Short-term effects of wildfire in boreal peatlands: Does fire mitigate the linear footprint of oil and gas exploration?

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Abstract. Exploration practices for oil sands developments in the boreal forest of western Canada create a network of thousands of kilometers of linear features, particularly seismic lines that dissect these forests posing significant environmental challenges. As wildfire is one of the prevalent stand-replacing natural disturbances in the Canadian boreal forest, it is an important driver of environmental change and stand development that may contribute to the mitigation of such linear industrial footprint. Here, we evaluate the short-term cumulative (also known as combined) effects of seismic lines and wildfire on biodiversity and site conditions. One year after the Horse River (Fort McMurray, Alberta, Canada) fire event in the spring of 2016, we compared dissected and undisturbed forests in burned and unburned boreal peatlands, assessing changes in overall stand structure and the responses of a variety of organisms. Soil moisture was significantly higher on seismic lines than in the adjacent forest, suggesting why most of the study sites within the fire perimeter showed little evidence of burning at the line in relation to the adjacent forest. Low fire severity on seismic lines seemed an important driver of local species diversity for ants, beetles, spiders, and plants in disturbed peatlands, resulting in similar species composition on seismic lines both within and outside the burned area, but different assemblages in burned and unburned adjacent forests. Our results suggest that fire did not erase seismic lines; rather, wildfire might increase the influence of this footprint on the recovering adjacent forest. Longer-term monitoring will be necessary to understand how boreal treed peatlands respond to the cumulative effect of wildfire and linear disturbances.

Key words: cumulative effects; edge effects; fire severity; habitat loss and fragmentation; habitat restoration; invertebrate and plant biodiversity; soil moisture.

Introduction

Fragmentation (i.e., dissecting contiguous forested areas into smaller areas) and edge effects (i.e., the influence of forest removal into the adjacent forest) have long been identified as important drivers of ecological change in forested landscapes (Lindenmayer and Fischer 2013). Depending on the degree and intensity of habitat change, fragmentation may lead to reduction in connectivity, degradation of forest interior habitats, loss of biodiversity, and ultimately decline of forest health, ecological integrity, and ecosystem function (Harper et al. 2005, Haddad et al. 2015, Hanski 2015, Wilson et al. 2016). Often neglected or underestimated (Ries et al. 2017), edge effects can pose important challenges to management goals of highly fragmented landscapes (Porensky and Young 2013), such as those resulting from oil and gas (OG) exploration and development (Rosa et al. 2017).

Much of the boreal forest in the province of Alberta (Canada), and particularly those areas where bitumen deposits (i.e., oil sands) are found, has experienced extensive industrial developments over the last few decades (Schneider 2002, Pickell et al. 2015). Given the very nature of OG exploration and extraction practices, in-situ landscapes have become heavily dissected (as defined by Jaeger [2000]) by a network of thousands of kilometers of linear features (seismic lines, pipelines, access roads, etc.), and other local disturbances (exploration pads, well-sites, and other industrial infrastructure; Timoney and Lee 2001, Pusher et al. 2013, Pattison et al. 2016, Stern et al. 2018). In many cases, this extensive footprint has shown little natural recovery (Revel et al. 1984, Lee and Boutin 2006, Jorgenson et al. 2010,
and natural disturbances (but see Riva et al. 2020), and the abundance, composition and distribution of many taxa (Hebblewhite 2017, Finnegan et al. 2018a, Fisher and Burton 2018). For instance, this footprint extends over much of woodland caribou (Rangifer tarandus caribou) habitat, contributing to population decreases via apparent competition with other ungulates (e.g., moose and deer) and interaction with predators (e.g., wolves and bears; James and Stuart-Smith 2000, Latham et al. 2011a,b, Tigner et al. 2014). Woodland caribou is currently listed as a threatened species under both the Canadian federal Species at Risk Act and the Alberta provincial legislation (Government of Canada 2002, Thomas and Gray 2002). As caribou home ranges normally extend over thousands of square kilometers (Environment Canada 2012), management approaches for improving critical habitat (including seismic line restoration) will likely benefit many other taxa typical of habitats occupied by this species (Bichet et al. 2016, Drever et al. 2019) that are inherently related to the natural dynamics typical of these landscapes.

Oil and gas development is not the only disturbance in the Alberta boreal zone, where large-scale perturbations resulting from other industrial developments (e.g., forest harvest, agriculture) and natural disturbance regimes (e.g., wildfire, insect outbreaks) are also of common occurrence (Weber and Stocks 1998). Stand-replacing natural disturbances are important drivers of environmental change, succession and stand development in the boreal forest (Bergeron et al. 2004, Brassard and Chen 2006, Burton et al. 2008, Thom and Seidl 2016), and wildfire is a critical element at both local and landscape scales (e.g., Reilly et al. 2006). Since moderate- to high-severity fires are known to reset stand conditions to early successional stages (Chen and Popadiouk 2002, Bergeron et al. 2014), it has been argued that wildfire could be exploited as a passive form of restoration (Fulé et al. 2004, Barros et al. 2018, Leverkus et al. 2019), potentially reducing the need for active human intervention in restoring degraded habitats. Wildfire might be considered as mitigating factor of the effects of exploratory OG industrial footprint if the influence of linear disturbances on forested landscapes is reduced post-fire. Although positive effects of wildfire on natural regeneration of jack pine (Pinus banksiana) have been documented along seismic lines in xeric forests (Filiceetti and Nielsen 2018), it is largely unknown to what extent this could be the case in lowland areas characterized by a shallow water table, such as treed peatlands, which are abundant in northern Alberta. Furthermore, little is known about biodiversity responses to the cumulative (also known as combined) effect of these anthropogenic and natural disturbances (but see Riva et al. 2020).

In the spring of 2016, the Horse River wildfire ignited southwest of Fort McMurray, in the oil sands region of northeastern Alberta. Between 1 May and 4 July, it burned close to 600,000 ha of boreal forest (MNP LLP 2017), including many areas with a significant human footprint from OG exploration and development. In this study, we assessed the potential effects of wildfire in mitigating the footprint associated to linear disturbances (i.e., conventional seismic lines created by removing trees and shrubs with heavy machinery in corridors of ~10 m wide). Specifically, we evaluated short-term cumulative effects of seismic lines and wildfire on biodiversity by assessing responses of spiders, ground beetles, ants, vascular plants, and non-vascular plants to site conditions (e.g., soil moisture, temperature, and stand structure) on burned and unburned seismic lines and adjacent forest. We hypothesized that, if fire had reduced the effect of the linear footprint, no differences would be detected between seismic line habitats and the adjacent forest in burned sites, whereas significant differences would be detected between seismic lines in burned and unburned sites, and seismic lines and adjacent forest in the unburned sites, as previously documented (Dabros et al. 2017). Although prescribed burning has been applied for restoration purposes in fire-prone systems (Hardy and Arno 1996), this tool has not been extensively used due to public safety concerns and liability issues (Toledo et al. 2013, Joshi et al. 2019). Results from this study will be useful to fill knowledge gaps in the management of boreal peatland forests, while enhancing the understanding of complex cumulative effects of anthropogenic and natural disturbances, and could be used as baseline knowledge required for the use of fire as a silvicultural approach to restoring forests dissected by anthropogenic disturbances.

**Materials and Methods**

**Study area**

This study took place south of Fort McMurray (Alberta, Canada) along the 2016 Horse River wildfire southwest perimeter (56°31’33” N, 111°18’10” W; Fig. 1). The study area (about 35 × 35 km) comprises a mosaic of boreal uplands and wetlands (Appendix S1). We selected 15 sites in treed peatlands dominated by black spruce (Picea mariana; Table 1), with nine sites within the fire (“Burn”) and six sites outside the burned area (“Unburn”). All sites were dissected by conventional seismic lines, were at least 200 m from roads, and were at least 2.4 km from each other to guarantee independent samples. Assessed seismic lines were established 15–20 yr before data collection (May–September 2017). General site characteristics were compiled from publicly available data from the Alberta Biodiversity Monitoring Institute (ABMI), including mean probability of occurrence of wetlands within a 100-m buffer around each site centroid (Wetland Probability OS; ABMI 2017), area and density of seismic lines and other anthropogenic footprint (Human Footprint Data...
Fig. 1. Study area along the southwest perimeter of the 2016 Horse River wildfire (Fort McMurray, Alberta, Canada). The location of burned (B1–B9) and unburned (U1–U6) sites is shown. Linear footprint (mostly seismic lines) is depicted for context and highlighted within a 1.2 km radius buffer around each site (site characteristics within buffer are provided in Table 1). Lower pictures depict the 1 × 1 m vegetation quadrat adjacent to a pitfall trap (the small white square is the trap roof).
Layers, ABMI 2016) and percentage of land cover types (Wall-to-Wall Land Cover Inventory; ABMI 2013), both within a 1.2-km buffer around each site (buffer defined as one-half the minimum distance between the two closest sites).

### Data collection

At each site, three 50-m transects were run parallel to each other within each of three habitat types: one transect along the center of the seismic line (“Line”), one transect along the forest edge (10 m from the line edge; “Edge”), and one transect in the adjacent forest (50 m from the line edge; “Forest”). Both Edge and Forest transects were located on the same side of the seismic line, with side selected randomly, except for sites in the burned area where only one side was available. A sampling point was placed every 10 m along each transect, for a total of 15 sampling points per site (overall, 225 sampling points). At each sampling point, we collected the following data.

Environmental and stand structure data. Soil moisture and temperature at 10–12 cm deep were obtained from the average of five readings (at the center and four corners of 1 \times 1 \text{ m quadrat}). Moisture was obtained using a portable time-domain reflectometer (Field Scout TDR-100; Spectrum Technologies, Plainfield, Illinois, USA) and recorded as percent volumetric water content (VWC). Soil temperature was obtained with a soil thermometer. As temperature readings were performed at different times during the day for different sampling points, values were standardized from air temperature readings collected at the same time (soil/air temperature). A 4 \times 4 \text{ m quadrat} was used to record additional variables. Stem basal area (m²/ha; total, live, and dead BA) and density (stems/ha; total, live, and dead density) were obtained from tree stems ≥1.0 cm in diameter at the base. Tree regeneration (<1.0 cm in diameter at the base) and shrub densities (number/ha) were obtained from the count of individual stems. Density of dominant shrub species (bog birch [Betula pumila], Labrador tea [Rhododendron groenlandicum], and willows [Salix spp.]) was also recorded. Downed woody material (DWM) volume (m³/ha) was estimated using the formula to calculate the volume of a tapered cone for pieces ≥1.0 cm in diameter at least at one end. DWM density (number/ha) was estimated from the number of pieces within the quadrat. Percent canopy cover was obtained from the average of four readings (each cardinal direction) at the center of each quadrat, using a concave spherical densiometer. Relative burn severity was estimated by counting the number of points of burned ground every 10 cm along five 4 m parallel transects separated from each other by 1 m and nested within the quadrat; counts were standardized in relation to the total point count (205 points) and expressed as percentage.

### Table 1. General characteristics of surrounding area of each study site within and outside the southwest perimeter of the 2016 Horse River wildfire (Fort McMurray, Alberta, Canada).

| Site ID | Wetland probability | Seismic lines (ha) | Other linear features (km) | Well pads (ha) | Seismic lines ( Density (m/ha) | Other linear features (Conifer, Mixed, Deciduous, Shrub/ grassland, Other) | Land cover (%) |
|---------|---------------------|--------------------|---------------------------|---------------|-------------------------------|-----------------------------------------------------------------|---------------|
| Within fire perimeter (Burn) |
| B1      | 0.88 (0.075)        | 3.8 (0.8)          | 13.8 (3.1)                | 0.7 (0.2)     | 56.0                          | 38.2                                                             | 16.7          |
| B2      | 0.29 (0.199)        | 5.8 (1.3)          | 18.3 (4.0)                | 1.1 (0.2)     | 82.2                          | 24.6                                                             | 43.8          |
| B3      | 0.46 (0.203)        | 4.8 (1.1)          | 24.6 (5.4)                | 2.5 (0.6)     | 65.8                          | 127.8                                                           | 54.7          |
| B4      | 0.60 (0.11)         | 6.8 (1.5)          | 17.6 (3.9)                | 0.6 (0.1)     | 94.4                          | 33.6                                                             | 61.0          |
| B5      | 0.64 (0.189)        | 6.1 (1.3)          | 25.6 (5.7)                | 1.0 (0.2)     | 86.6                          | 28.0                                                             | 72.5          |
| B6      | 0.64 (0.111)        | 9.0 (2.0)          | 40.0 (8.8)                | 0.3 (0.1)     | 227.9                         | 73.4                                                             | 50.8          |
| B7      | 0.62 (0.214)        | 2.4 (0.5)          | 35.3 (7.8)                | 1.9 (0.4)     | 77.3                          | 145.6                                                           | 69.8          |
| B8      | 0.65 (0.113)        | 4.6 (1.0)          | 35.8 (7.9)                | 0.3 (0.1)     | 63.9                          | 106.5                                                           | 51.4          |
| B9      | 0.55 (0.155)        | 3.2 (0.7)          | 23.2 (5.1)                | 5.0 (1.1)     | 47.9                          | 61.4                                                             | 87.2          |
| Outside fire perimeter (Unburn) |
| U1      | 0.77 (0.168)        | 5.9 (1.3)          | 5.1 (1.1)                 | 1.9 (0.4)     | 138.4                         | 34.5                                                             | 85.6          |
| U2      | 0.82 (0.238)        | 18.3 (4.0)         | 5.6 (1.2)                 | 8.3 (1.8)     | 453.6                         | 25.7                                                             | 67.0          |
| U3      | 0.73 (0.236)        | 5.8 (1.3)          | 9.9 (2.2)                 | 2.7 (0.6)     | 81.9                          | 21.7                                                             | 55.3          |
| U4      | 0.63 (0.16)         | 5.8 (1.3)          | 14.6 (3.2)                | 1.1 (0.2)     | 81.2                          | 51.9                                                             | 73.8          |
| U5      | 0.60 (0.259)        | 2.2 (0.5)          | 14.6 (3.2)                | 1.9 (0.4)     | 77.0                          | 115.0                                                            | 42.3          |
| U6      | 0.82 (0.153)        | 1.5 (0.3)          | 45.7 (10.1)               | 2.1 (0.5)     | 34.1                          | 201.3                                                            | 38.5          |

**Notes:** Site IDs correspond to those in Fig. 1. Mean wetland probability (with SD in parentheses) was obtained within a 100-m buffer around each site; all other values were obtained within a 1.2-km buffer (depicted in Fig. 1). Land cover values are out of the total buffer area (452 ha) with percent cover in parentheses. Values under Other linear features include roads, trails and their verges. Values under Other land cover include developed, water, rock, and exposed land. Land cover percentages are from pre-fire conditions.
Ground dwelling arthropods were collected using one pitfall trap at each sampling point (five traps/transect and 15 traps/site). Traps consisted of plastic containers (11 cm diameter) dug into the ground with the rim leveled at the surface (Spence and Niemelä 1994). Propylene glycol was used as preservative and a square roof of corrugated plastic was suspended on a wire over the trap to reduce rain and debris falling into the container. Traps were serviced every three weeks from 20 May to 15 September 2017, with spiders, carabid beetles, and ants sorted and identified to species level. Spider nomenclature followed the World Spider Catalog (2020), carabid beetle nomenclature followed Lindroth (1961–1969) and ant nomenclature followed Bolton (1995), Ellison et al. (2012), and Glasier et al. (2013). Voucher specimens are deposited in the Northern Forestry Centre Arthropod Collection (Natural Resources Canada, Canadian Forest Service, Edmonton, Alberta).

Vegetation data were collected using a 1 × 1 m quadrat placed adjacent to each pitfall trap. Percent cover of all plant species was visually estimated to the nearest 0.1% (Schulz et al. 2009), from the ground to the overstory level. We used 1 m height as the threshold to distinguish understory (≤1 m) and overstory (>1 m). Since our identification approach and designation to a given vegetation type was based on the taxonomic identity and the size of an encountered individual, same species could be considered to be either understory or overstory, depending on their size and maturity (this pertains particularly to immature and mature tree species). Overstory was assessed visually by estimating percent cover taken up by the stem(s) of a given species, plus the cover of branches of tall shrubs and small trees falling into the quadrat, had they been brought down to the ground. Non-vascular plants and lichens were assessed at least to the genus level (e.g., Calliergon spp., Sphagnum spp., Polytrichum spp., and some unidentified mosses), also to the nearest 0.1% (hence, we only measured plants species richness and diversity for vascular plants, but percent cover for all plants; see Species diversity). Plant data were collected and species identified in the field by the same person (A. Dabros) between 10 and 17 July 2017. Nomenclature followed the Database of Vascular Plants of Canada (VASCAN; Brouillet et al. 2018) and the Integrated Taxonomic Information System (ITIS 2018), for non-vascular plants.

Species diversity.—Pitfall samples were pooled for the entire collection period. Due to differences in sampling effort as a result of trap disturbance by wildlife, trap catches were standardized to number of individuals per trapping days, and estimated to a total of 120 trap-days at the transect level. For this, we divided the total number of individuals from each trap by the total number of days the trap was active and multiplied it by 120. Then, values from the five traps in each transect were pooled for analyses. Plant data were also analyzed at the transect level, with mean percent cover of individual plant species (or genus for some non-vascular plants) obtained from the five quadrats within each habitat type. Three vegetation types were considered: (1) understory, including all herbaceous plants (forbs and graminoids), low shrubs, and tree seedlings and saplings below 1 m; (2) overstory (not to be confused with percent canopy coverage as described above for stand structure), including trees and tall shrubs above 1 m; and, (3) non-vascular species (bryophytes and lichens). Although not true plants, lichens were considered under non-vascular vegetation on the basis of similarity to the low-to-the-ground growth form of bryophytes and lack of vascular system. The effects of fire and habitat type on species richness (S), diversity (D; exponential of Shannon–Wiener’s index [Jost 2006]; vascular species only) and abundance/percent cover (all vegetation types) were analysed as above, fitting mixed-effects models and post hoc multiple comparisons, except for arthropods, in which S and D were estimated for fire by habitat combinations using coverage-based rarefaction (Jost 2007, Chao and Jost 2012, Chao et al. 2013), with differences assessed from experimental units to test differences among habitats (Line vs. Edge vs. Forest). Post hoc pre-planned comparisons using Tukey’s HSD P value adjustment were carried out to assess potential differences among habitats within burn or unburned areas, and for the same habitat type between burned and unburned sites. Variance structures were included in most models to improve assumptions on model residuals. For models in which residuals still did not meet assumptions, response variables were transformed accordingly, but contrasts of back-transformed least-squared mean estimates were obtained. The model for relative burn severity excluded unburned sites, but given that habitats within each site were still spatially correlated, a mixed-effects approach was also used. Constrained ordination by means of redundancy analysis (RDA; Legendre and Rao 1964, Legendre 2012) was used to assess multivariate changes in site conditions as a function of fire by habitat combinations, by fitting a regression model with only variables that showed significant differences. These variables (as in Fig. 2d) were standardized (mean = 0 and variance = 1) prior to model fitting to account for differences in measurement units. Model significance was assessed after 5,000 permutations restricted by site to account for spatial correlation among habitats.
non-overlapping 95% confidence intervals returned by the rarefaction procedure. Rarefaction for ants was based on incidence data, as ant abundance may be biased due to their social behavior.

Species composition.—The effects of fire and habitat for arthropods and plants were analyzed using RDA. Species with five or less individuals (for spiders and carabids) or one or two occurrences (for plants), were removed. Hellinger transformation (Legendre and Gallagher 2001) was applied to the resulting species data prior to RDA to improve model. Model for ants was based on presence/absence. Model significance was also assessed after 5,000 permutations. Confidence intervals (95% CI) were constructed around group centroids and overlaid on the ordination plots to compare groups, with differences assessed by the overlap between intervals.

All analyses were carried out in R version 3.6.3 (R Core Team 2020). General mixed-effects models were fit using nlme (Pinheiro et al. 2020) with least-squares mean estimation using emmeans (Lenth 2020). Estimated richness and diversity using coverage-based rarefaction were computed using iNEXT (Hsieh et al. 2020). Diversity estimation was computed using vegetarian (Charney and Record 2012). Constrained ordination models (RDA) were fit using vegan (Oksanen et al. 2019).

RESULTS

General characteristics of the study area (Appendix S1)

Selected sites were located within relatively wet areas, with an average wetland probability of 0.65 ± 0.150 (mean ± SD) in a 100-m buffer, with three burned sites with a probability lower than 0.6 (Table 1). Before the wildfire event, the conifer (consisting mostly of black spruce) cover within a 1.2-km buffer dominated all sites (57.5% ± 14.63%), with relatively lower contributions of mixed and deciduous cover in the surrounding landscape (11.3% ± 8.53% and 12.5% ± 8.58%, respectively). Based on the data collected at the transect level at unburned sites, black spruce accounted for 95.8% ± 6.21% of stems tallied at each site, with an estimated density of 6,812–13,125 stems/ha. The seismic line area and density among sites (1.2-km buffer) varied considerably (1.5–18.3 ha and 34.1–453.6 m/ha, respectively). The higher values were a result of development of low impact seismic lines around some sites (U1, U2,
and B6 in Fig. 1), which are normally constructed in a grid fashion, about 50–100 m from each other. Due to access constraints, all sites were located close to main roads (and their verges), which were the other main linear footprint present in the area, and their contribution to the disturbed area in each 1.2 km buffers (22.0 ± 12.49 ha) was much greater than that of seismic lines (5.7 ± 4.00 ha), but with lower density (73 ± 56.53 m/ha vs. 115.7 ± 107.56 m/ha; Table 1). The area disturbed by human activities (i.e., seismic lines, well pads, and other linear features) represented on average 6.6% ± 2.5% of the 1.2-km buffer around each site, ranging from 2.9% to 10.9% (Table 1).

Site conditions

For the sites within the fire perimeter, relative burn severity was consistently and significantly lower on seismic lines (15.2%) with forest (70.3%) and edge (67.6%) habitats showing higher and similar evidence of fire (Fig. 2a). For the remaining variables, no statistical differences were detected between seismic lines in burned and unburned sites (Table 2, Appendix S2). Soil volumetric water content (VWC) was significantly higher along seismic lines regardless of whether sites had burned (50.5% vs. 18.0% at the edge and 21.9% in the forest) or not (40.1% vs. 18.9% at the edge and 17.2% in the forest; Fig. 2b). Many of the remaining variables were related to stand structure, and expectedly showed significant differences among habitats, particularly with conditions at the seismic lines (Table 2). Thus, canopy cover was higher in the forest and edges, particularly in unburned sites. Likewise, snag BA and density were higher in forest and edge habitats, in both burned and unburned sites, with the forest showing greater values and seismic lines showing much lower values. Similarly, live tree BA and density were higher in forest and edge habitats, but expectedly only in unburned sites. However, overall stem BA and density (both dead and live stems) were no different between burned and unburned sites and differences were only between seismic lines and forest/edge habitats. Although no differences were detected in tree seedling density among habitats, it tended to be higher along seismic lines in burned sites but lower along lines in unburned sites. Seedling density, however, was significantly higher in unburned forest and edge habitats than in the same habitats in burned sites. Willow density was greater on seismic lines than in the forest or edge habitats but no differences were detected between burned and unburned sites. In contrast, Labrador tea density was higher in unburned sites, but consistently lower in the lines compared to forest and edge habitats in both burned and unburned sites. No differences were detected for bog birch density, as well as for DWD volume and density or soil temperature.

The RDA model for environmental conditions was highly significant ($F_{5,39} = 14.34, P < 0.001$) explaining 60.3% of the total variation (adjusted $R^2$), with the first axis (RDA1, 56.6% of the constrained variation) attributed mostly to a habitat gradient (Line vs. Forest/Edge) and the second axis (RDA2, 40.7%) showing mostly a fire gradient (Burned vs. Unburned; Fig. 2c,d). No differences were detected between the forest and edge for either burned or unburned sites, with tree density and basal area, tree regeneration density and Labrador tea density highly correlated with unburned forest and edge habitats, and snag density and basal area, highly correlated with burned forest and edge habitats. No differences were observed between seismic lines in burned and unburned sites, which shared similar environmental conditions (e.g., higher VWC and willow density, and low stem BA and density).

Species richness, diversity, and abundance

A total of 423 species were collected among the different taxonomic groups (spiders, 215 species and 3,557 individuals; carabids, 46 species and 1,454 individuals; ants, 20 species and 9,441 individuals; plants, 142 species [understory, 103; overstory, 16; non-vascular, 26]; Table 3, Appendix S3). Seven spider species, six wolf spiders (Lycosidae), and one ground spider (Gnaphosidae), accounted for more than 60% of the total spiders (Pardosa hyperborea, 16.9%; Pardosa uintana, 11.1%; Pardosa moesta, 8.4%; Alopecosa aculeata, 6.0%; Pirata bryantae, 5.2%; Pirata insularis, 3.0%; and Gnaphosa microps, 10.2%; Appendix S3). Four carabid and four ant species accounted for more than 75% and 85% of the total catch in each group, respectively (carabids, Pterostichus punctatissimus, 42.5%; Pterostichus adstrictus, 18.0%; Agonum gratiosum, 9.7%; Stereocerus haematopus, 5.6%; ants, Formica aserva, 31.7%; Myrmica alaskensis, 28.0%; Myrmica fracticornis, 14.1%; Formica neorygibarbis, 11.4%). The most common plant taxa were encountered in more than one-half of the plots, and included Labrador tea (74.2%), lingonberry (Vaccinium vitis-idaea, 70.7%), sphagnum moss (Sphagnum spp.; 56.0%), and common horsetail (Equisetum arvense, 51.6%; Appendix S3).

Richness (S) and diversity (D) varied considerably among taxonomic groups (Table 3, Appendix S2). Spider richness (sample coverage [SC] = 99.5%) increased from forest to line habitats in unburned sites, with a significantly larger richness along the lines compared to the adjacent forest. Spider richness was significantly lower in unburned forest sites compared to burned forest sites, and no differences were detected between unburned and burned sites for edge and line habitats. Spider diversity (SC = 99.5%) also increased from forest to line habitats, but only in burned sites, where it was lowest in forest and edge habitats; however, no differences were observed between seismic lines in burned and unburned sites. Carabid richness (SC = 96.5%) was highest in the forest and lowest in the edge habitat in burned sites, while it was higher in the unburned seismic lines compared to the edges. In contrast, carabid diversity (SC = 96.5%)
| Condition                      | Burned forest | Burned edge | Burned line | Unburned forest | Unburned edge | Unburned line |
|-------------------------------|---------------|-------------|-------------|-----------------|---------------|---------------|
| Burn severity                 | 70.3 (7.63)²  | 67.6 (7.63)² | 15.2 (7.63)¹ | 18.9 (4.84)²    | 17.2 (3.55)¹  | 40.1 (7.32)²  |
| Soil VWC (%)                  | 21.9 (3.95)¹  | 18.0 (2.90)¹ | 50.5 (5.97)² | 50.5 (0.066)¹  | 50.0 (0.066)  | 0.62 (0.066)  |
| Soil temp (°C)                | 0.67 (0.054)² | 0.68 (0.054)² | 0.71 (0.054)² | 0.71 (0.054)²  | 0.71 (0.054)² | 0.68 (0.054)² |
| Stem BA (m²/ha)               | 17.8 (2.94)²  | 14.6 (2.38)² | 0.0 (0.01)³  | 21.4 (3.60)²    | 20.9 (2.91)²  | 0.0 (0.01)³   |
| Tree BA (m²/ha)               | 0.13 (0.088)² | 0.21 (0.127)² | 0.01 (0.01)³ | 19.6 (3.85)²    | 20.1 (3.93)²  | 0.0 (0.01)³   |
| Snag BA (m²/ha)               | 17.6 (4.18)²  | 14.4 (2.48)² | 0.0 (0.25)³  | 1.6 (0.40)²     | 0.8 (0.34)²   | 0.0 (0.30)²   |
| Stem den. (stems/ha)          | 1,0027.8 (1,336.72)² | 12,138.9 (1,962.74)² | 69.4 (75.82)² | 10,291.7 (1,637.15)² | 11,583.3 (2,403.8)² | 104.2 (92.9)²   |
| Tree den. (stems/ha)          | 111.1 (88.79)² | 347.2 (179.80)² | 13.9 (24.62)² | 9,437.5 (1,697.61)² | 10,916.7 (1,857.60)² | 20.8 (36.64)² |
| Snag den. (stems/ha)          | 9,917.2 (1,697.33)² | 11,792.4 (1,697.33)² | 0.0 (1697.33)² | 854.5 (190.11)² | 667.4 (190.11)² | 0.0 (0.001)² |
| Seedling den. (stems/ha)      | 1,014.5 (540.14)² | 1,014.1 (540.14)² | 3,306.5 (1,157.0)² | 16,771.4 (4,040.21)² | 16,271.2 (3,962.4)² | 11,292.1 (3,130.25)² |
| Shrub den. (stems/ha)         | 118,014.1 (19,057.1)² | 145,902.9 (19,981.80)² | 129,639.4 (29,954.00)² | 181,813.2 (23,393.33)² | 174,563.5 (22,023.20)² | 121,604.2 (36,685.67)² |
| Bog birch den. (stems/ha)     | 3,028.3 (2,001.20)² | 8,541.9 (4,819.48)² | 1,986.2 (1,400.24)² | 14,521.5 (9,252.93)² | 4,479.5 (3,415.43)² | 11,229.1 (7,441.94)² |
| Labrador tea den. (stems/ha)  | 86,902.7 (19,271.93)² | 91,542.2 (19,271.93)² | 40,000.0 (19,271.93)² | 151,563.2 (23,604.36)² | 155,167.5 (23,604.36)² | 63,708.4 (23,604.36)² |
| Willow den. (stems/ha)        | 20,014.0 (13,979.40)² | 36,471.7 (13,979.40)² | 64,819.5 (13,979.40)² | 7,874.8 (6,311.63)² | 9,771.0 (6,311.63)² | 32,688.2 (6,311.63)² |
| DWD vol. (m³/ha)              | 11.3 (3.73)²   | 7.4 (3.73)²   | 9.7 (3.73)²   | 7.3 (4.56)²     | 2.5 (4.56)²   | 2.7 (4.56)²   |
| DWD den. (stems/ha)           | 1,514.2 (324.03)² | 1,194.1 (247.03)² | 1,681.2 (802.08)² | 1,104.1 (397.04)² | 750.1 (302.03)² | 1,188.1 (983.01)² |
| Canopy cover (%)              | 23.3 (5.59)²   | 21.2 (4.94)²   | 5.6 (2.37)³   | 58.4 (6.84)²    | 56.2 (6.05)²  | 6.9 (2.90)³   |

**Notes:** Values are averages (with SE in parentheses). Different letters denote significant differences (α = 0.05). Uppercase letters denote differences between burned and unburned sites by habitat (e.g., burned forest vs. unburned forest). Lowercase letters denote differences between habitats within each fire category (i.e., forest vs. edge vs. line in burned sites, or forest vs. edge vs. line in unburned sites). VWC, volumetric water content; temp., temperature; BA, basal area; den., density; DWD vol., downed woody debris volume.

†Cubic root applied to meet model assumptions; estimated means and standard errors obtained from back-transformed data.
was highest in line habitats, regardless of sites being burned or unburned. No differences were observed in ant richness or diversity (SC = 95.0%) among habitats or between fire categories. Richness and diversity of vascular understory plants were significantly higher on the lines than on edge or forest habitats, but no differences were detected between the latter two or between fire categories. No differences in richness and diversity of overstory plants were detected among habitats in burned areas; however, edges showed the lowest values in unburned areas with no differences between forest and line habitats (Table 3, Appendix S2).

In terms of abundance (Table 3, Appendix S2), spiders were significantly more abundant in forest and edge habitats in burned sites than in unburned sites; however, no difference among habitats was detected within either fire category. Carabid abundance was highest in burned lines; however, variation was large and no statistical differences were detected among habitats. In terms of percent cover, non-vascular plants showed higher cover in edge and line habitats in burned sites, with no differences among habitats in unburned sites, and no differences between seismic lines in burned and unburned sites. Understory plants exhibited greater cover along seismic lines in burned sites, but no differences were observed among habitats in unburned sites. Cover of understory plants was higher, however, in unburned forest and edge habitats compared to these habitats in burned sites. In unburned sites, overstory plants showed highest cover along edges, with no differences between forest and line habitats. No differences among habitats were observed in burned sites. However, overstory cover was higher in both forest and edge habitats in unburned sites compared to burned sites, with no difference between lines.

### Species composition

Patterns in species composition revealed by RDA (Fig. 3) were consistent to those presented above for site conditions. The models for spiders (\(F_{3,39} = 2.73, P < 0.001\); Fig. 3a), carabids (\(F_{3,39} = 1.72, P < 0.001\); Fig. 3b), ants (\(F_{3,39} = 1.14, P = 0.011\); Fig. 3c), non-vascular plants (\(F_{3,39} = 4.12, P < 0.001\); Fig. 3d) and understory plants (\(F_{3,39} = 1.64, P < 0.001\); Fig. 3e) were significant, while the overstory plants model was marginally significant (\(F_{3,39} = 1.99, P = 0.055\); Fig. 3f). The variance explained was relatively large only for non-vascular plants (adjusted \(R^2 = 26.6\%\)) and spiders (16.4%), while for the remaining taxa it was much lower (overstory plants, 10.8%; carabids, 7.5%; understory plants, 6.8%; ants, 1.6%). The first axis in the non-vascular plants and spider models (64.2% and 46.6% of the constrained variation, respectively) explained mostly a fire gradient (Burned vs. Unburned), while the second axis (27.3% and 43.2% of the constrained variation, respectively) explained mostly a habitat gradient (Line vs. Forest). In most models, no major differences in composition were detected between the forest and edge habitats in either burned or unburned sites (Fig. 3); however, differences in composition were evident

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**Table 3.** Species richness, diversity, and abundance/percent cover of various taxonomic groups in forest, edge, and seismic line habitats at burned and unburned peatlands along the southwest perimeter of the 2016 Horse River wildfire (Fort McMurray).

| Group         | Burned forest | Burned edge | Burned line | Unburned forest | Unburned edge | Unburned line |
|---------------|---------------|-------------|-------------|-----------------|---------------|---------------|
| **Species richness** |               |             |             |                 |               |               |
| Spiders       | 138.0 (13.97)b | 146.1 (12.40) | 147.5 (8.40) | 110.3 (8.39)ab  | 130.9 (16.72)ab | 151.7 (15.34)b |
| Carabids      | 41.3 (10.35)bc | 17.2 (2.48)ab | 24.7 (2.25)b | 13.7 (3.21)ab   | 9.1 (2.60)ab   | 19.5 (5.03)b   |
| Ants          | 19.0 (6.65)   | 19.5 (4.96)  | 16.1 (2.34)  | 21.5 (5.34)     | 14.5 (1.89)    | 16.1 (1.69)    |
| Understory plants | 13.7 (1.82)a | 12.7 (1.71)a | 21.6 (3.45)b | 13.7 (2.23)ab   | 11.0 (2.09)a   | 21.5 (4.23)b   |
| Overstory plants | 2.5 (0.46)   | 2.3 (0.36)   | 3.7 (0.69)   | 2.7 (0.46)ab    | 1.8 (0.44)a    | 4.7 (0.84)b    |
| **Species diversity** |               |             |             |                 |               |               |
| Spiders       | 19.4 (0.91)ab | 21.5 (0.89)ab | 30.7 (1.08)c | 31.0 (1.73)b    | 27.1 (1.30)b   | 31.5 (1.35)b   |
| Carabids      | 5.5 (1.04)c   | 4.9 (0.72)ab | 10.0 (0.99)b | 4.5 (1.05)ab    | 3.2 (0.52)ab   | 8.0 (1.54)b    |
| Ants          | 12.7 (2.71)   | 14.6 (2.47)  | 13.4 (1.64)  | 16.1 (3.10)     | 12.6 (1.85)    | 14.7 (1.47)    |
| Understory plants | 6.8 (0.99)   | 6.7 (0.91)   | 9.4 (1.58)   | 6.3 (1.21)      | 4.8 (1.11)     | 9.1 (1.94)     |
| Overstory plants | 1.7 (0.27) | 1.7 (0.17) | 2.3 (0.39)    | 2.2 (0.27)b     | 1.2 (0.21)a    | 2.6 (0.47)b    |
| **Abundance/percent cover** |         |              |             |                 |               |               |
| Spiders†      | 656.9 (62.41)b | 602.9 (37.06)b | 604.5 (81.62) | 442.2 (62.71)b | 474.3 (40.26)A | 541.3 (94.60) |
| Carabids‡     | 29.6 (6.07)   | 28.9 (7.22)  | 46.2 (12.08)b | 21.2 (5.32)     | 21.1 (6.46)    | 18.0 (5.75)A   |
| Non-vasc. ‡   | 17.5 (3.91)A,a | 21.6 (6.12)Ab | 47.1 (11.64)b | 96.1 (11.21)B,a | 91.7 (14.88)B,a | 79.6 (18.55)   |
| Understory plants | 19.0 (4.48)Ab | 24.0 (4.15)A | 60.1 (8.54)B | 37.6 (4.48)B,a  | 41.6 (5.08)B   | 47.1 (10.46)   |
| Overstory plants | 1.5 (1.63)A  | 3.1 (1.77)A  | 7.0 (1.89)   | 9.9 (1.64)R,a   | 18.5 (2.17)R,b  | 9.3 (2.31)A    |

**Notes:** Values are averages (with SE in parentheses), except for arthropod richness, which are estimated via coverage-based rarefaction (95% confidence interval; differences are assessed by visual inspection). Different letters denote significant differences (α = 0.05). Uppercase letters denote differences between burned and unburned sites (e.g., burned forest vs. unburned forest). Lowercase letters denote differences between habitats by fire category (e.g., forest vs. edge vs. line in unburned sites). Non-vasc., non-vascular plants.

Square root (†) and logarithm (‡) transformations were applied to meet model assumptions; estimated means and standard errors obtained from back-transformed data.
between seismic lines in burned and unburned sites, particularly for spiders and carabid beetles. Patterns among habitats for the other taxa were relatively similar, but much less marked and with greater overlap between confidence intervals.

**DISCUSSION**

We investigated the immediate cumulative effects of seismic lines and wildfire on boreal treed peatlands one year following fire, demonstrating that both forest disturbances determine site characteristics, resulting in particular species composition patterns across the taxa here assessed, which are relatively consistent among spiders, carabid beetles, non-vascular plants and vascular understory plants. The Horse River fire event was classified as a severe crown wildfire (MNP LLP 2017), killing on average 97% of the trees in our study plots. At the peak of the growing season the following year, sites exhibited low regeneration of the burned understory cover. We observed, however, a wide variation in burn severity on the forest floor (excluding seismic lines), with values ranging from no burn evidence in a few plots to plots completely burned (CV 38.6%). Fire severity in peatlands is highly variable and particularly...
influenced by local microtopography (hummocks and hollows) and proximity to water table (Zoltai et al. 1998, Turetsky and Wieder 2001, Bengtson et al. 2005, 2015), variables that also have a direct effect on species distribution (Nicholson and Vitt 1990, Vitt 1990, Riva et al. 2018a). Despite this natural range of variability in the observed burn severity across all sites, seismic lines burned in a consistently lower proportion, compared to forest and edge habitats. Although there were a few plots along seismic lines that burned more than 50% (n = 5), over three-quarters did not show any (n = 24) or very little (below 25% burn severity; n = 10) evidence of fire, resulting in a much higher understory vegetation cover along the seismic lines and a charred landscape crossed by a network of green linear features.

Presumably, the relatively low burn severity along seismic lines is a result of lower fuel loadings and high soil water content in these environments. There is evidence that seismic lines are often wetter than the adjacent habitat (Dabros et al. 2017, Strack et al. 2018, Deane et al. 2020), with increased soil moisture along seismic lines being the result of the interaction of various factors. These include reduced plant water uptake and evapotranspiration due to the lack of mature trees on seismic lines (Vitt et al. 1975), soil compaction and seismic line subsidence (Williams et al. 2013, Lovitt et al. 2018, Stevenson et al. 2019), and the dominance of sphagnum moss (Deane et al. 2020), which is known for its water retention capacity (Hayward and Clymo 1982, Kellner and Hall din 2002, Shetler et al. 2008). Although we did not measure microtopography, evidence shows that seismic lines in boreal peatlands lay lower than the adjacent habitat (Lovitt et al. 2018), even if sites had experienced wildfire (Stevenson et al. 2019). Further, when comparing Forest plots to Line plots in unburned sites, we did observe higher sphagnum moss occurrence and cover along seismic lines (87% vs. 67% of the plots and 83% vs. 49% mean cover), as well as much higher volumetric water content (40.1% vs. 18.9%) and lower coarse fuel levels (2.7 vs. 7.3 m3/ha). Several species with known association and/or preference to wet habitats were commonly observed/collected along seismic lines, highlighting the particular environmental conditions of these features. These included, for example, the spiders *P. bryantae*, *P. insularis*, *Dolomedes striatus* (Don dale and Redner 1990), the carabids *Agonum affine*, *A. gratiosum*, *Bembidion concretum* (Lindroth 1961–1969), and sedges, particularly *Carex aquatilis* (Dabros and Waterway 2008). Prevalent habitat conditions thus likely prevented seismic lines from burning extensively, with fire essentially skipping over the lines and spreading through the surrounding forest, with burn evidence on the lines mostly attributed to burned trees that fell onto the seismic line (based on field observations).

Low fire severity on seismic lines in comparison to the adjacent forests had an important influence on the response of local site conditions and species composition. Except for seedling density, which was overall higher in unburned sites regardless of the habitat, no differences were observed among any of the remaining environmental variables between seismic lines within and outside the fire perimeter, suggesting that habitat conditions along lines within the burned area were not altered much. This, in turn, resulted in similar richness, diversity (in the case of plants, only for vascular species), abundance/percent cover (except for carabids that showed lower abundance in lines at unburned sites) and composition (except for spiders and beetles) between lines in burned and unburned sites. Further, the lack of change in ant species richness and diversity both between fire categories and among habitats is consistent with past studies on boreal ants (Lafluer et al. 2006, Glasier et al. 2015). As ants are able to seek refuge from fire in subterranean nests and are able to adapt to disturbances by changing their foraging behaviors (Parr and Andersen 2008, Glasier et al. 2015), we believe this taxon to be less influenced by changing conditions due to fire.

Although we were not expecting major differences between habitats in burned sites as a result of the assumed erasing effect of fire, differences in unburned sites were anticipated, specifically between seismic lines and the adjacent forest. There is plenty of evidence that describe these differences (e.g., Lee and Boutin 2006, van Rensen et al. 2015, Pattison et al. 2016, Dabros et al. 2018, Finnegan et al. 2019), which confirms our observations showing little tree regeneration on lines; however, knowledge of such differences following wildfire is scarce (but see Dawe et al. 2017, Riva et al. 2018a, 2020). We expected abundance/percent cover, richness, and diversity, particularly that of understory vegetation, to be higher on the seismic lines than in the adjacent forest in unburned sites, where the canopy of mature trees would outcompete shade-intolerant species, and late seral species would be more common and abundant. Overstory percent cover in these sites was highest but diversity lowest along edge habitats (in unburned sites), where tree growth and density is often more pronounced (Bella 1986), owing to the higher light levels along the line edge compared to interior forest away from the line edge (Dabros et al. 2017). Mature black spruce trees had by far the highest percent cover within the edge habitat, compared to forest and line habitats (17.5%, 4.4%, and 2.1%, respectively, but below 1% at all locations on burned sites). Higher canopy growth along the edges could lead to higher shade and stronger competition on shade-intolerant understory species, resulting in lower plant species diversity overall. Although we did not detect significant differences in vascular understory vegetation diversity among habitats, it was on average lower along the edges. For the non-vascular species, it should be noted also that although we did not estimate species diversity and richness (due to some taxa grouped at the genus level), we observed that the lines were often dominated by *Sphagnum* species, whereas in the adjacent habitats (forest and edges) several species of bryophytes, notably feather moss *Pleurozium schreberi* and
Hylocomium splendens, Politrichum species, as well as various species of Sphagnum were common. This allows us to speculate that while species richness and diversity of bryophytes might have been similar between the lines and the forest, species composition and dominance were different. On the lines most of the diversity could have resulted from diversity of different Sphagnum species (which we did not assess), whereas the adjacent forest would present overall higher diversity of bryophytes at the genus level. These plausible differences in composition, richness and diversity of non-vascular species between the lines and the forest would have been present there before the fire event, and would not have changed much due to fire event, since the lines presented such a low burn severity. Richness and diversity for the other groups of organisms were generally higher along seismic lines, but responses were not consistent and varied considerably among taxa, highlighting the challenges for ecological restoration of these industrial footprints, especially from the perspective of managing biodiversity.

In conclusion, although wildfire is an important natural disturbance in the Canadian western boreal forest (Burton et al. 2008, Bergeron et al. 2014) and particularly in peatlands (Kuhry 1994, Turetsky et al. 2004), its effectiveness to burn and mitigate the footprint resulting from OG seismic exploration in wet areas seems limited (at least in the short term), due primarily to changes in the local and landscape hydrology resulting from soil compaction and reduced evapotranspiration (i.e., reduced canopy) along seismic features, and low fuel loadings. Our study, in agreement with a recent assessment of butterflies and plants in the same area (Riva et al. 2020), provides strong evidence that wildfire did not erase the linear footprint across burned sites as we hypothesized, despite the fact that this fire event was particularly severe and intense (MNP LLP 2017). If this was the case, no major differences would have been observed between the three studied habitats within the fire perimeter, and strong differences would have been observed between lines in burned sites compared to those in unburned sites, which is not what we observed. More importantly, low fire severity along seismic lines in peatlands may further increase the effects of this linear footprint in the recovering post-fire landscape, with currently unknown consequences to the medium- to long-term regeneration along the interface between the seismic lines and the adjacent forest. Hence, low fire severity along lines not only has important implications for post-fire recovery patterns (or the lack of, along seismic lines), but to the spatial distribution and composition of species across these landscapes. Seismic lines may serve as habitat refuge for certain species, including some rare butterflies (Riva et al. 2020), but these long corridors of open habitat also facilitate movement of other species (Hebblewhite et al. 2007, Latham et al. 2011b, Riva et al. 2018b, Dickie et al. 2020), which might help in maintaining population of species that otherwise would have been removed from burned areas. The latter should be taken with caution; unburned seismic lines may contribute as a population source for the recovering adjacent burned forest, but many of these species are typical of disturbed and open habitats (van Rensen et al. 2015, Finnegan et al. 2019), which may influence post-fire recovery patterns in the adjacent forest. The results presented here evaluate overall responses one year following the fire event, therefore we can only speak to the short-term and immediate potential of wildfire as a passive restoration approach to mitigate the extensive linear footprint in peatlands, which given the evidence seems to be limited, and active human intervention (e.g., Rochefort and Lode 2006) would likely be required to accelerate recovery. These observations, however, have important implications, as they suggest a divergence in the successional pathways and recovery patterns between the burned adjacent forest and the unburned line, potentially resulting in the persistence of linear footprints as these landscapes regenerate from fire. Monitoring site conditions and biodiversity will be crucial to evaluate longer-term responses to the cumulative effect of the linear footprint and wildfire, and to assess potential impacts in the natural recovery of fragmented peatlands as a result of OG industrial development.

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**Supporting Information**

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2281/full

**Data Availability**

Data are available from the Dryad Digital Repository (Pinzon et al. 2020): https://doi.org/10.5061/dryad.6djh9w105