natural Region (at the Alberta provincial scale), where small changes in topography (~0.5 m change in elevation) can result in abrupt changes of ecosite due to differences in the water table (Natural Regions Committee 2006). Widths of seismic line disturbances ranged from just under 3 m to just over 12 m (see Fig. 1 for examples). None of the seismic lines in this study were replanted or subjected to any silvicultural treatment or mechanical site preparation.

Here, treed peatlands, representing as much as 60% of the overall regional landscape, include bogs, poor fens, rich fens, and poor mesic ecosites. Peatlands are wetlands that can accumulate >40 cm of organic matter (peat) from vegetation, most often from mosses. There are numerous classifications for peatlands, but here we use the definition from terrestrial data collection protocols (Alberta Biodiversity Monitoring Institute 2018) and the *Encyclopedia of Ecology* (Vitt 2008). There are four types of peatland ecosites, they are: bog, poor fen, rich fen, and poor mesic.

Bogs are characterized as ombrotrophic, acidic (pH of 3.5–4.5), dominated by sphagnum mosses, with black spruce [*Picea mariana* (Mill.) B.S.P.] often being the exclusive tree present.

Poor fens are characterized as minerotrophic, acidic (pH of 3.5–5.5), dominated by sphagnum mosses with black spruce and a minority of tamarack [*Larix laricina* (Du Roi) K. Koch].

Rich fens are characterized as minerotrophic, neutral (pH of 5.5–8.0), dominated by true mosses (or brown mosses) with black spruce and tamarack. Rich fens are often distinguished from poor fens by being wetter and richer in nutrients.

Poor mesic sites are not technically a wetland or peatland ecosite because the depth to water table is slightly greater than the other ecosites mentioned, but poor mesic sites occur in the same locations often transitioning into peatlands. Poor mesic sites are dominated by feather mosses with black spruce and a minority of jack pine (*Pinus banksiana* Lamb.), aspen (*Populus tremuloides* Michx.), and white spruce (*Picea glauca* Moench. Voss).

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. Six wildfires were selected for having multiple ecosites and being large enough to contain at least 12 sites to sample, as well as accessibility and variation in stand age (1, 6, 8, 15, 18, and 22 years prior to sample collection). Locations were selected from a random set of available possible locations within 3.4 km (\bar{x} = 580 m) of roads, with each site requiring consistent forest stand conditions (i.e., height, density, age) across an area large enough to be sampled (>1 ha). A random toss of a metal stake was used to determine specific starting location of all plots. All of the field work occurred

in the summer of 2017, with 143 sites sampled. Each site being represented by a pair of plots with one plot on a seismic line and the other 25 m into the adjacent reference forest ($n = 286$ plots); a coin toss was used to randomly assign which side of the seismic line the adjacent forest plot would be located. Distribution of plots by ecosites was 29 bogs (58 plots), 61 poor fens (122 plots), 23 rich fens (46 plots), and 30 poor mesic forests (60 plots). Of the 143 sites, 68 sites (48%) had not experienced a wildfire in over 65 years (we defined as “unburnt”), while 75 of the sites (52%) had experienced a wildfire in the last 22 years (defined as “burnt”). Sites that had experienced a wildfire in the last 22 years, by ecosite, were as follows: bogs at 19 sites (38 plots or 65%); poor fens at 32 sites (64 plots or 52%); rich fens at 10 sites (20 plots or 44%); and poor mesic at 14 sites (28 plots or 47%).

Each plot represented a 30 m belt transect with the seismic line transect located in the center of the seismic line, while the adjacent paired control transect was located 25 m into the adjacent forest running parallel to the seismic line (see Filicetti and Nielsen 2018 for more details). Regeneration density, shrub density, and tree density were measured within belt-plots along each 30 m transect. Regeneration density [1 cm diameter at breast height (DBH)] and shrubs were counted in 1 m \times 30 m belt quadrats (30 m²), while trees (≥ 1 cm DBH) were counted in 2 m \times 30 m belt quadrats (60 m²). All of the stem densities were calculated to a common scale of 100 m² (0.01 ha) for modeling, but in some cases were reported as stems per hectare for ease of comparison with the literature. Additional stand information was collected for the adjacent forest plot, including fire severity (defined as percent overstory tree mortality), stand basal area by species using a 2-factor metric prism (m²/ha) at the midpoint of the adjacent forest transect (15 m), stand age of representative mature trees in the same plot using dendrochronological aging via tree cores, and representative tree height using a Haglof Vertex IV (Sweden) hypsometer.

Effects of fire and seismic line presence on regeneration density

We first visualized the main experimental effects on regeneration density by plotting the mean and standard errors of regeneration density for all tree species against the presence of a recent (22 years) wildfire, ecosite type, and seismic line presence (versus adjacent forest). Initial analyses found no difference between wildfire ages, except for the most recent (1 year old) fire, but this difference was eliminated after considering each ecosite separately. It was apparent that ecosite differences were substantial, and thus we analyzed regeneration density for each ecosite to account for these ecosite level complexities. We then used mixed-effects negative binomial models (*xtnbreg* command in STATA 15.1/SE; StataCorp 2017) to test for significant differences in regeneration density in units of trees per 100 m² of wildfire (burnt versus unburnt) and seismic line presence by ecosite. Site ID was used as a random effect to account for the paired nature of the seismic line and adjacent control forest plots within a single site. Separate binary dummy variables were used 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. Model selection of predictor variables was limited to the interaction of two main treatment variables [binary fire presence and binary seismic line presence (versus adjacent forest)], regardless of their significance. Initial collinearity among variables was assessed using Pearson correlations. We found only two variables considered colinear ($|r| = >0.7$), stand height and stand age at $r = 0.71$. We therefore did not include stand height and stand age together in the same model. We report coefficients from negative binomial models, but also interpret them as percentage change in regeneration density per one unit change in the predictor variable by exponentiating them, subtracting one, and multiplying by 100% $\{[\exp(\text{var}) - 1] \times 100\}$. Finally, a

mixed-effects negative binomial model was used with the combination of presence/absence of wildfire and seismic line presence (burnt line, unburnt line, burnt forest, unburnt forest), to predict regeneration density, and a pairwise test with a Bonferroni adjustment (*pwcompare mcompare (bonferroni)*; STATA 15.1/SE StataCorp 2017) to test for significance between variables within ecosites.

Effects of stand, fire severity, and seismic line characteristics on regeneration density

For this analysis, regeneration density was defined as any tree on the seismic line regardless of its DBH with the analysis restricted to only seismic line plots. This allowed us to directly examine the effects of fire severity and seismic line characteristics, such as line orientation and line (forest gap) width. We also considered the effect of the adjacent stand on regeneration density within lines including tree height, stand basal area, stand age, and their interaction with seismic line (forest gap) width and orientation. Because we removed the adjacent forest plot from the paired design (random effect) from the section on *Effects of fire and seismic line presence on regeneration density*, we used standard negative binomial regression count models (*nbreg* command in STATA 15.1/SE; StataCorp 2017). Model selection of predictor variables was based on the inclusion of variables for seismic line and stand characteristics only if significant (at $\alpha = 0.05$). Line width varied between 3 and 12 m ($\bar{x} = 5.9$ and SE = 0.1), while 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 (76%). In addition to line characteristics, we examined the effects of graminoid, woody debris, lichen, bare ground, bryophyte, *Sphagnum fuscum*, and open water (only woody debris, bryophyte, and open water were found to be significant and thus used in our models) on regeneration density based on their average percent cover within six quadrats (2 m \times 5 m) along the transect. Again, all analyses of regeneration density were at a scale of 100 m². Finally, contour graphs were used to illustrate predictions from our models explaining regeneration density as a function of different seismic line and stand characteristics.

Effects of microtopography and water table on regeneration density

For a subset of sites ($n = 102$) we measured microtopographic patterns along the transect to characterize microtopographic complexity (the measure of how much the hummocks and hollows vary in their peaks and troughs along the central 20 m length of the 30 m transect at 25 cm intervals), and depth of topographic depression (average height difference between the center of the seismic line and the adjacent forest; where positive values mean belowground elevation compared with the adjacent forest) on the seismic line based on data reported in Stevenson et al. (2019), and here related to regeneration density within those same plots. Specifically, we used a ZIPLEVEL PRO-2000 (Technidea® Corporation, Escondido, California, USA) high-precision hydrostatic altimeter. We also considered terrain wetness as measured topographically from the compound topographic wetness index (CTI, Moore et al. 1991) using a 15-m Lidar-derived digital elevation model. Because terrain wetness was measured at a meso-scale, it will not resolve differences within paired plots, but should provide a general gradient of wetness between sites. Standard negative binomial regression models (*xtnbreg* and *nbreg* command in STATA 15.1/SE; StataCorp 2017) were again used to relate regeneration density (per 100 m²) to microtopography, terrain wetness, and their interactions with variables retained only if significant ($\alpha = 0.05$). Because of the smaller sample sizes where microtopography was measured ($n = 102$ sites), all of the ecosites were used in analyses of microtopography. Initial analyses, however, demonstrated clear differentiation between unburnt and burnt seismic lines, so we

Table 1. Stand characteristics and tree regeneration densities (per hectare) for 143 sites sampled on seismic lines and adjacent forests (286 plots) in northeast Alberta, Canada.

Stand variable	Minimum	Median	Maximum	Mean (SE)
Age (years)	1	22	158	34.4 (2.7)
Height (m)	0	5.1	24.8	5.9 (0.4)
Basal area (m ² /ha)	0	8	36	8.9 (0.6)
Tree stems per ha (DBH < 1 cm)				
Seismic line	0	9667	156 333	20 385 (2285)
Adjacent stand	0	9667	115 000	13 887 (1216)
Tree stems per ha (DBH ≥ 1 cm)				
Seismic line	0	0	19 833	903 (207)
Adjacent stand	0	11 333	37 333	13 196 (672)

further divided data into unburnt ($n = 42$) and burnt ($n = 60$) seismic lines groups for the final analyses.

Results

Stand characteristics and overall regeneration density patterns

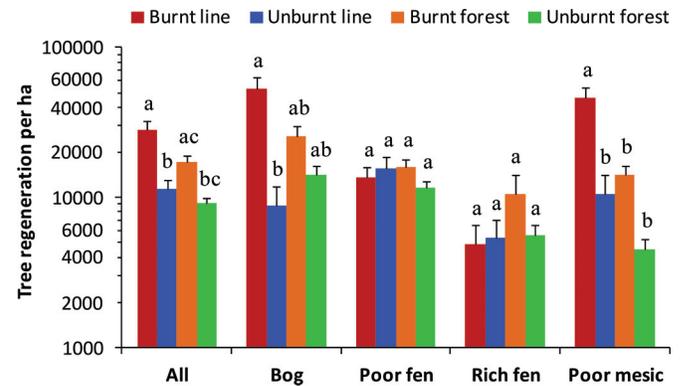
The age of the stands ranged from 1 to 158 years ($\bar{x} = 34.4$, $SE = 2.7$); stand height varied from 0 to 24.8 m ($\bar{x} = 5.9$, $SE = 0.4$); basal area in adjacent stands varied from 0 to 36 m²/ha ($\bar{x} = 5.9$, $SE = 0.8$); and trees per hectare ranged from 0 to 37 333 stems ($\bar{x} = 13 196$, $SE = 672$), see Table 1. The most common tree species, in order of most to least common, were: black spruce at 83%, tamarack at 10%, jack pine at 4%, Alaska birch at 1.7% (*Betula neoalaskana* Sarg.), aspen at 1.5%, and balsam poplar at 0.6% (*Populus balsamifera* L.); similarly the most common shrubs were: willow at 45% (*Salix* spp. L.), bog birch at 40% (*Betula pumila* L.), and prickly rose at 8% (*Rosa acicularis* Lindl.).

On average, the burnt lines had 28 500 ($SE = 3875$) regenerating stems/ha, unburnt lines had 11 440 ($SE = 1640$) regenerating stems/ha, the adjacent burnt forests had 18 210 ($SE = 2090$) regenerating stems/ha, and the adjacent unburnt forest had 9520 ($SE = 990$) regenerating stems/ha. The burnt lines, therefore, had 2.5-times more regenerating stems per hectare than the unburnt lines ($p < 0.001$), 1.7-times more regenerating stems per hectare than burnt forest, but not statistically significant ($p = 0.999$), and 3.1-times more regenerating stems per hectare than unburnt forest ($p = 0.048$) (Fig. 3). The burnt forests had 1.9-times more stems per hectare than unburnt forests ($p = 0.999$) and 1.5-times more stems per hectare than unburnt lines ($p = 0.024$). There were, therefore, more regenerating tree stems on the burnt seismic lines, compared with the unburnt lines, adjacent burnt forest, and adjacent undisturbed forests, illustrating that wildfires, regardless of their severity or timing, can promote natural regeneration density (passive restoration) of most linear disturbances in peatlands.

Effects of fire and seismic line presence on regeneration density for each ecosite

The interaction between seismic line presence and wildfires within the last 22 years was only significant for bogs and poor mesic sites, demonstrating a positive effect on regeneration density (see Fig. 3 and Table 2). Overall, regeneration density in bogs was 4% higher in the burnt versus unburnt sites, 42% less on the seismic lines versus adjacent forest, but 146% higher for the burnt seismic lines (see Fig. 3 and Table 2). The regeneration density in poor fens was 2% higher in the burnt versus unburnt sites, 11% less on the seismic lines versus adjacent forest, and 4% less for the burnt seismic lines. The regeneration density in rich fens was 17% lower in the burnt versus unburnt sites, 49% less on the seismic lines versus adjacent forest, and 3% less for the burnt seismic lines. The regeneration density in poor mesic stands was 97% higher for a wildfire in the adjacent forest versus the unburnt adjacent forest, while decreasing by 13% on seismic lines and in-

Fig. 3. Tree regeneration (DBH < 1 cm) across all sites (All) and separately for each of the four peatland ecosites for both burnt and unburnt conditions. Significance of treatments within each ecosite were tested using a mixed-effects negative binomial model with a pairwise comparison (Bonferroni adjustment) with different letters indicating significant differences within an ecosite at $p < 0.05$ (error bars are standard errors).



creasing by 225% in the presence of a wildfire on a seismic line (see Fig. 3 and Table 2).

Effects of stand, fire severity, and seismic line characteristics on regeneration density

When eliminating the adjacent paired forest plots and only assessing seismic lines based on surrounding stand characteristics (basal area, stand height, stand age), line characteristics of line width (gap) and bearing, fire severity, and ground cover, the differences in regeneration density on seismic lines between ecosites was more apparent. Wildfire age was often non-significant, and both fire severity and fire presence were consistently better predictors; this remained true even when considering interactions between wildfire age and fire severity.

The regeneration density on lines within bogs were moderately influenced by fire severity, with a 2% increase in regeneration density per 1 unit increase in fire severity. The regeneration density increased by 36% per 1 m increase in line width, and increased by 101% on north-south lines compared with the east-west lines (see Fig. 4 and Table 3). Regeneration density in both fen types was not related to wildfire presence or severity, but the regeneration density in poor fens was positively related to basal area of black spruce and negatively related to the cover of open water within the plot. Specifically, there was a 4% increase in regeneration density per 1 m²/ha increase of black spruce and a 4% decrease in regeneration density per one unit increase in cover of open water. In contrast, the regeneration density in rich fens was influenced by line bearing, coarse woody debris, and bryophyte cover. Specifically, regeneration density decreased by 390% on north-south lines compared with east-west lines, increased by 213% per one unit increase in woody debris cover, and increased by 8% per one unit increase in bryophyte cover (Fig. 4 and Table 3). Finally, regeneration density in poor mesic ecosites was positively related to fire severity, increasing by 2% per one unit increase in fire severity and negatively related to stand basal area of non-black spruce trees decreasing by 27% per 1 m²/ha of non-black spruce trees.

Effects of microtopography and water table on regeneration density

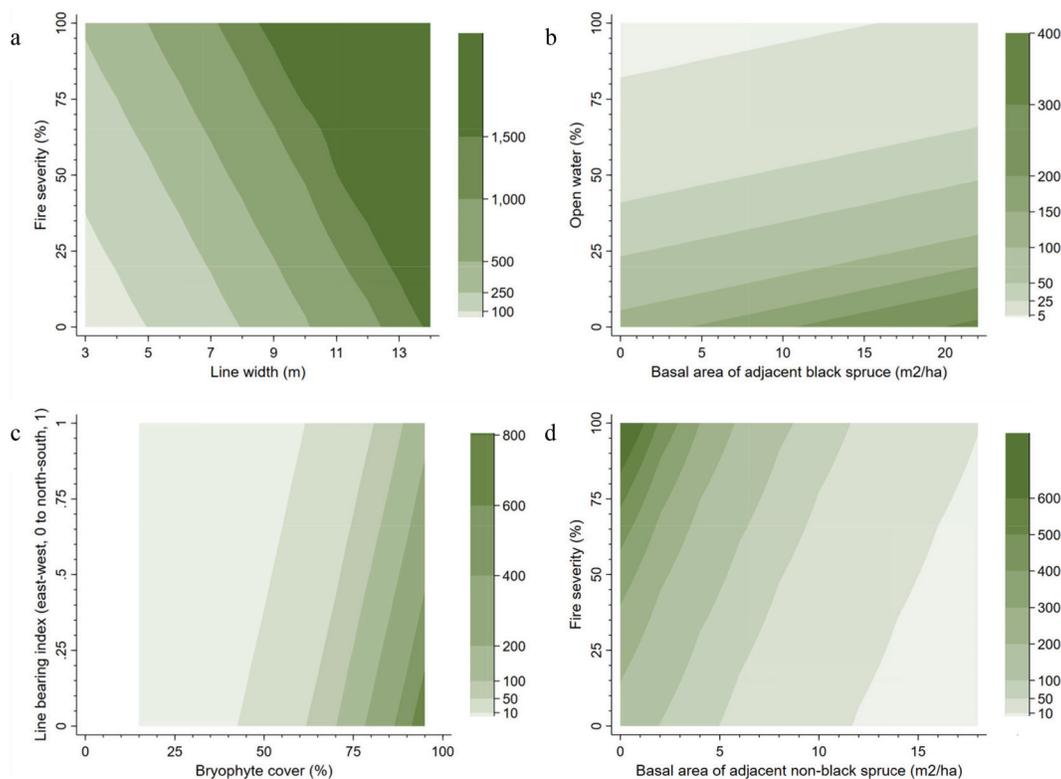
For unburnt seismic lines, microtopographic complexity was the only explanatory variable negatively related to regeneration density (15% decrease in regeneration density per one unit increase in microtopographic complexity), but this was weak overall ($p = 0.062$, Table 4) suggesting less support for the hypothesis that a lack of microtopographic complexity limits regeneration

Table 2. Mixed-effects negative binomial regression model parameters (coefficient, β ; and standard error, SE) relating regeneration density (DBH < 1 cm) of all tree species to the presence of fire and the presence of a seismic line (vs. adjacent forest control).

Tree density (stems/100 m ²)	Bog β (SE)	Poor fen β (SE)	Rich fen β (SE)	Poor mesic β (SE)
Constant (intercept)	0.40 (0.35)	0.18 (0.19)	-0.22 (0.28)	-0.23 (0.26)
Fire				
Presence of fire	0.04 (0.32)	0.02 (0.21)	-0.19 (0.38)	0.68 (0.29)*
Fire \times seismic line	0.90 (0.40)*	-0.04 (0.29)	-0.03 (0.60)	1.18 (0.38)**
Seismic line presence				
Seismic line plot	-0.54 (0.34)	-0.12 (0.21)	-0.68 (0.37)	-0.14 (0.31)
Model statistics				
<i>n</i>	58	122	46	60
Log likelihood	-380.6	-585.2	-228.7	-348.2
Wald χ^2	9.14	0.95	5.62	63.49
Prob > χ^2	0.027	0.813	0.132	<0.001

Note: The presence of both fire and seismic line were included regardless of significance, given that they were study design (treatment) variables; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Fig. 4. Predicted density of all trees regenerating on seismic lines (negative binomial count model) in the four peatland ecosites based on a combination of site factors: (a) bogs, using line width and fire severity with the example here being north-south bearing lines; (b) poor fens, using basal area of adjacent black spruce and ground cover of open water; (c) rich fens using bryophyte ground cover and line bearing; and (d) poor mesic, using basal area of adjacent non-black spruce trees and fire severity. Note that scales of regeneration density (contour colors) differ between ecosites. [Colour online.]



density on unburnt seismic lines in peatland forests. In contrast, regeneration density on burnt seismic lines was significantly and negatively related to both the compound topographic wetness index (CTI) and the amount of microtopographic depression on the line (see Fig. 5 and Table 4) suggesting stronger limitations in regeneration density post-fire to microtopography. Specifically, terrain wetness and microtopographic depression were both negatively related to regeneration density, with a 23% decrease in regeneration density per one unit increase in terrain wetness and a 4% decrease in regeneration density for every centimeter of depression on the seismic line (see Fig. 5 and Table 4).

Discussion

Effects of fire and seismic line presence on regeneration density

Unburnt seismic lines had similar regeneration density rates to adjacent forests, contrary to prior observations of a general lack of tree recruitment on lines (Lee and Boutin 2006; van Rensen et al. 2015; Filicetti et al. 2019). However, we would expect higher regeneration density in forest openings, such as seismic lines, where seed sources are nearby (adjacent to line) and sunlight more available than in the adjacent forest understory (Stern et al. 2018). In contrast to unburnt lines and forest, wildfires consistently increased regeneration density in adjacent forest stands across all ecosites

Table 3. Standard negative binomial regression model parameters (coefficient, β ; and standard error, SE) relating the regeneration density of all tree species on seismic lines to fire severity (% tree mortality), line characteristics, stand variables, and percent ground cover.

Tree density (stems/100 m ²)	Bog β (SE)	Poor fen β (SE)	Rich fen β (SE)	Poor mesic β (SE)
Constant (intercept)	2.38 (0.78)**	4.82 (0.23)***	-1.29 (1.65)	5.07 (0.27)***
Fire				
Severity	0.016 (0.004)***			0.016 (0.004)***
Stand				
Bearing (0–1 index)	0.70 (0.34)*		-1.59 (0.69)*	
Width (m)	0.31 (0.13)*			
Black spruce (m ² /ha)		0.04 (0.02)*		
Non-black spruce (m ² /ha)				-0.24 (0.04)***
Ground cover (%)				
Woody debris			1.14 (0.45)*	
Open water		-0.04 (0.02)*		
Bryophytes			0.08 (0.03)*	
Model statistics				
<i>n</i>	29	61	23	30
LR χ^2	24.60	8.84	12.45	25.76
Prob > χ^2	<0.001	0.012	0.006	<0.001

Note: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

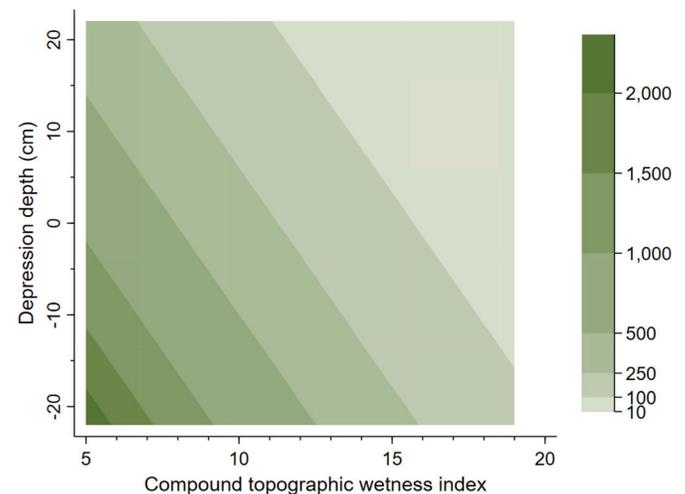
Table 4. The best fitting negative binomial model for predicting tree regeneration for (A) unburnt and (B) burnt (excluding fire related variables) seismic lines.

Parameters	β	SE	<i>p</i>
(A) Non-burnt seismic lines only			
Intercept	5.543	0.427	<0.001
Microtopographic complexity	-0.136	0.073	0.062
(B) Burnt seismic lines only			
Intercept	7.851	0.653	<0.001
Terrain wetness (CTI)	-0.207	0.058	<0.001
Depression depth	-0.043	0.019	0.026

Note: The best model for unburnt seismic lines (A) included only microtopographic complexity, while the burnt seismic line model (B) included line depression depth and the compound topographic index (CTI) representing terrain wetness (higher values = wetter).

when compared with unburnt forest stands. Likewise, regeneration density increased on burnt seismic lines compared with unburnt seismic lines in bogs and poor mesic sites, but not poor and rich fens. This suggests that seismic lines have a long-term detrimental effect on regeneration density in one type of peatland — fens. One possible mechanism by which seismic lines reduce regeneration density in peatlands, and especially within fens, is the elimination of microtopographic complexity (hummocks–hollows; Lieffers et al. 2017) and the depression of the ground on seismic lines due to the mechanical nature of their creation (Stevenson et al. 2019). This results in a shallower water table and thus changes in vegetation, even to the extreme of converting lines to sedge-dominated communities with standing water that restricts any tree recruitment (Lieffers et al. 2017). If a tree can establish within certain microsites, there is no guarantee that it will eventually thrive because of the abnormally high mortality rates for trees above a certain size (Lieffers et al. 2017). Although microtopographic changes in peatland ecosystems are similar (Stevenson et al. 2019), their effect on regeneration density in fens appears to be much more negative, even after wildfires. One study found substantial increases in the natural regeneration density on treated (mounded) seismic lines in fens, even above the regeneration density for trees that were planted as part of the treatments (Filicetti et al. 2019), demonstrating that the main limitation of tree recruitment in fens is the depth of the water table and lack of microtopography. Moreover, measures of regeneration density on these mounded treatments were 4 years post-treatment compared with untreated

Fig. 5. Predicted tree regeneration (negative binomial count model) in burnt seismic lines as a function of compound topographic wetness index (CTI; higher values representing greater wetness at a meso-scale) and depression depth (cm) at local scales (transect). Note that positive values of depression depth relate to greater belowground depths of the line compared to that of the adjacent forest and thus more likely to be near the water table or wet. [Colour online.]



lines disturbed by the creation of seismic lines ~22 years prior demonstrating how restoration of the microtopography can promote rapid natural regeneration on the mounds.

Effects of stand, fire severity, and seismic line characteristics on regeneration density

It was surprising to find that time to the last wildfire was often non-significant for regeneration density, and that fire severity was consistently the better predictor. It is likely that wildfire age was not particularly useful for regeneration density because of seed abscission patterns post-fire, where black spruce cones release 70% of their seeds within 2 years, and 90% within 5 years post-fire, whereas jack pine cones release 90% of their seeds within the first year (Greene et al. 2013). Additionally, the viability of tree seeds stored in the boreal forest floor is generally low (Bonan and Shugart 1989), where black spruce lose their ability to germinate within 10 to 16 months (Fraser 1976). Therefore, with most seed

abscission and germination occurring within 5 years, it should not be too surprising that time post-wildfire >5 years (only one wildfire sampled in this paper was within 5 years post-fire) has little to no additional recruitment.

The regeneration density of trees on seismic lines in bogs was positively related to fire severity, positively related to width of line (forest gap size), and the bearing of lines (north–south lines being more beneficial). These results are similar to responses observed by Filicetti and Nielsen (2018) in (xeric) burnt jack pine sites that were dominated by trees with serotinous cones, and in bogs with north–south oriented seismic lines (Filicetti et al. 2019). Because black spruce has semi-serotinous cones that release substantial amounts of seed post-fire, and bogs are dominated by black spruce, it is not surprising to observe increased regeneration density post-fire in these communities. Here we found that the regeneration densities in bogs post-fire were more than double that observed on seismic lines treated with mounding and planting (Filicetti et al. 2019), suggesting that in specific scenarios, wildfires could result in leave-for-natural regeneration that would be beneficial and cost-effective. Increased regeneration densities for wider seismic lines are likely to be associated with increases in sunlight (Filicetti and Nielsen 2018; Stern et al. 2018). They also receive higher wind speeds in northeastern Alberta (Roberts et al. 2018; Stern et al. 2018). Higher winds could lead to increased seed dispersal (Roberts et al. 2018) and evapotranspiration. Evapotranspiration plays an important role in regulating the water table, with the removal of trees raising the water table (Jutras et al. 2006). Regardless, the effect of line bearing and width appears to be reduced post-fire, possibly due to increases in sunlight and (or) changes in hydrology (higher evaporation rates and increased depth to water table leading to more available microsites) (Thompson et al. 2014).

Patterns of regeneration density on seismic lines in poor fens were best explained by the basal area of black spruce in the adjacent stand and the cover of open water on the seismic line. The positive relationship of regeneration density in poor fens to a higher basal area of black spruce are not related to their cones' semi-serotinous nature, or wildfires. Fens with more black spruce than tamarack are associated with greater overall tree abundance and size. Fens with more black spruce than tamarack are also characterized by a shift away from rich fens, because rich fens evolve into poor fens and then bogs (Kuhry et al. 1993), with a corresponding decrease in tamarack with site-decreases in nutrients, a lower water table, and increased competition for sunlight (Lieffers and Rothwell 1987; Froelking et al. 2001). The cover of open water was related to wetter sites with a higher water table, fewer available microsites, lower cover of bryophytes (Pearson correlation, $r = -0.47$), and greater cover of graminoids ($r = 0.37$) that increase competition and litter (Hogg and Lieffers 1991). Regeneration density in rich fens was positively related to the east–west bearing of the seismic line, and increases in woody debris and bryophyte cover. This may mean that rich fens, which typically have short trees (on average 6.7 m in this study) and fewer trees per unit area than other ecosites, may receive more sunlight on east–west lines, especially on their northern edge. Bryophytes, particularly *Sphagnum*, are required for hummock formation and are therefore crucial to tree establishment (Caners and Lieffers 2014). Likewise, woody debris provides structural support for bryophytes to establish (Crites and Dale 1998). Although cover of woody debris had a large effect on regeneration density compared with bryophytes (increase in regeneration density of 213% per one unit increase of woody debris cover versus an increase of 8% per one unit increase of bryophyte cover), bryophyte cover was on average 45-times higher than woody debris overall, suggesting that bryophytes had a larger contribution to regeneration density. In rich fens, bryophyte cover was negatively related to cover of graminoids ($r = -0.67$) and open water ($r = -0.40$), both of which appear to limit regeneration density in both poor and rich fens.

And finally, regeneration density in poor mesic sites depended on fire severity and cover (basal area) of non-black spruce trees. The relationship with fire severity in poor mesic sites is expected, given that it is dominated by black spruce, and to a lesser extent jack pine, which are semi-serotinous and serotinous, respectively. Here we found that regeneration density on burnt seismic lines in poor mesic sites was more than 4-times that of observed on seismic lines treated with ripping and planting from another study (Filicetti et al. 2019), suggesting that fire is highly effective in initiating natural regeneration in poor mesic sites like bogs. Similar to bogs, wildfires in poor mesic sites could be a beneficial and cost-effective leave-for-natural solution utilized in specific situations.

The negative effect of the cover (basal area) of non-black spruce trees on regeneration density in poor mesic seismic lines suggests less non-black spruce regeneration as the ecosite shifts to transitional uplands where aspen, birch, and especially jack pine dominate. Basal area of non-black spruce may reflect conditions where jack pine fares better on seismic lines post-fire, but tends not to regenerate in the absence of fire (Filicetti and Nielsen 2018). Therefore, the closer a poor mesic site lies to the xeric side of the spectrum (more jack pine), the less regeneration there is in the absence of fire.

Effects of microtopography and water table on regeneration density

Regeneration density on burnt seismic lines were negatively related to terrain wetness and line depression where conditions limit regeneration density because of both a higher water table and fewer available microsites (Filicetti et al. 2019). Yet, in unburnt seismic lines, microtopography and terrain wetness did not fully explain local patterns of regeneration, owing to risk of flooding (high water table) and loss of microtopography. We did not, however, expect differences between burnt and unburnt lines as a high-water table and a lack of microtopographic complexity would limit regeneration density regardless of recent fire disturbance history. One possible reason for this unexpected result is that wildfires can exaggerate microtopographic complexity (Benscotter et al. 2015), although differences in microtopographic complexity were not observed between the burnt and unburnt seismic lines in our sites (Stevenson et al. 2019). Seismic lines also act as wildfire barriers or skips (refugia) as observed here (see Fig. 1) and elsewhere (Riva et al. 2019). We therefore think a change in microtopography post-fire is an unlikely explanation. Another possibility is that, although not significant, bogs and poor mesic seismic lines were less depressed post-fire than poor and rich fens (Stevenson et al. 2019), which may affect the regeneration densities observed here. Wildfires can also alter hydrology in peatlands, with burnt peatlands having higher evapotranspiration that can lower water tables (Thompson et al. 2014). This pattern is especially apparent in *Sphagnum*-dominated peatlands (bogs) and is more dramatic under more severe fires (Kettridge et al. 2019) that occur less often in fens.

Management implications

The mechanized creation of seismic lines alters the establishment and growth trajectories of regenerating forests, in some cases resulting in clearings (open corridors) that last decades or longer. Reforestation of these cleared lines is important for woodland caribou, yet difficult and costly to apply because of the narrow and long nature of seismic lines and their vast numbers across a large landscape. Distinguishing which locations benefit from active restoration and which can be left-for-natural (passive) restoration, particularly after wildfire, has the potential to save substantial investments in restoration and caribou conservation. Sites with more serotinous and semi-serotinous species do recover at denser rates post-fire. Microtopography and terrain wetness could explain regeneration density on burnt lines, but not unburnt lines. In unburnt and burnt seismic lines sunlight, micro-

topography, and depth of water table seem to play critical roles in regeneration density, particularly in fens, where restoring trees is the most inhibited of the peatland ecosites, even post-fire. Triage of where to spend limited conservation dollars (including restoration) is an ongoing debate in conservation biology. Here we are not suggesting to simply wait for wildfire to restore seismic lines. We are instead suggesting that recently burnt sites, and possibly areas likely to experience wildfires in the near future, should be considered lower priority for restoration. With climate change, large parts of the boreal forest, including northeastern Alberta, are expected to receive more intense, more frequent, and larger wildfires (Flannigan et al. 2009a, 2009b). Locally, there are large variations in fire frequency within the landscape, owing to natural landscape features (Nielsen et al. 2016), dominant tree species (Larsen 1997), time since last fire (Beverly 2017), and fuel loads (Johnston et al. 2015). Areas with caribou herds, if caribou conservation is an agreed upon objective, should clearly get priority, but otherwise we do not promote widespread use of limited restoration dollars without considering trade-offs associated with natural recovery, especially with that of wildfire.

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