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 recovery often governing the vegetation trajectory for decades. Here, we investigated post-fire vegetation changes in dry boreal forests of the Northwest Territories, Canada, during the first 5 years following the unusually severe 2014 wildfire season. We sampled post-fire tree regeneration and the understory plant community at 1, 3, and 5 years post-fire across different stand types within fires that burned in 2014. Post-fire trajectories of tree recruitment, understory cover by plant functional types, and plant diversity varied widely among sampled stands, as well as among years post-fire. Tree seedling density reached relative equilibrium by 3-years post-fire, whereas trends in understory plant cover and understory species assemblages suggested an ongoing change that will extend beyond 5 years of observation. In almost half of sampled stands, the composition of recruited trees differed from that of the pre-fire stand, suggesting a change in tree species dominance. An analysis of regional climate revealed 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.

Keywords Post-fire regeneration · Understory community dynamics · Repeated sampling · Boreal forest · Wildfire ecology

Introduction

Boreal systems are inherently resilient to changes in climate and fire activity (Gauthier et al. 2015; Hart et al. 2019). However, in recent decades, there is mounting evidence of accelerating shifts in tree dominance across the boreal biome, a trend that is especially pronounced across its western extent (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). As such, while recent
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 behavior through increased fire intensity (Wotton et al. 2017), while concurrently causing a deterioration of the environmental conditions necessary 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), with evidence suggesting that current and future climate-induced changes are occurring at an unprecedented rate, leading to large uncertainties in future ecological outcomes (Stralberg et al. 2018).

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 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 3 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 enable them to thrive or fail (Bergeron et al. 2002; Whitman et al. 2018a).

While classic ‘direct regeneration’ dynamics predominate across the boreal 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 spruce (Picea mariana) and white spruce (Picea 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; Baltzer et al. 2021). 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).

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 was to investigate vegetation development during the first 5 years following wildfires of the unusually severe 2014 wildfire season (Northwest Territories Environment and Natural Resources 2015) in a dry boreal forest of the Northwest Territories and northern Alberta, in northwestern Canada. Specific objectives consisted of (1) monitoring post-fire tree recruitment and tree dominance shifts from the pre-fire state, (2) evaluating changes in understory plant composition (i.e., functional types) and structure, (3) comparing the evolution of understory plant species assemblages, and (4) examining the trends in temperature and moisture availability that may have affected the 2014 wildfire season and subsequent vegetation trajectories. These objectives were achieved by sampling 32 forested sites originating from 2014 wildfires at 1, 3, and 5 years after fire across different fire severities and stand conditions.
types, as determined by pre-fire tree composition and topoedaphic characteristics.

**Methods**

**Study area**

Field sites were established in five lightning-caused fires from 2014 that burned in the Northwest Territories and northern Alberta in an area stretching from 59.7° to 62.5° latitude and −117.0° to −112.2° longitude, with the southern portion of the study area located within Wood Buffalo National Park (Fig. 1). Much of this area is flat and situated on deep, ancient marine sediment. A smaller part of the area, underlain by the rocky bedrock of the Canadian Precambrian Shield, is characterized by rolling hills. Wetlands, predominantly in the form of peatlands (peat-forming wetlands with organic layer depths ≥ 40 cm), cover approximately a third of the area (Tarnocai et al. 2011). Mean annual temperatures range from −4.3 °C in the north to −1.8 °C in the south (Ecological Stratification Working Group 1995). The mean annual precipitation in the 2015–2019 period, during which field sampling took place, ranged from 279 to 357 mm (Wang et al. 2016), making it one of the driest parts of the boreal biome of North America. 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). Although forest types are similar in composition and structure throughout the area, the dominance of conifer species increases northward at the expense of broadleaf trees.

Due to its high latitude and low vegetation productivity, there is very little agriculture and industrial forest harvesting in the area 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-renewing wildfires (Johnson 1992; Boulanger et al. 2012), the 2014 fire season was particularly severe, with drought-driven wildfires burning more than 3 million ha (Northwest Territories Environment and Natural Resources 2014).

![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.](image)

**Fig. 1** Samples 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.
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), despite burning an uncommonly large area, the 2014 wildfires considered here 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, as shown in Fig. 2.

Field methods

We established 32 field sites one year after fire (2015; as reported in Whitman et al. 2018a, 2018b) to capture an array of different forest types and burn severities (Table 1). Each site was placed in an area of homogeneous burn severity, topoedaphic setting (upland or wetland), and dominant vegetation extending ≥ 60 m in any direction and located > 100 m from roads. Some remote sites (n = 3) were accessed by helicopter. Site centers were located a minimum of 103 m from each other. Sites were subsequently resampled 3 and 5 years post-fire (2017 and 2019). We note that Whitman et al. (2018a, 2018b) initially established 52 sites in 2015; however, resampling visits were limited to forested sites (open wetland sites excluded, n = 18), and some sites that had experienced human disturbance after the initial sampling year were discarded (n = 2), resulting in the subset of 32 sites analyzed here.

In the first sampling year (2015), sample plots were 30 × 30 m, with two 30-m transects oriented in the cardinal directions and crossing at the plot center. We measured overstory composition by tree species, percent overstory mortality, stem density (stems ha⁻¹), and basal area (m² 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 center. We used semi-continuous classes for understory cover estimations: 1%, 2.5%, and increments of 5% for 5–100% cover. Vegetation cover of short
shrubs (<0.5 m tall) was assessed in the understory vegetation plots; counts and species of tall shrubs (≥0.5 m tall) that intersected the transect line were sampled along the two 30-m transects (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 that crossed the original plot center 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 35 m 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’s 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 as low (CBI 0.5–1.25), moderate (CBI >1.25–2.25), and high (CBI >2.25). We classified fires resulting in <50% overstory tree mortality in this first post-fire year (2015) as surface fires. Basal sections were collected from fire-scarred trees, or in their absence, mature dominant trees, to determine time since stand origin 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 by moisture class and species dominance into 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 the inner corners of the burn severity/seedling density subplot, with three soil cores collected at the plot center 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.

### Table 1 Post-fire characteristics of stand types

| 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    | m² 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) |

Values indicate the median value of sites by stand type, with the range of values shown in parentheses (n = 32 sites total)
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 (1) the total stem density of living seedlings and saplings, (2) the stem density of coniferous and broadleaf tree species separately, and (3) the proportion of broadleaf regeneration. 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 these metrics of regeneration, as well as 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 post hoc 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 before analysis to better visualize changes in groups with large differences in regenerating stem density. 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 after fire. Post-fire dominance was described for each sampling year as the species that was the most prevalent among post-fire seedlings and saplings. We then represented 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 that initially did not see recruitment experienced delayed regeneration of $>5000$ stems ha$^{-1}$ of the pre-fire dominant by 5-year post-fire (2019) and was thus removed from the regeneration failure group.

We examined understory vegetation communities by functional group (forbs, graminoids, shrubs), 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 detrended correspondence analysis (DCA) in the package ‘vegan’ (Oksanen et al. 2020). The DCA allowed us to measure the effects of environmental gradients, expressed here as two orthogonal axes, on each site’s understory vegetation progression through time. The inclusion of both treed wetland and upland (black spruce, jack pine, and mixedwood) site types on the ordination plot resulted in a broad first DCA axis; to confirm their inclusion did not affect the interpretation of the upland results, we also performed the analysis on only upland sites. The resulting ordination did not have disproportionate effects on our interpretation, and, as such, we display results from all site types in our ordination results. 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. Species that had been present within a site in the previous year but not found during the following year of field sampling were represented as extinctions. Conversely, colonizations were calculated as the number of unique species found within a site that had not been present at that site in the previous year of field sampling. We attributed all plants observed in the first year to colonizations.

Climate and fire analyses

To characterize trends in regional climate and fire activity, we produced multiple time series for a study...
area corresponding to the Boreal Plains, Taiga Plains, and Taiga Shield ecoregions (Ecological Stratification Working Group 1995) of the Northwest Territories and the portion of Wood Buffalo National Park that extends into the province of Alberta. We extracted all fire perimeters between 1965 and 2020 that intersected the study area from the Canadian National Fire Database (CNFDB; Natural Resources Canada 2021). 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 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 vapor pressure deficit (VPD; hPa), and annual number of frost-free days (NFFD). For each point, we calculated the Theil–Sen non-parametric 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 derived Sen’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 to account for serial autocorrelation (Ebisuzaki 1997). We used the natural logarithm of the area burned for cross-correlations. We note that, despite being produced from sophisticated interpolation algorithms, the climate data are based on observations from weather stations that may be located hundreds of kilometers from one another, which constitutes a perennial challenge in large-scale studies in North America.

**Results**

Post-fire tree regeneration

Post-fire tree recruitment was 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. 3A1). However, high rates of recruitment in treed wetlands from 2015 to 2017 and from 2015 to 2019 in black spruce (Fig. S1) resulted in these stand types achieving similar regeneration densities to mixedwood and jack pine stands by 2019. Despite high initial variability in coniferous and broadleaf regeneration stem density (Fig. 3A2–3), recruitment at each sampling year was similar across stand types, with the exception of mixedwood stands, which had higher initial recruitment of broadleaf species than other types (Fig. 3A3). The rate of coniferous and broadleaf recruitment was similar across all stand types, except for treed wetlands, which saw substantial increases in recruitment in the 2015 to 2017 period (Fig. 3A2–3). Percent broadleaf remained 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 outpaced broadleaf recruitment (Fig. 3A4). No statistical differences were observed in recruitment metrics within each sampling year by fire severity class (Fig. 3B1–4), although recruitment
density did increase within each severity class through time (Fig. 3B1–3).

Tree species dominance fluctuated considerably from pre-fire to post-fire. 53% of sites saw dominant post-fire recruitment in 2019 from the pre-fire dominant overstory species (Fig. 4). However, many sites experienced post-fire dominance shifts to competitor species within the 5-year post-fire period, particularly in a subset of sites experiencing poor establishment and even post-fire regeneration failure of the pre-fire dominant species (Fig. S2). In particular, many sites switched dominance from spruce or jack pine to trembling aspen in the 5 years following fire. This phenomenon occurred across all stand types (Fig. S3 and S4). Aspen dominance was observed in 41% of 2019 sites’ regeneration as compared to 6% of the pre-fire overstory, and 69% of sites saw an increase in the proportion broadleaf from the pre-fire overstory to post-fire recruitment (Fig. S4). The only sites in which fire did not increase the proportion of aspen were northern treed wetland sites and a subset of jack pine stands that had little to no aspen in the overstory (Fig. S3 and S4). Although aspen recruited successfully across most sites, a subset of these sites were surface fires or otherwise retained some proportion of live overstory conifer trees in which the new pulse of aspen was overtopped by the residual living trees.

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Fig. 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.
Understory vegetation communities

Although the total vegetation cover increased over time in all stand types, the composition of that cover between categories of forbs, graminoids, and shrubs varied among stand types (Fig. 5). In particular, the increase observed in mixedwood forest vascular plant cover was dominated by forbs, whereas treed wetlands saw substantial increases in shrubs, particularly from 3 to 5 years post-fire (2017 to 2019). Across all the upland sites (all stand types except treed wetland), bryophytes and lichens recovered similarly over time. In the treed wetland stands, less bryophyte and lichen cover was consumed by fire, resulting in initially higher cover amounts than in the upland stand types 1 to 3-years post-fire, until these upland sites had experienced sufficient time to recover in 2019. Exposed mineral soil cover after fire was initially highest and most sustained in jack pine stands, although amounts were statistically similar to those observed at some mixedwood sites in 2015 and 2019. Although upland sites had similar amounts of CWD one-year post-fire, mixedwood and black spruce stands, in particular, seemed to accumulate CWD more rapidly in the 3-year post-fire period (Fig. 5).

Vegetation community dissimilarities along DCA axis 1 were primarily related to topoedaphic characteristics distinguishing wetlands from upland sites, such as site moisture and organic soil depth (Fig. 6). As a result, treed wetland sites were most dissimilar from all other stand types. Mixedwood and jack pine stands shared many post-fire understory stem density at that year of sampling. Sites that 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.

Fig. 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
community characteristics, with intermingled trajectories of community change over time. With time, all sites tended to move down DCA axis 2, with community recovery most correlated to greater time since last fire (TSLF) and overstory tree basal area (BA), although also moving toward communities characteristic of drier, sandier sites. Greater community dissimilarity was observed between years 3 to 5 than in years 1 to 3, with the greatest amount of change observed in black spruce stands. Surface fires also displayed 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 tended to be similar within any given year (Fig. 7). Species evenness converged over time (Fig. 7B), while conversely, species richness appeared to be potentially diverging (Fig. 7A), with the number of new species in black spruce stands, in particular, plateauing from three to five-year post-fire. A similar number of colonizing species was observed in 2017 as in 2015, although shrinking in number between 2017 and 2019 (Fig. 7C). Substantial species turnover was apparent in all stand types, as gains in new colonizing species were also accompanied by loss.

**Fig. 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).
Climate and fire analyses

The majority of the study area experienced significant increases in summer maximum temperature between 1965 and 2020. Those areas without a significant trend nonetheless had positive Theil–Sen’s slopes, indicating a non-significant increase in temperature (Fig. 8A). On average, the entire study area experienced an approximate increase in summer TMax of 1.1°C since 1965, exhibiting a significant increasing trend (Fig. S5; \(p < 0.001\)). The volume of summer PPT significantly increased in some of the northwest portions of the study area; however, the extent of these increases was 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 was a significant overall increase in mean summer PPT volume (Fig. S5; \(p = 0.001\)). Some locations within the study area underwent both significant increases and decreases in summer VPD. The southernmost portion of the study area experienced the strongest trends of increasingly dry conditions; the northeastern portion of the
study area also demonstrated increasing evaporative demand over a large area during the observation period. Overall, the average summer VPD within the study area significantly increased, indicating a drying trend, despite increasing summer rain inputs (Fig. S5; $p = 0.02$). 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 were in the south of the study area and likely already had longer frost-free periods relative to the rest of the region. The increase in mean NFFD since 1965 consisted of 11 additional frost-free days, with a significantly increasing trend throughout the study area (Fig. S5; $p < 0.001$).

All of the climate variables of interest were significantly correlated to the fire activity measures of the annual area burned by large ($\geq 200$ ha) fires and the annual number of large fires, with the exception of summer PPT volume, which did not exhibit a significant relationship to fire activity (Fig. 9). Even considering the significant positive correlations with climate variables that underwent changes over time, the fire activity variables did not exhibit such strong trends during this period (1965–2020; Fig. 9, Fig. S5). 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. S5), despite being positively correlated with the number of large fires (Fig. 9).

### Discussion

The heterogeneous collection of 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. Our results provide further support to the idea that the self-replacement paradigm is too simplistic for our study area (Whitman et al. 2018a), as well as the observation that shifts in tree dominance are a likely outcome of climate-induced change (Baltzer et al. 2021). Coherent with other studies in the northern boreal forest of North America, tree seedling composition appeared to be reaching some equilibrium merely a few years

### 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 | 495–54,494   |
| 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        |
after fire (e.g., Johnstone et al. 2004). However, repeated observations demonstrated that some stands continued to experience substantial change—including tree dominance—several years after the fire, hinting at the possibility of a return to a stand’s pre-fire tree dominance. Post-fire understory species assemblages were particularly fluid, with evidence of ongoing species turnover and understory communities diverging with time. Climate in this region has trended toward warming and drying, with the potential to reinforce these pre- to post-fire changes and contribute to further shifts in forest stand composition.

Tree recruitment and dominance

Despite the differences in post-fire tree regeneration among—and within—stand types, the rate of seedling recruitment slowed and densities appeared to converge as microsites suitable for germination (i.e., “safe sites”) became occupied (Green 1983; Turnbull et al. 2000). The average rate of increase in seedling density from 2015 to 2019 was similar among stand types, except for wetlands, whose low initial recruitment reflected the sparse pre-fire tree cover and higher water tables of these ecosystems, both factors limiting tree recruitment (Walker et al. 2020). Fire may have, in fact, improved the

Fig. 7 Post-fire understory species A richness, B evenness, and C unique species colonization (unique species not observed in the previous timestep) and extinctions (species present in the preceding timestep but not the year displayed) across stand types and time. Points and bar heights 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
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 have been partly due to the slow juvenile growth of the species, which is outpaced by pines and broadleaf trees in early stages of stand development (LeGoff and Sirois 2004). In many of these stands that had been dominantly black spruce prior to fire, trembling aspen was absent or poorly represented in the overstory, yet made substantial gains post-disturbance and is likely to persist unless the fire-free interval is lengthy (e.g., > 100 years; Johnstone et al. 2010). Our results also suggested a rise in the prominence of ‘pine-mixedwood,’ whereby jack pine largely or entirely replaces the more usual mix of white spruce or black spruce with trembling aspen (cf. Macdonald and Fenniak 2007).

Fig. 8 Maps of trends (1965—2020) in A summer maximum temperature (TMax), B summer precipitation (PPT), C summer vapor pressure deficit (VPD), and D annual number of frost-free days within the study area. Gray 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).
Only negligible differences in tree regeneration were observed among fire severity classes. The lack of an effect of severity observed in this study contrasts with results in Whitman et al. (2018a) in the same area (and partially 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 was assuredly obscured by the unbalanced representation of each severity class resulting from the more limited dataset used here than in Whitman et al. (2018a) (Table 1), from which several sites were dropped (see Methods). Despite this, our results align with that of previous work in which stand-type effects were generally more important than fire severity to post-fire communities in this region (Day et al. 2017; Whitman et al. 2018a).

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 in the northern boreal forest, it occurred in only a slight majority of our sites (as observed by Rowe and Scotter 1973). Within this study, our observation of increasing dominance of broadleaf tree species, which are favored both by frequent wildfire and warmer climates (Prasad et al. 2020), may be an indicator of the ongoing shift in forest composition observed throughout western boreal forests (Searle and Chen 2017). We cannot discount the possibility that newfound aspen dominance in stands previously dominated by conifers is transitory and aspen may eventually be replaced by late-successional species, thereby following the typical succession observed in boreal mixedwood forests that populate more southerly boreal landscapes (Peters et al. 2006). Although it is plausible that the stands sampled here could eventually revert to a state similar to pre-fire conditions through succession toward long-lived conifer species, we posit that this is unlikely at a regional scale, if wildfire activity increases at a rate similar to that observed elsewhere in western Canada (Hanes et al. 2019; Hart et al. 2019). The dual forcing from a drying regional climate and increasing fire activity is likely to render the stand-level changes persistent with lasting impacts on regional forest dynamics and ecosystem services (Hansen et al. 2021; Mack et al. 2021).

Retention of pre-fire compositional dominance following a wildfire does not preclude a change in structure, namely an opening of the tree cover (Girard et al. 2008; Buma et al. 2013). For instance, we observed stands in which the pre-fire tree species—all conifers in this study—remained poorly stocked 5 years after fire. Although 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), as observed at one site that initially underwent a regeneration failure but subsequently saw substantial recruitment (> 5000

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**Fig. 9** A Time series of annual fire activity (1965–2020) as represented by area burned [log(ha)] and number of fires ≥ 200 ha. Area burned for low-quality fire perimeters was adjusted as in Skakun et al. (2021). B Spearman correlations between climate and fire activity variables. Significant \((p \leq 0.05)\) correlations are indicated with an asterisk.
stems ha⁻¹) of the pre-fire dominant spruce. Our study also followed the trajectory of several stands that experienced surface fires (non-lethal to most large trees), analogous to some “dry” forests of the western USA. Stands that are the outcome of one or more surface fires constitute an underappreciated component of the landscape fire mosaic of our study area and promote unique compositional and structural attributes (Heinselman 1973; Whitman et al. 2018b). Although these stands experienced limited coniferous seedling recruitment following surface fire, they differed from other, poorly stocked coniferous sites in that a sufficient overstory seed source of the pre-fire dominant species remains to provide an opportunity for future regeneration. Nonetheless, these stands may also eventually experience compositional shifts if they remain undisturbed for long timeframes, allowing the overtopped seedlings and saplings (usually aspen) to achieve site dominance over time.

There is a growing appreciation for the biotic interactions that influence post-fire stand recovery and, as such, may help explain the variation observed among stands (Evans et al. 2020). Alongside the “visible” factors associated with stand development (e.g., pre-fire structure and composition, 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). Browsing by large mammals, namely moose (Alces alces), may also have influenced our observations of forest trajectories (Conway et al. 2017; Leroux et al. 2021), although, similar to Johnstone et al. (2020), we found little indication of mammalian herbivory in our sites. Post-fire understory communities or particular species may also facilitate or impede the development of trees (Greene et al. 1999). This is often the case when a vigorous cover of ericaceous shrubs captures potential germination sites before trees can establish (Malik 2003, Fisichelli et al. 2014). Although assessing the effect of biotic interactions was beyond the scope of this study, it constitutes an important, yet understudied, area of research.

Development of post-fire plant communities

The succession of non-arboreal vegetation assemblages and surface cover varied considerably among stand types in the study area, but, unlike that of tree regeneration, appeared to diverge rather than converge through time. The legacy of pre-fire assemblages was evident in many stands as non-arboreal plants, notably shrubs (Salix spp., Betula spp., Alnus spp.), sucker or resprout from their burned bases (Stickney 1986). 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 sprouting from seed banks. In some low-intensity fires, many vascular and non-vascular species survived, providing an alternate pathway to the restoration of understory vegetation cover. The plant succession reported here followed an expected trajectory in which the incidence of novel colonizing species declined over time and species richness plateaued, as species infilled available space and used changing resources (e.g., light availability; Hart and Chen 2007; Day et al. 2017).

This study provides additional support to the assertion that large wildfires promote regional heterogeneity by enabling a reshuffling of biological communities. Even though the pre-fire species assemblages of the sampled stands was largely unknown, the large, patchy wildfires of 2014 likely increased the plant diversity of the regional mosaic, by virtue of adding stand structure and development classes (i.e., stand ages) that were poorly represented in the landscape prior to wildfire (Harper et al. 2005; Whitman et al. 2019a). The apparent homogenization of plant diversity immediately (i.e., one year) after fire, in terms of vegetation cover and understory species richness, was highly transitory as communities began diverging as a result of rapid species turnover. Although jack pine and mixedwood stands seemed to share consistently similar species assemblages, rates of turnover were similar among stand types and additional time may result in compositionally distinct understory communities (Hart and Chen 2008). A longer observation period (i.e., closer to a state of relative equilibrium) could have allowed us to refine our insights concerning the development of plant species assemblages in the study area. While it is impossible to know the trajectories these stands will follow, it is highly likely that the (ongoing) climate warming observed over the last half-century and the projected climate changes in the north—among the most pronounced in North
Recent climate change and fire activity

Despite some spatial variability, nearly ubiquitous increases in temperature throughout the study area have been accompanied by a simultaneous rise in precipitation. The study area has undergone a 1.1°C increase in maximum summer temperature since 1965, as well as a concurrent 22-mm increase in average summer precipitation. Relative to an average annual precipitation of 124 mm (1961–1990 normals), this translates to an approximate 17% increase in summer precipitation. 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. Over the last three decades, the increase in precipitation within the study area appears to have kept pace with increasing temperature, acting to somewhat offset the effect of increased evaporative demand on flammable vegetation (i.e., fuels) and therefore fire activity. 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 due in part to this increase in summer precipitation.

Although average precipitation inputs may have buffered the effect of temperature on fire activity within the study area broadly, 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, when it outstrips precipitation inputs, will likely have implications for both fire and vegetation. The climate conditions in much of 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. S5; Kochtubajda 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 vapor pressure deficits continue on their trajectories toward 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). Such changes are already ongoing in the western USA, with decreasing humidity explaining much of the increase in fire weather severity (Jain et al. 2022). Increasing fire occurrence in the study region, as indicated by a positive trend in the annual number of large fires, could catalyze boreal vegetation transformation, with fire acting to mediate climate-driven changes in vegetation community composition and function (Stevens et al. 2015; Day et al. 2020), as well as the likelihood of tree recruitment and shifts in stand structure (Coop et al. 2020).

Conclusion

By measuring vegetation attributes of forest stands at multiple points in time, we gained insights into stand development in dry boreal forests that may be missed through single one-time sampling or using a space-for-time approach. The results of this study suggest that the wildfires of 2014, while being particularly large and severe, have also 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. The forests of boreal Canada have undergone some of the most significant climate warming experienced globally during the last half-century. As such, identifying how sensitivity to current and future conditions may influence the generation and persistence of vegetation communities post-disturbance is a critical aspect of promoting climate resiliency within this region.

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**Declarations**

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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