

Initial Succession After Wildfire in Dry Boreal Forests of Northwestern North America

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Abstract

Wildfires in the boreal forest of North America are generally stand renewing, with the initial phase of vegetation recovery often governing the vegetation trajectory for decades. Here, we investigate post-fire vegetation changes in dry boreal forests of the Northwest Territories, Canada, during the first five years following the unusually severe 2014 wildfire season. We sampled post-fire tree regeneration and the overall plant community at one, three, and five years post-fire across different fire severities and stand types within fires that burned in 2014. Post-fire trajectories of tree recruitment, cover by plant functional types, and plant diversity varied widely among sampled stands, as well as among years post-fire. Tree seedling density reaches relative equilibrium by three years post-fire, whereas trends in understory plant cover and understory species assemblages suggest an ongoing change that will extend beyond five years of observation. In almost half of sampled stands, the composition of recruited trees differs from that of the pre-fire stand, suggesting a change in tree-species dominance. An analysis of regional climate reveals a significant, albeit spatially variable, warming and drying trend that will further accelerate forest-stand transformation through both climate drivers of plant community composition and indirectly through increasing fire activity. While the 2014 wildfires enhanced the structural and compositional heterogeneity of the region, they also triggered vegetation changes that are likely to be persistent. As such, this study exemplifies the speed and variability that characterizes post-fire stand development in a strongly moisture-limited part of North America.

Introduction

The persistence of forest cover in the boreal biome of North America is usually contingent on immediate and vigorous post-fire tree recruitment. The magnitude of this recruitment is dependent on sufficient propagule presence prior to burning, as well as the availability of suitable regeneration substrates and weather conducive to germination and early seedling growth after the wildfire (Brown and Johnstone 2012). Post-fire recruitment is facilitated by various adaptations of keystone vascular plant species to high-intensity wildfire, such as serotiny, resprouting, and rapid juvenile growth rates (Greene et al. 1999). Unlike the forests of many other biomes, where tree recruitment may span decades, in northern boreal forests, the first few years following a fire are critical to the development of the stand; in fact, vegetation trajectories are often set after merely three years (Johnstone et al. 2004; Boulanger et al. 2018). Careful monitoring of vegetation communities during that period is therefore necessary for understanding the fate of these stands, as well as the biophysical factors that allow them to thrive or fail (Bergeron et al. 2002, Whitman et al. 2018a).

While the classic 'direct regeneration' dynamics predominate across the biome, patterns of post-fire early tree recruitment and stand development regularly diverge from this model. For example, tree regeneration can be greatly limited, leading to the replacement of pre-fire dominant trees by a different species or, if regeneration fails altogether, a conversion to non-forest vegetation (Baltzer et al. 2021). Conifers, and in particular spruce species such as black (*Picea mariana*) and white spruce (*P. glauca*), have been losing ground to pines (*Pinus spp.*) and broadleaf species, namely poplars (*Populus spp.*) and birches (*Betula spp.*) (Lavoie and Sirois 1998, Johnstone et al. 2010). When trees completely fail to regenerate following a wildfire, profound and long-lasting changes in ecological dynamics may occur (Splawinski et al. 2019). On the other end of the severity spectrum, surface fires that are generally non-lethal to dominant trees commonly occur in some areas, as evidenced by multiple-scarred trees (Rowe and Scotter 1973, Van Wagner 1983). Evidence from local studies suggests the prevalence of

surface burning, which is the dominant fire type in much of boreal Eurasia (de Groot et al. 2013), is underestimated in the North American part of the biome (Heinselman 1973, Whitman et al. 2018b).

Boreal systems are inherently resilient to changes in climate and fire activity (Hart et al. 2019), but there is mounting evidence of accelerating shifts in tree dominance across the boreal biome in recent decades, and this is especially true for the western part of the biome (Baltzer et al. 2021). These changes are most often triggered by large wildfires, which are themselves an outcome of top-down environmental (i.e., climatic) factors (Erni et al. 2017). This said, while warmer and drier conditions reported for much of North America—especially in the West—exert direct pressure on plants, the effect of climate change on boreal forests is exacerbated through a change in the fire regimes that govern boreal landscape dynamics (Boucher et al. 2020, Coop et al. 2020). More intense heat and drought can affect fire behaviour through increased fire intensity (Wotton et al. 2017), while concurrently causing a deterioration of the conditions for early seedling establishment (Hogg and Wein 2005). Greater recurrence of short (i.e., <20 years in the North American boreal biome) intervals between wildfires, an almost-certain outcome of increased fire activity, is prompting rapid and enduring changes to vegetation composition and structure (Whitman et al. 2019a, Hayes and Buma 2021). Major shifts in vegetation have been reported throughout the Holocene in the western boreal forest of North America (MacDonald 1987, Higuera et al. 2009); however, evidence suggests that the current and future climate-induced changes are occurring at an unprecedented rate, leading to large uncertainties in future ecological outcomes (Stralberg et al. 2018).

Examining the initial stages of post-fire vegetation development in boreal forests will help us understand how ecological heterogeneity originates among boreal stands, and shed light on the biophysical factors that mediate vegetation change. Monitoring stands through time allows us to capture insights, such as patterns of divergence or convergence, that may be obscured in single-observation studies. As such, the goal of this study is to investigate the vegetation development during the first five years following wildfires of the unusually severe 2014 wildfire season in a dry boreal forest of the Northwest Territories, in northwestern Canada. Specific objectives consist of: (1) monitoring tree recruitment and tree dominance shifts from the pre-fire state, (2) evaluating changes in stand composition (i.e., functional types) and structure, (3) comparing the evolution of plant species assemblages, and (4) examining the trends in temperature and moisture availability during the years prior, the year of, and the years following the 2014 wildfires. This was achieved by sampling 32 forested sites originating from 2014 wildfires at one, three, and five years after fire across different fire severities and stand types, as determined by pre-fire tree composition and topographic characteristics.

Methods

Study Area

Field sites were established in five, lightning-caused fires from 2014 that burned in the Northwest Territories and Wood Buffalo National Park (Fig. 1). Most of the area is sitting on ancient marine sediment having deep sedimentary soil; this area is particularly flat, except for a few plateaus. A smaller part of the area is underlain by rocky bedrock that is part of the Canadian Precambrian Shield, which is characterized by rolling hills. Wetland areas cover approximately a third of the area (Tarnocai et al. 2011), with peatlands (peat-forming wetlands with organic layer depths ≥ 40 cm) making up the majority of wetlands in the study area. Mean annual temperatures range from -4.3°C in the north to -1.8°C in the south, whereas the mean annual precipitation in the 2015-2019 period range from 279 to 357 mm (Ecological Stratification Working Group 1995, Wang et al. 2016), making it

one of the driest parts of the boreal biome. Forests of the study area are dominated by jack pine (*Pinus banksiana*), black spruce, white spruce, and trembling aspen (*Populus tremuloides*), with paper birch (*Betula papyrifera*), eastern larch (*Larix laricina*), and balsam poplar (*Populus balsamifera*) present in smaller proportions (Ecological Stratification Working Group 1995).

Due to its high latitude and low vegetation productivity, there is very little agriculture and industrial forest harvesting in the areas and, as a result, active fire management is limited and focused around communities. Although the fire regime of the northwestern Canadian boreal forest is characterized by infrequent, stand-replacing wildfires (Boulanger et al. 2012; Johnson 1992), the 2014 fire season was particularly severe, with drought-driven wildfires burning more than 3 million ha (Northwest Territories Environment and Natural Resources 2015). Large wildfires such as these comprise a small proportion of the total number of wildfires that burn within the boreal forest, but contribute the vast majority of total area burned (Stocks et al. 2002). As reported by Whitman et al. (2018b), sampled stands were highly variable in terms of severity, ranging from surface fires to high-intensity crown fires with complete overstory mortality, and leaving many patches unburned within the fire's perimeter.

Field methods

Thirty-two field sites were established one-year post-fire (2015) in areas of homogenous burn severity, topographic setting (upland or wetland), and dominant vegetation extending ≥ 60 m in any direction in locations >100 m and ≤ 2 km from roads. Some sites ($n = 3$) were accessed by helicopter. Site centres were located a minimum of 103 m distant from each other, with a mean distance between centres of all sites of 170 m. Sites were subsequently resampled three and five years post-fire (2017 and 2019).

In the first sampling year (2015), sample plots were 30×30 m, with two 30-m transects oriented in the cardinal directions crossing at the plot centre. We measured overstory composition by tree species, percent overstory mortality, stem density (stems ha^{-1}), and basal area ($\text{m}^2 \text{ha}^{-1}$) of mature trees in the pre-fire stand, for 32 trees ≥ 3 cm diameter at breast height (DBH) using the point-centered quarter method (Cottam et al. 1953, Mitchell 2015) at eight evenly-spaced points along the two transects. Burn severity (described further below) and seedling density were measured in four 10×10 m subplots at the corners of each 30×30 m macroplot. Understory vegetation cover was estimated by species in five 1×1 m plots located at the inner corner of each burn severity/seedling density plot and the plot centre. Vegetation cover of shrubs was separated for short shrubs (<0.5 m tall), which was assessed in the understory vegetation plots, and counts and species of tall shrubs (≥ 0.5 m tall,) which were sampled along the two 30-m transects where they intersected the transect lines (Alberta Environment and Sustainable Resource Development 2014). Coarse woody debris (CWD) loading was measured along each transect out to a length of 25 m, using a line-intercept method and a go-no-go gauge, following McRae et al. (1979) with sampling intensity (length along the transect for which a size class was measured) decreasing with decreasing fuel size-class.

In 2017 and 2019, seedling density, sapling density, tall shrub density, and overstory stand characteristics were remeasured using a north-south oriented 35×2 m belt transect which crossed the original plot centre at 17.5 m. Seedlings were counted and identified to species along varying belt transect lengths as a function of seedling height, with seedlings 0-10 cm counted for 10 m, >10 -50 cm counted for 20 m, and seedlings > 50 cm counted for the full 35 m of the belt transect. We counted and identified saplings (live trees > 1.33 m with a DBH < 3 cm) and tall shrubs for the full 35×2 m transect. Overstory tree species basal area was measured using an angle gauge

(BAF factor 10), at 0, 17.5 and 35m along the transect, with tree species, mortality status, and decay class noted. Finally, understory vegetation cover was estimated by species at five 1 × 1 m plots placed at 0, 7, 14, 21, and 28 m along the belt transect. CWD was remeasured along the length of the 35-m transect, and beyond to an extended length of 50 m to match the initial year sampling efforts.

Environmental variables and initial post-fire characteristics were sampled in 2015 (see Whitman et al. 2018a for detailed descriptions). At this time, surface burn severity was measured using the Burn Severity Index (Dyrness and Norum 1983, Loboda et al. 2013), and generalized fire severity across all forest strata was measured using the composite burn index (CBI; Key and Benson 2006). CBI was later used to classify fire severity into low (CBI 0.5-1.25), moderate (CBI >1.25-2.25), and high (CBI >2.25). We classified surface fires as those resulting in <50% overstory tree mortality in this first post-fire year. Basal sections were collected from fire-scarred trees, or in their absence, mature, dominant trees, to determine time since stand origin (TSO) and time since last fire (TSLF) of the stand, using dendrochronological methods. Site moisture was classified from hydric to xeric according to Beckingham and Archibald (1996), with sites later generalized into dominant four stand types: treed wetland, upland black spruce, upland mixedwood, and upland jack pine (from wettest to driest). Post-fire organic soil depth was measured at inner corners of the burn severity/seedling density subplot, with three soil cores collected at the plot centre and inner corners of the southwest and northeast subplots. Physicochemical properties of oven-dried mineral and organic samples were measured in the lab. These included: pH, electrical conductivity (EC; mS cm⁻¹), percent total nitrogen (N), percent total carbon (C) measured by loss on ignition, calcium (Ca; mg kg⁻¹), potassium (K; mg kg⁻¹), magnesium (Mg; mg kg⁻¹), and sodium (Na; mg kg⁻¹), as well as the relative percentages of sand, silt, and clay in mineral soils.

Field data analysis

All analyses were performed in R version 4.0.5 (R Core Team 2021). We analyzed tree regeneration as a function of total stem density of living seedlings and saplings, as well as the separated stem density of coniferous and broadleaf tree species, and proportion of broadleaf regeneration. We examined shifts in tree dominance from pre- to post-fire using tree species compositional data. We identified the dominant pre-fire tree species at each site as the tree species with the greatest proportion of the site's overstory stem density, as measured one-year post-fire. Post-fire dominance was described for each sampling year as the species that was the most prevalent amongst the post-fire seedlings and saplings. We then visualized shifts in species dominance at each plot using an alluvial diagram from the package 'ggsankey' (Sjoberg 2021). For this analysis, white spruce and black spruce were combined into one category (*Picea* spp.) to limit errors in differentiating between white and black spruce seedlings at early ages (i.e., they are often indistinguishable). Within this analysis, we took note of sites seemingly experiencing regeneration failure, defined as non-surface fires in which no regeneration of the pre-fire dominant species was observed one-year post-fire. One site which initially did not see recruitment of the pre-fire dominant experienced delayed regeneration of >5000 stems/ha at year 5 and was thus removed from the regeneration failure group, highlighting the utility of repeated sampling in identifying longer-term trends.

We examined understory vegetation communities by functional group (forbs, graminoids, shrub), as well as the total vascular cover. We ordinated the Bray-Curtis dissimilarities of post-fire understory vascular plant communities for all years and sites using a detrended correspondence analysis (DCA) in the package 'vegan' (Oksanen et al. 2020). We fitted environmental variables and initial post-fire characteristics as sampled in 2015, along with two derived metrics (described below) to the DCA axes and assessed goodness of fit (R^2) for all

significant variables ($\alpha = 0.05$). The two derived metrics were 'percent broadleaf', which described the percentage of regenerating stems that were broadleaf species and 'broadleaf increase', a binary indicator of whether the percent broadleaf of regeneration in a sampling year exceeded the percent broadleaf observed in the pre-fire overstory canopy.

We then assessed understory vegetation diversity by calculating vascular species richness and evenness by stand type, also using the 'vegan' package. We further assessed species compositional shifts by calculating the number of unique vascular plant species 'extinctions' and 'colonizations' at each site over time. Extinctions were counted as species that had been present within a site in the previous year but not found during the next year of field sampling. Conversely, colonizations were considered to be the number of unique species found within a site that had not been present at that site in the previous year of field sampling, with all plants observed in the first year attributed to colonizations.

To detect varying temporal responses among stand types and fire severity classes, we tested for significant differences ($\alpha = 0.1$) within each sampling year for tree seedling and sapling density, understory vegetation cover classes, understory community diversity metrics, and CWD loading, among both stand classes and fire severity classes using non-parametric Kruskal-Wallis rank sum tests (Conover 1999) in the 'agricolae' package (de Mendiburu 2021). We conducted posthoc comparisons of rank means using Fisher's least significant difference tests, with Holm-adjusted p -values (Holm 1979) to determine which groups were meaningfully different. Tree seedling and sapling data were log-transformed prior to analysis to better visualize changes in groups with large differences in regenerating stem density.

Climate and fire analysis

To characterize trends in regional climate and fire activity we produced multiple time series within a study area corresponding to the boreal plains, taiga plains, and taiga shield ecoregions (Ecological Stratification Working Group 1995) within the Northwest Territories, as well as the portion of Wood Buffalo National Park that extends into the province of Alberta. We extracted all fire perimeters from the Canadian National Fire Database (CNFDB; Natural Resources Canada 2021) that intersected the study area, between 1965 and 2020. The starting point of 1965 was selected due to the lack of consistent fire data reporting prior to the 1960s in this region. We cropped the fire perimeters to the study area extent and calculated the area burned in hectares (ha) for each fire. We adjusted area burned estimates for fires that were not mapped from satellite or aerial photo sources, using the NWT model for area burned adjustment reported in Skakun et al. (2021). Finally, we removed any fires that were smaller than 200 ha from the dataset (i.e., because of inconsistent reporting of small fires) and then calculated the annual number of large fires and total annual area burned for the entire study area.

We produced a 50 × 50 km grid of points over the study area and extracted an elevation value from the North America Elevation dataset (Commission for Environmental Cooperation 2007) for each location. If a point fell inside of a waterbody we removed the point from the dataset. Using ClimateNA (Wang et al. 2016), we downscaled PRISM (Daly et al. 2008) and WorldClim (Hijmans et al. 2005) climate data grids to the local elevation points. We selected climate variables that are known to be related to fire activity: annual summer (JJA) maximum temperature (Tmax; °C), annual summer precipitation (PPT; mm), annual summer mean vapour pressure deficit (VPD) in hectopascals (hPa), and annual number of frost-free days (NFFD). For each point, we calculated the Theil-Sen nonparametric slope ('Sen's Slope') of the time series of climate data, for the same period used to examine fire activity (1965 - 2020). We tested the significance ($\alpha = 0.05$) of the slope at each point

using a two-tailed Mann-Kendall trend test, with a variance correction for serially autocorrelated data (Hamed and Rao 1998) using the 'modifiedmk' package (Patakamuri and O'Brien 2021). We then summarized the climate data within the study area by calculating an annual average value for each climate variable, creating four time series of regional climate trends.

We then derived Sens's slopes for the six regional time series (number of fires, area burned, TMax, PPT, VPD, NFFD) and also calculated variance-corrected one-tailed Mann-Kendall trend tests to determine their significance. We estimated Spearman correlation values indicating the relationship between the climate and fire time series and tested their significance, using the 'astrochron' package (Meyers 2014) to generate phase-randomized surrogate time series for cross-correlation in order to account for serial autocorrelation (Ebisuzaki 1997). We used the natural logarithm of the area burned for cross-correlations.

Results

Post-fire tree regeneration

Post-fire tree recruitment is initially lowest in treed wetland and black spruce sites, with mixedwood and jack pine stands achieving similar total regeneration density in the first year post-fire (Fig. 3a). However, high rates of recruitment in treed wetlands from 2015 to 2017 and from 2015 to 2019 in black spruce (Fig. S1.1) result in these site types achieving similar regeneration densities to mixedwood and jack pine stands by 2019. Despite high variability in coniferous and broadleaf regeneration stem density, recruitment at each sampling year is similar across site types, with the exception of mixedwood stands, which have higher initial recruitment of broadleaf species than other stand types. The rate of coniferous and broadleaf recruitment is similar across all stand types, except for treed wetlands, which see substantial increases in recruitment in the 2015 to 2017 period. Percent broadleaf remains relatively stable through time in mixedwood stands, with a net increase in percent broadleaf observed across all other stand types from 2015 to 2019, despite decreases in the percent broadleaf from 2017 to 2019 as conifer recruitment outpaces broadleaf recruitment. No statistical differences are observed in recruitment metrics within each sampling year by fire severity class, though recruitment does increase within each severity class through time (Fig. 3b).

Species dominance fluctuates considerably from pre-fire to post-fire, with changes in dominance observed for some sites at every sampling period time step (Fig. 4). Fifty-three percent of sites have the potential for the initial, pre-fire overstory species to self-replace and retain post-fire dominance, provided that the dominant regenerating species sampled five years post-fire in 2019 is preserved into the future. However, many sites experience post-fire dominance shifts to competitor species, particularly in a subset of sites experiencing poor establishment and even post-fire regeneration failure of the pre-fire dominant species (Fig. S1.2). In particular, many sites switch dominance from spruce or jack pine to trembling aspen. This phenomenon occurs across all stand types (Fig. S1.3 and S1.4) and is more likely to occur in sites in the southern portion of the study area (Fig. 1). Aspen dominance was observed in 41% of 2019 sites as compared to 6% of the pre-fire overstory, and 69% of sites see an increase in the proportion broadleaf from pre-fire to post-fire (Fig. S1.4). The only sites in which fire did not increase the proportion of aspen are northern treed wetland sites and a subset of jack pine stands that had little to no aspen in the overstory (Fig. S1.3 and S1.4). Although aspen recruit successfully across most sites, some of these sites retain live overstory conifer trees, and the new pulse of aspen is subdominant to the residual living stand.

Understory vegetation communities

Although the total vegetation cover increases over time in all stand types, the composition of that cover between categories of forbs, graminoids, and shrubs varies among stand types (Fig. 5). In particular, the increase observed in mixedwood forest vascular plant cover is dominated by forbs, whereas treed wetlands see substantial increases in shrubs, particularly from three to five years post-fire (2017 to 2019). Bryophytes and lichens see similar recovery with time across all the upland sites, whereas lower burn severity and greater retention of organic soil (Table 1) lend themselves to higher preservation of bryophytes in the treed wetland sites one-year post-fire. Conversely, despite evidence of recovery through time, higher burn severities within the jack pine stands surveyed (Table 1) result in the sustained larger exposure of mineral soil as compared to other stand types. Although upland sites have similar amounts of CWD one year post-fire, mixedwood and black spruce stands, in particular, seem to accumulate CWD more rapidly in the three years post-fire period.

Table 1

Post-fire characteristics of stand types. Values indicate the median value of sites by stand type, with the range of values shown in parentheses ($n= 32$ sites total)

Environmental variable	Units	Stand type			
		Treed Wetland	Jack Pine	Mixedwood	Black Spruce
# sites	-	5	14	10	3
Burn severity index	-	2.3 (0.8-2.5)	3.2 (1.9-4)	2.6 (1.3-4)	2.7 (2.2-2.8)
Time since last fire	years	54 (15-130)	43.5 (9-130)	61 (9-101)	118 (59-151)
Pre-fire basal area	m ² ha ⁻¹	3 (0.6-12.2)	14.5 (0.02-30.1)	18.2 (0.2-53.5)	23.3 (7.8-31.6)
Overstory mortality	% stems	100 (94-100)	100 (6-100)	92.19 (38-100)	100 (31-100)
Post-fire organic soil depth	cm	10 (3.25-10)	0.5 (0-5.12)	1.6 (0-4)	3.9 (3.8-9.1)
Percent sand in mineral soil	% mass	0 (0-0)	78 (47-94)	61 (47-95)	63 (59-66)

Table 2

Abbreviations, mean, and range of significant explanatory environmental variables ($p < 0.05$) used in the detrended correspondence analysis (DCA) of understory community dissimilarities

Environmental variable	Abbreviation	Units	Mean	Range
Total carbon	TC	% mass	13.72	0.75-52.80
Site moisture	Moisture	Xeric-Hydric (converted to a numerical scale)	4.88	2-9
Post-fire organic soil depth	OSD	cm	3.37	0-13.5
pH	pH	-	6.27	3.21-8.12
Total nitrogen	Total N	% mass	0.34	0.03-1.39
Percent sand in mineral soil	% Sand	% mass	59.47	0-95
Calcium	Ca	mg kg ⁻¹	8670.31	495-54494
Basal area	BA	m ² ha ⁻¹	15.94	0-59.69
Magnesium	Mg	mg kg ⁻¹	751.04	49-4858
Sodium	Na	mg kg ⁻¹	79.53	39-205
Electrical conductivity of soil	EC	mS cm ⁻¹	0.45	0.05-2.49
Indicator of broadleaf increasing from pre-fire to post-fire	Broadleaf increase	-	0.66	0-1
Time since last fire	TSLF	years	61.38	9-151
Potassium	K	mg kg ⁻¹	335.06	105-1148
Burn severity index	BSI	-	2.75	0.77-4
Percent broadleaf	% broadleaf	% stems ha ⁻¹	45	0-100

Vegetation community dissimilarities along DCA axis 1 are primarily related to topo-edaphic characteristics distinguishing wetlands from upland sites, such as site moisture and organic soil depth (Fig. 6). As a result, treed wetland sites are most dissimilar from all other site types. Mixedwood and jack pine stands share many post-fire understory community characteristics, with intermingled trajectories of community change over time. With time, all sites tend to move down DCA axis 2, trending towards characteristics descriptive of community recovery, such as greater time since last fire (TSLF), and overstory tree basal area (BA), though also moving towards communities characteristic of drier, sandier sites. Greater community dissimilarity is observed between years three to five than in years one to three, with the greatest amount of change observed in black spruce stands.

Surface fires also display greater clustering within the ordination than canopy fires. Despite dissimilarities in vegetation community composition, the overall number of species, evenness of species, and number of unique species extinctions and colonizations tend to be similar within any given year (Fig. 7). Species evenness, in particular, converges over time, while conversely, species richness appears to be potentially diverging, with black spruce stands particularly plateauing in the number of new species observed from three to five years post-fire.

Climate and fire analysis

The majority of the study area has experienced significant increases in summer maximum temperature between 1965 and 2020. Those areas without a significant trend nonetheless have positive Theil-Sen slopes, indicating a non-significant increase in temperature (Fig. 8A). Overall, the study area has experienced an approximate increase in summer TMax of 1.1 °C since 1965, exhibiting a significant increasing trend (Fig. S1.5; $p < 0.001$). The volume of summer PPT has significantly increased in some of the northwest portions of the study area; however, the extent of these increases is more limited than the widespread temperature increases (Fig. 8B). Despite the mix of significant increases in summer PPT and non-significant trends, including some areas with decreasing precipitation, there has been a significant increase in mean summer PPT volume (Fig. S1.5; $p = 0.001$). Locations within the study area have undergone both significant increases and decreases in summer VPD. The southernmost portion of the study area has experienced the strongest trends of increasingly dry conditions; the eastern taiga shield region also demonstrated increasing evaporative demand over a large area during the observation period. Overall, the average summer VPD within the study area has significantly increased, indicating a drying trend, despite increasing summer rain inputs (Fig. S1.5; $p = 0.02$). The central portion of the study area either indicated no trends in summer VPD or decreasing trends (Fig. 8C). Furthermore, the majority of the study area underwent a significant increase in the NFFD, pointing to a lengthening of the fire season (Fig. 8D). The locations lacking significant trends in NFFD are in the south of the study area, and likely already have longer frost-free periods relative to the rest of the region. The increase in mean NFFD since 1965 consists of 11 additional frost-free days, with a significantly increasing trend throughout the study area (Fig. S1.5; $p < 0.001$).

All of the climate variables of interest were significantly correlated to the fire activity measures of the annual area burned by large (≥ 200 ha) fires, and annual number of large fires, with the exception of summer precipitation volume which did not exhibit a significant relationship to fire activity (Fig. 9). Despite the significant positive correlations with climate variables that have undergone significant changes over time, the fire activity variables did not exhibit such strong trends during this period (1965 - 2020; Fig. 9, Fig. S1.5). The annual number of large fires significantly increased by approximately 24 fires per year since 1965 (one-tailed Mann-Kendall trend test, $p = 0.03$), but the annual area burned did not demonstrate a significant trend over time (Fig. S1.5), despite being positively correlated with the number of large fires (Fig. 9).

Discussion

The heterogeneous forest stands selected for monitoring in this study yielded diverse ecological outcomes, but with a substantial reshuffling of tree species dominance compared to their pre-fire state. Although shifts in tree dominance are likely a symptom of climate-induced change (Baltzer et al. 2021), the self-replacement paradigm may also be too simplistic for our study area (Whitman et al. 2018a). Coherent with other studies in the northern boreal forest of North America, tree seedling composition appears to be reaching some equilibrium merely a few years after fire (e.g., Johnstone et al. 2004). Particularly dry conditions during the year after fire (2014 and 2015)

likely retarded seedling establishment, especially in drier sites, affecting the overall development of stands. Repeated observations demonstrate that some stands continue to experience substantial change—including tree dominance—several years after the fire. The understory species assemblages are particularly fluid and, even after the early colonizers are replaced by the more enduring species associated with mature forest stands, species turnover is likely ongoing.

Tree recruitment and dominance

Despite the differences in post-fire tree regeneration among—and within—stand types there appears to be some convergence in terms of seedling densities as “safe sites” for germination became occupied. The average rate of increase in seedling density from 2015 to 2019 was similar among stand types, except for wetlands, whose low initial recruitment reflects the sparse pre-fire tree cover and higher water tables, both factors limiting tree recruitment (Walker et al. 2020). Fire may have, in fact, improved the substrate for germination in wetlands due to the creation of suitable microsites by the fire (Benscoter et al. 2015) and thus facilitated the sudden increase in recruitment from one to three years post-fire. Delayed recruitment in black spruce-dominated stands (also the dominant tree in most wetlands) may be partly due to the slow juvenile growth of the species, which is outpaced by pines and hardwoods in early stages of stand development (LeGoff and Sirois 2004). In many of these stands, trembling aspen is absent or poorly represented prior to the fire, yet has made substantial gains and is likely to persist unless the fire-free interval is lengthy (e.g., >100 years; Johnstone et al. 2010). Surprisingly, only negligible differences in tree regeneration were observed among fire severity classes, somewhat contradicting the results in the Whitman et al. (2018b) in the same area (and using the same data) and those from other parts of the boreal biome (Johnstone and Chapin III 2006, Lecomte et al. 2006). The effect of severity is assuredly obscured, however, by the confounding effect of the unbalanced representation of stands in each severity class in the more limited dataset of the current study.

Our results provide supporting evidence for the diversity of trajectories possible in boreal forests following fire (Baltzer et al. 2021), but also show that dominance shifts can occur at different time steps in the early stages of development. While self-replacement of trees remains common, it occurs in only a slight majority of sites (as observed by Rowe and Scotter 1973); this apparent state of equilibrium may in fact be precarious and change several years after the fire. Furthermore, maintenance of compositional dominance does not preclude a change in structure, namely an opening of the tree cover (Girard et al. 2008, Buma et al. 2013). We observed stands in which the pre-fire tree species—all conifers in this study—remain poorly stocked five years after fire. Though their fate remains uncertain, they may persist as open woodlands (e.g., Arseneault 2001) or, in contrast, experience delayed recruitment and regain considerable densities (Bergeron 2000, Peters et al. 2006). An interesting case considered in this study is that of stands that have been maintained by frequent surface fires (non-lethal to large trees), analogous to some “dry” forests of the western USA. These stands constitute an underappreciated component of the landscape-fire mosaic of our study area by promoting unique compositional and structural attributes.

Development of post-fire plant communities

The succession of non-arboreal vegetation assemblages and surface cover varied considerably amongst stand types in the study area, but, unlike that of tree seedlings and saplings, appeared to diverge rather than converge through time. The legacy of pre-fire assemblages is evident in many stands as plants, notably shrubs (*Salix spp.*, *Betula spp.*, *Alnus spp.*), sucker or resprout from their burned bases. In stands where few fire “endurers” were

present prior to the fire, or where the severity of the burn prevented any carryover (e.g., as in many pine stands), early-succession species ensured early revegetation through invasion and possible seed banking. In some lightly burning fires, many vascular and nonvascular species survive, providing an alternate pathway to restoring understory vegetation cover. Despite this, we found no link between fire severity and biotic cover, as reported in other studies from western boreal forests, though this effect is minor compared to that of stand type (Hollingsworth et al. 2013, Day et al. 2017). After the 1988 wildfires of Yellowstone National Park, USA, an environment that is considered 'boreal-like', Turner et al. (1997) showed that species assemblages were affected by wildfire size and fire severity to a lesser extent than the stand location (hence, the pre-fire state of the stand) and that they reached relative equilibrium after five years. While the idiosyncratic vegetation trajectory of stands is coherent with the results of Turner et al. (1997), in our study area the proportion of plant functional types will undergo further change as stands develop.

This study provides additional support to the assertions that large wildfires of 2014 are promoting regional heterogeneity by enabling a reshuffling of biological communities. Alongside the "visible" factors associated with stand development (e.g., pre-fire vegetation, stand age, fire severity), it is likely that other processes, such as those governed by soil biota, also come into play (Day et al. 2019, Whitman et al. 2019b). Our results, for instance, suggest a rise in the prominence of 'pine mixedwood', whereby jack pine largely or entirely replaces the more usual mix of trembling aspen with white spruce or black spruce (*cf.* Macdonald and Fenniak 2007). Plant communities of black spruce-dominated stands are experiencing the greatest overall change, indicating the transformation of this stand type may not be limited to tree composition. Even though the pre-fire species assemblages of the sampled stands is largely unknown, the large, patchy wildfires of 2014 likely increased the plant diversity of the regional mosaic, by virtue of adding stand-classes that were poorly represented in the landscape prior to wildfire (Harper et al. 2005, Whitman et al. 2019a). While it is impossible to know the trajectories in which these stands will engage, it is highly likely the (ongoing) climate warming observed over the last half-century and the projected climate changes in the north—among the most pronounced in North America—will lead to increased floristic changes (Stralberg et al. 2018).

Recent climate change and fire activity

At present, the increases in precipitation within the study area appear to have kept pace with temperature increases, acting to somewhat offset the effect of increased evaporative demand on flammable vegetation (i.e., fuels), and therefore fire activity. Flannigan et al. (2016) calculated that a 15% increase in precipitation input was necessary for every 1 °C of climate warming, in order to compensate for the effect of warming temperatures on fine fuel moisture. Within the study area, which has undergone a 1.1 °C increase in maximum summer temperature since 1965, there has been a concurrent 22 mm increase in summer precipitation. Relative to an average annual precipitation of 124 mm (1961 - 1990 normals), this translates to an approximate 17% increase in summer precipitation. It is possible that the lack of a significant trend in area burned in this region, despite warming summer temperatures and lengthening fire seasons, is explained in part by summer precipitation increases.

Although precipitation inputs may have buffered the effect of temperature on fire activity at a regional scale, local patterns of moisture deficits are variable, with most of the study area either becoming increasingly dry or not demonstrating any meaningful trend. In this dry portion of the boreal biome, moisture deficits are already common, and increasing evaporative demand will likely have implications for both fire and vegetation, where they outstrip precipitation inputs. The climate conditions throughout the study area at the time of the 2014 fire

season were warm and dry but were not without historical precedent in the area (Fig. S1.5; Kotchtubajda et al. 2019). The drought conditions at the time likely interacted with convective lightning-producing storms to enable many fires to start and then, uninhibited by wet fuels, grow to a great size. If summer temperatures, fire season length, and vapour pressure deficits continue on their trajectories towards increasingly fire-conducive conditions, fire activity in this region will likely follow suit, given the significant correlations between these top-down drivers of fire activity (Flannigan et al. 2005). Increasing fire occurrence in the study region, as indicated by a positive trend in the annual number of large fires, could open boreal vegetation to change through the dual influence of severe and extensive disturbances from fire, and altered post-fire weather and climate for regenerating plants. Within our field plots, we observed increasing dominance of broadleaf tree species, which are favoured both by frequent wildfire and warmer climates (Prasad et al. 2020). Although it is plausible that the stands could eventually revert to a state similar to pre-fire conditions through succession towards long-lived conifer species, this is unlikely at a regional scale if wildfire activity increases at a rate similar to those observed elsewhere in western Canada (Hanes et al. 2019, Hart et al. 2019). The shift towards tree species and vegetation communities favoured by warmer conditions and frequent fire is likely an indicator of ongoing background changes in forest composition throughout western boreal forests (Searle and Chen 2017). Given the interacting forces of a warming and drying regional climate alongside increasing fire activity these stand-level changes are expected to be persistent, and will likely have lasting impacts on regional forest dynamics and ecosystem services (Hansen et al. 2021, Mack et al. 2021).

Limitations

The conclusions of this study are contingent on some limitations related to the sampling design, field data collection, and climate-data quality. Although an effort was made to sample the variability in terms of stand type, drainage, and fire severity, the sparseness of our dataset limited the robustness of our analyses. Similarly, a longer observation period (i.e., closer to a state of relative equilibrium) may have allowed us to refine our insights, notably with respect to the development of plant-species assemblages. Our results allow us to make some conclusions about the fate of stands, but only further monitoring can ascertain whether—and how—the changes we observed in the initial post-fire phase persist in time. This is particularly true if one considers the immense uncertainty surrounding the future of the boreal biome (Price et al. 2013). Finally, we note that, in spite of being produced from sophisticated interpolation algorithms, the climate data is based on observations from weather stations that may be hundreds of kilometers from one another, which constitutes a perennial challenge in large-scale studies in North America.

Conclusion

By measuring vegetation attributes of stands at multiple points in time, we gained insights into stand development in dry boreal forests that may be missed by looking at a single point in time, or using a space-for-time approach. The results of this study suggest that the wildfires of 2014, despite being particularly large and severe, have enhanced landscape heterogeneity. At the same time, these wildfires initiated stand-level changes in tree-species dominance and associated plant assemblages that are certain to alter ecosystem function and associated services. While the persistence of these changes is uncertain and will require further monitoring, the ongoing—and accelerating—rates of climate change make it unlikely for stands to revert to their pre-fire state due to both moisture stress on plants and associated increases in fire activity. Identifying how sensitivity to current and future conditions may determine the maintenance and persistence of vegetation communities is, therefore, a

critical aspect of promoting climate-resilient landscapes. The forests of boreal Canada have undergone some of the most significant climate warming experienced globally thus far. As such, how the climate following wildfires influences post-fire vegetation community development is a particularly important knowledge gap to fill in this dry forest region, given the interaction of wildfires with other climate-controlled northern forest disturbances (e.g., permafrost thaw, large insect outbreaks).

Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

D.A.D, M.-A.P, and E.W. contributed to the development of methods for this manuscript. D.A.D, A.V.D., and E.W. performed data analysis. D.A.D, M.-A.P, and E.W. contributed to field data collection and the preparation and writing of the manuscript. E.W. designed the initial study from which the data was used.

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Figures

Figure 1

Sampled site locations within 2014 wildfires in the Northwest Territories (NT) and Wood Buffalo National Park, in the NT and northern Alberta. The study area's relative location in Canada is outlined in red on the inset map.

Figure 2

Representative photos of site progression from one to five years post-fire. All sites pictured had been dominated by jack pine prior to fire. Sites include (from left to right) a high-severity fire recovering to a mix of jack pine and aspen, a short-interval reburn in which only aspen is regenerating, and a surface fire in which much of the overstory survived, providing an opportunity for future jack pine regeneration despite low post-fire recruitment.

Figure 3

Post-fire tree species regeneration separated by A) stand type and B) fire severity class. Points represent means across sites ($n=32$) and error bars represent standard errors. Letters separate significantly different means within each year. All letters are identical in years in which no significant difference was found among vegetation communities or fire severity at $p < 0.1$. Note that the y-axis differs within the broadleaf density plot stratified by stand type.

Figure 4

Species dominance changes with time for surveyed sites. Pre-fire species dominance indicates the overstory species with the greatest stem density prior to wildfire; subsequent measurements of species dominance indicate species with the most prevalent living seedling and sapling stem density at that year of sampling. Sites which experienced regeneration failure are denoted with an asterisk; surface fires are denoted with a diamond shape. One surface fire site had zero seedlings in 2019 and therefore has no alluvial line for the last sampling year

Figure 5

Post-fire understory vegetation cover change over time displayed by plant group and stand type. Points represent means across sites ($n=32$) and error bars represent standard errors. Letters separate significantly different means within each year. All letters are identical in years and plant groups in which no significant difference was found among vegetation communities at $p < 0.1$. Shrubs include percent cover of both short and tall shrubs (see Methods).

Figure 6

Detrended correspondence analysis (DCA) of post-fire understory plant community Bray-Curtis dissimilarities in different stand types. In plot A), normal confidence ellipses of each stand type over all years of analysis are shown, with successional vectors linking the annual centroid of each community type to describe compositional change through time. Environmental vectors are overlain for significant variables at $p < 0.05$ (variables are further

described in Table 2). Plot B) is drawn from the same ordination as plot A) but faceted to further describe the trends of sites in ordination space over time, with confidence ellipses shown for each year. Points represent individual sites ($n=32$) within the ordination space, with shape distinguishing surface and crown fires.

Figure 7

Post-fire understory species A) richness, B) evenness, and C) unique species colonization and extinctions (i.e., unique species not observed in the previous timestep) across stand types and time. Points represent means across sites ($n=32$) and error bars represent standard errors. In plots A) and B) letters separate significantly different means within each year. All letters are identical in years in which no significant difference was found at $p < 0.1$.

Figure 8

Maps of trends (1965 - 2020) in A) summer maximum temperature (TMax), B) summer precipitation (PPT), C) summer vapour pressure deficit (VPD), and D) annual number of frost-free days within the study area. Grey outlines around a point indicate significant ($p < 0.05$) trends in Sen's slope, as determined by a two-tailed Mann-Kendall trend test with a variance correction for serial autocorrelation (Hamed and Rao, 1998).

Figure 9

A) Time series of annual fire activity (1965 - 2020) as represented by area burned ($\log(\text{ha})$) and number of fires ≥ 200 ha. Area burned for low-quality fire perimeters was adjusted sensu Skakun et al. (2021). B) Spearman correlations between climate and fire-activity variables. Significant ($p \leq 0.05$) correlations are indicated with an asterisk.

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