ARTICLE

The influence of postfire recovery and environmental conditions on boreal vegetation

Alexis Gardiner Jorgensen[1] | Raquel Alfaro-Sánchez[1,2] | Steven G. Cumming[3] | Alison L. White[1,4] | Geneviève Éliane Degré-Timmons[1,3] | Nicola Day[1,5] | Merritt Turetsky[6] | Jill F. Johnstone[7] | Xanthe J. Walker[8] | Jennifer L. Baltzer[1]

[1]Department of Biology, Wilfrid Laurier University, Waterloo, Ontario, Canada

[2]Department of Agroforestry Technology and Science and Genetics, School of Advanced Agricultural and Forestry Engineering, University of Castilla La Mancha, Campus Universitario, Albacete, Spain

[3]Department of Wood and Forest Sciences, Laval University, Québec, Québec, Canada

[4]Ministry of Natural Resources and Forestry, Peterborough, Ontario, Canada

[5]School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand

[6]Institute of Arctic and Alpine Research, Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, Colorado, USA

[7]Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

[8]Department of Biological Sciences, Northern Arizona University, Center for Ecosystem Science and Society, Flagstaff, Arizona, USA

Correspondence
Alexis Gardiner Jorgensen
Email: alexis.jorgensen27@gmail.com

Abstract

Climate change is increasing the frequency and extent of fires in the boreal biome of North America. These changes can alter the recovery of both canopy and understory vegetation. There is uncertainty about plant and lichen recovery patterns following fire, and how they are mediated by environmental conditions. Here, we aim to address these knowledge gaps by studying patterns of postfire vegetation recovery at the community and individual species level over the first 100+ years following fire. Data from vegetation surveys collected from 581 plots in the Northwest Territories, Canada, ranging from 1 to 275 years postfire, were used to assess the influence of time after fire and local environmental conditions on plant community composition and to model trends in the relative abundance of several common plant and lichen species. Time after fire significantly influenced vegetation community composition and interacted with local environmental conditions, particularly soil moisture. Soil moisture individually (in the absence of interactions) was the most commonly significant variable in plant and lichen recovery models. Patterns of postfire recovery varied greatly among species. Our results provide novel information on plant community recovery after fire and highlight the importance of soil moisture to local vegetation patterns. They will aid northern communities and land

managers to anticipate the impacts of increased fire activity on both local vegetation and the wildlife that relies on it.

INTRODUCTION

Climate change is causing more widespread and frequent fires in the boreal biome of North America (Kasischke & Turetsky, 2006; Veraverbeke et al., 2017). Both the number of ignitions and annual area burned in boreal North America have increased significantly since the 1960s, particularly in western regions, and these trends are expected to continue (Kasischke & Turetsky, 2006; Kochtubajda et al., 2006; Veraverbeke et al., 2017). Although boreal forest vegetation is well adapted to the historic fire regime, there is some uncertainty about how these systems, and the species that inhabit them, will respond to the increased fire activity predicted under climate change.

Fire is the main disturbance agent in the boreal forest, initiating cycles of secondary succession, driving vegetation dynamics, and significantly influencing carbon and nutrient cycling (Simard et al., 2001; Walker, Rogers, et al., 2018; Ward et al., 2014), abiotic and biotic soil conditions (Day et al., 2019; Holden et al., 2016; Simard et al., 2001), and local permafrost thaw (Gibson et al., 2018; Holloway et al., 2020). Both overstory and understory plants are well adapted to fire disturbance, employing a variety of strategies for survival or recolonization (Hollingsworth et al., 2013; Markham & Essery, 2015; Viereck, 1982, 1983; Walker, Baltzer, et al., 2018). Vegetation recovery patterns following fire are influenced by fire severity, which is defined here as the proportion of the soil organic layer (SOL) combusted (Day et al., 2020; Hollingsworth et al., 2013; Schimmel & Granström, 1996). Low-severity fires tend to favor plants that resprout from underground structures or survive the disturbance in residual patches (Day et al., 2020; Hollingsworth et al., 2013). High-severity fires favor species regenerating from seed, either from the local seedbank or by dispersal from more distant sources. More severe fires also favor plants that are competitive on thin organic layers or bare mineral soil (Day et al., 2020; Hollingsworth et al., 2013; Schimmel & Granström, 1996).

In the boreal forests of North America, fire severity is regulated by soil moisture, with complete combustion of organic soils generally limited to dry sites (Hollingsworth et al., 2013; Kane et al., 2007; Walker, Baltzer, et al., 2018). This, in turn, influences site resilience, defined as the ability of an area to recover to a similar vegetation community after disturbance, which tends to be more common on wetter sites or after lower severity burns (Day et al., 2020; Johnstone et al., 2016). Soil moisture also directly influences both overstory and understory vegetation community in the boreal forest, highlighting the importance of local environmental conditions on plant community composition and structure (Day et al., 2020; Echiverri & Macdonald, 2019; Hollingsworth et al., 2013; Taylor & Chen, 2011). A range of other environmental conditions such as the presence of ground ice, which influences soil temperature, water availability, and site structure (Connon et al., 2014; Osterkamp et al., 2000; Young-Robertson et al., 2017), and active layer depth, which influences plant productivity and site drainage (Anderson et al., 2020), are also expected to impact boreal vegetation. However, the comparative influence that such variables have on both individual boreal species and full vegetation community is not well understood.

Establishment of both trees and understory vegetation occurs rapidly following fire in boreal forests, setting the long-term successional trajectory of the site within the first few years (Black & Bliss, 1978; Day et al., 2017; Johnstone et al., 2020; Kurkowski et al., 2008). However, there is limited information about the recovery patterns of boreal plant species over the long term and how environmental conditions mediate such recovery. In particular, temporal patterns of abundance, biomass, or cover postfire are known for few if any understory species (though see Greuel et al., 2021). Systematic changes to site conditions over time, such as overstory canopy closure, will influence understory composition by reducing or eliminating shade-intolerant plants (e.g., fireweed; *Chamaenerion angustifolium* (L.) Scop.), while the abundance of other species (e.g., *Empetrum nigrum* L.) tends to increase as the site matures (Black & Bliss, 1978; Hart & Chen, 2006; Lieffers & Stadt, 1994). In general, both the richness and abundance of vascular plants tend to increase rapidly over the first few years following fire, then decrease more gradually over time due to reductions in light, soil nutrients, and pH (Hart & Chen, 2006; Routh & Nielsen, 2021). It is uncertain how increasing fire due to climate change will influence such processes, with implications for the structure and composition of boreal plant communities.

Previous research has suggested that increased fire frequency and severity combined with drier conditions are likely to lead to higher levels of deciduous and grassland cover over time, as well as reductions in spruce (*Picea* spp.) across the landscape (Baltzer et al., 2021; Barber et al., 2018; Hart et al., 2019; Mack et al., 2008). Reindeer lichen (primarily of genus *Cladonia* spp.) are also likely to decrease in abundance with more frequent burning, as these species can take upwards of 30–81 years to recover to prefire biomass depending on the geographic region and local site conditions (Greuel et al., 2021). Such general predictions of vegetation change under the altered fire regime are valuable, but we believe a more quantitative approach, examining specific species under differing environmental conditions, is also needed to help anticipate the impacts of increasing fire activity on boreal vegetation.

We quantified vegetation recovery patterns in two ecoregions of the Northwest Territories (NWT), Canada, following wildfire considering both full vegetation community and individual species or species groups. Vegetation data from a chronosequence of burn sites ranging from 1 to 275 years postfire were used to address the following questions:

1. What are the patterns of vegetation recovery after fire for both full plant community composition and common individual plant and lichen species?
2. How are such recovery patterns mediated by environmental factors?

Though we anticipate variation among individual plant and lichen species, in general we expect that recovery patterns will reflect the trends noted above, with spruce and lichen recovering slowly after fire while graminoids and deciduous species increase more rapidly but potentially decline in abundance over time.

METHODS

Study area

The study area includes parts of the Taiga Plains (hereafter, Plains) and Taiga Shield (hereafter, Shield) ecological regions of the NWT (Government of the Northwest Territories, 2008, 2009) and encompasses the Tłı̨chǫ and Sahtú settlement areas, as well as Dehcho and Akaitcho unsettled traditional territories. The Plains covers most of the central NWT and extends from the southern border of the territory (~60° N) to north of Inuvik (68°21′ N). This region is characterized by relatively flat topography with rolling hills and extensive peatlands. Black and white spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb and *P. glauca* (Moench) Voss) forests are the dominant cover for the Plains. However, forests dominated by paper birch (*Betula neoalaskana* Sarg. or *Betula papyrifera* Marshall) and trembling aspen (*Populus tremuloides* Michx.) are scattered throughout the region and relatively species-rich, mixed-wood stands including white or black spruce, aspen, and/or paper birch are common in warmer southern areas. Jack pine (*Pinus banksiana* Lamb.) stands also occur below ~66° N in well-drained locations. The Shield covers much of the eastern half of the NWT, and runs from the NWT–Saskatchewan border, north to the western shore of Great Bear Lake (66°11′ N). The Shield is characterized by extensive areas of eroded bedrock, often either exposed or covered by glacial till, eskers, outwash, or lacustrine deposits. Black and white spruce forests are also the dominant cover for this region, though the Shield contains extensive areas of pure aspen and paper birch. In addition, both jack pine and mixed-wood stands, which may include any of these species, do occur, particularly further south. Both the Plains and Shield experience long cold winters and short summers, limiting tree growth, and cover extensive areas of discontinuous permafrost (average temperature: −2.5°C in the Plains [Hay River] and −4.3°C in the Shield [Yellowknife; Environment and Climate Change Canada, 2013a, 2013b]).

Field sampling

In the summers of 2015–2018, 580 plots were established within 237 sampling sites in burn scars ranging from 1 to 50 years postfire and in areas with no recorded fire history (>50 years postfire) located from 60°34′ N to 65°53′ N (Figure 1). Multiple sampling sites were established within most burn scars for practicality. However, burn scars generally covered wide geographic areas and were often formed by multiple fires that coalesced into large fire complexes. Because of this, burn scars tended to represent a mosaic of burn date and severity. For new burns (2014 fire season), sites were selected using a stratified random sampling approach, with a set of random points generated within different density strata (low-, medium-, and high-density conifer) and leading species class (black spruce or jack pine) available within each burn scar using the Land Cover Map of Canada 2005 (LCC05; Latifovic et al., 2008; see Walker, Baltzer, et al., 2018, for more detail). Points were constrained to within 1 km of a road or shoreline for accessibility. For burns prior to 2014, the land cover classes listed above, as well as other dominant land cover types such as shrub- and herb-dominated areas, wetlands, and mixed-wood forests, were sampled in proportion to their abundance within each burn scar, though
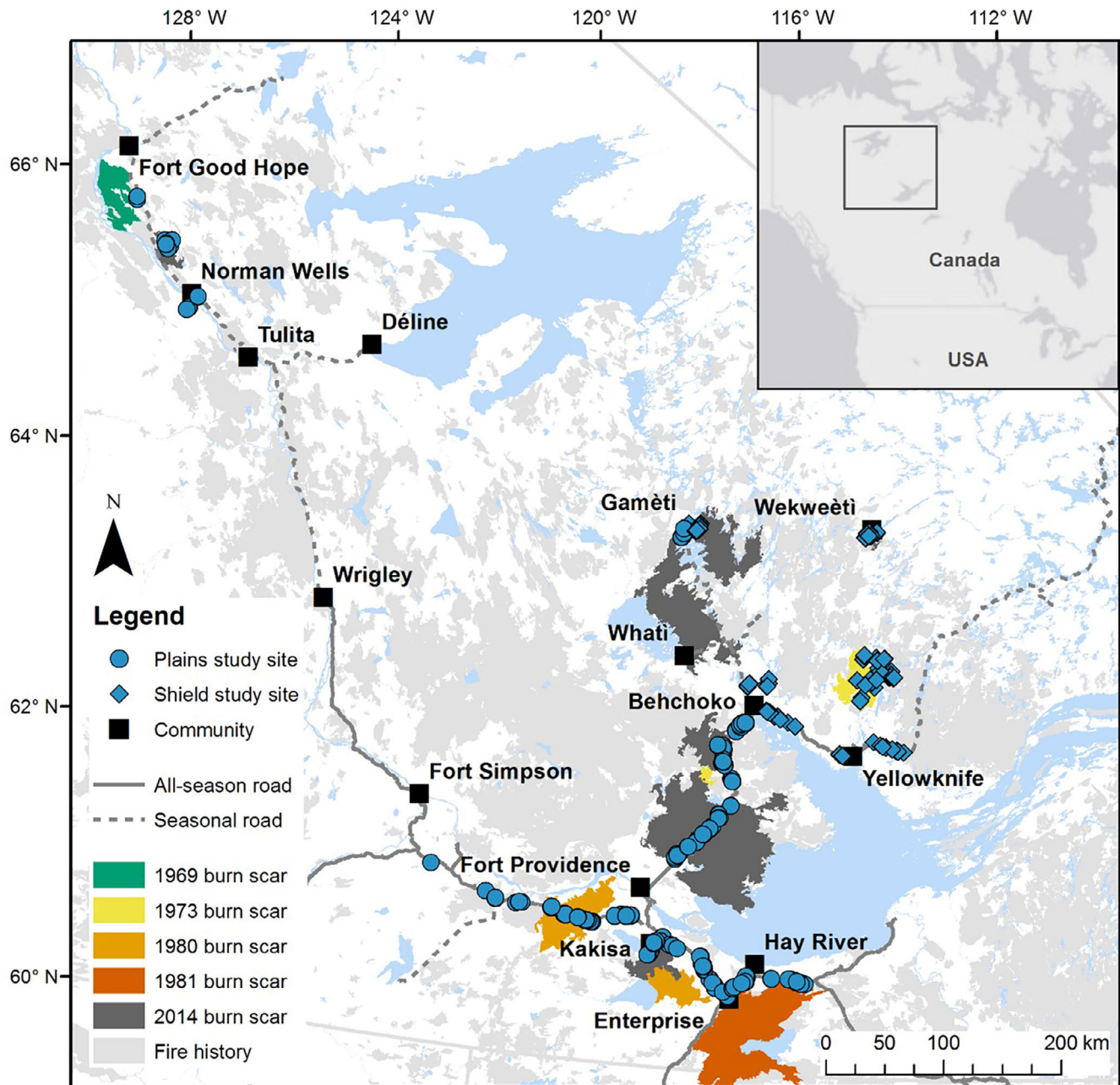
FIGURE 1 Locations of sampling sites ($n = 237$) and sampled burn scars ($n = 41$) of different ages in the Northwest Territories, Canada. Inset shows the location of the study area in North America.

coniferous strata remained the most common (see Day et al., 2020). Sites with no recorded fire history were chosen to represent the prefire conditions of burn areas. These sites were spatially paired with a local burn that shared approximately the same slope, aspect, and tree cover to the prefire conditions of 2014 burned areas.

During plot establishment, a goal was to capture the full range of soil moisture conditions proximal to each random location (Day et al., 2020; Walker, Baltzer, et al., 2018). As such, nests of plots were established at each site. Upon locating a random sampling point, soil moisture was

classified on a six-step scale from xeric to subhygric according to Johnstone et al. (2008), though was reclassified into dry (xeric and subxeric), mesic (subxeric to mesic and mesic), and wet (mesic to subhygric and subhygric) categories prior to analysis. One or usually two additional plots encompassing different moisture classes were then established within 500 m of the original plot, and no less than 100 m apart. These three plots made up a single sampling site. Each plot had an area of 60 m² and was comprised of two parallel 30-m transects running from south to north positioned 2 m apart.

To assess ground cover and vegetation, 1-m² quadrats were established at 0, 6, 12, 18, and 24 m along the east transect. All species of vascular plants within each quadrat were identified and recorded as present/absent. Each species was then assigned a relative abundance from 0 to 5 per plot, defined as the number of quadrats within the plot in which it occurred. All tree seedlings/saplings <1.3 m tall within each quadrat were counted and identified to the species level. In addition, percent cover of nonvascular plant and lichen functional groups was recorded (e.g., acrocarpus moss, feathermoss, *Sphagnum* spp., reindeer lichen, liverworts, *Ceratodon*/*Pohlia* spp.). Reindeer lichen refers to terricolous lichens belonging to the genus *Cladonia* spp., including *Cladonia mitis*/*arbuscula*, *C. rangiferina*/*stygia*, *C. stellaris*, and *C. uncialis* (see Greuel et al., 2021, for more details). Percent cover values were converted to relative abundance (presence in 0–5 quadrats per plot) prior to analysis for consistency with vascular plant data.

The depth of the SOL (depth to the organic–mineral interface or depth to frozen ground or ice) was measured adjacent to each vegetation quadrat in small soil pits or with soil cores. A 2-m steel rod was used in the same locations to determine the soil permeability depth (SPD), defined as the depth to rock, ice, frozen ground, or gravel. The mean values of each SPD and SOL depth per plot were then calculated. All rooted trees and shrubs ≥1.3 m tall within each plot, both living and dead, were counted and used to calculate stem density.

Determining time after fire

The age of young plots (<5 years since fire) was known from fire history records as they were established within a few years of burning. Stand age was used as time after fire for all plots other than those in the 2014 burns, as most fires in boreal North America are stand replacing and trees tend to establish rapidly postfire (Greene & Johnson, 1999; Viereck, 1983). To determine stand age, cores or basal cookies were taken just above the root collar from five trees of the (co)dominant conifer species within each plot, representing the dominant size class. Samples were sanded with increasingly finer grits before being scanned to a resolution of 4800 dpi and their rings counted using dendrochronology software (see Walker, Baltzer, et al., 2018, for more details).

Individual plant and lichen species selection

Selection of individual species and species groups for modeling was based on their value as wildlife forage, as there are community and government concerns about wildfire impacts on wildlife forage availability. The individual species analyzed in this research represent a range of common species in boreal North America including trees, shrubs, graminoids, forbs, and lichens.

Statistical analyses

Statistical analyses were conducted in R 3.6.1 (R Core Team, 2019) and graphs were made with package ggplot2 (Wickham, 2016). Data from the Shield and Plains were separated for all analyses because of the distinct environmental conditions that the vegetation in these regions is exposed to, resulting in compositional differences (Day et al., 2020).

Influence of time after fire and environmental variables on full plant community

To assess similarities and differences in plant community composition among plots, the vegan package (Oksanen et al., 2019) was used to perform principal coordinates analysis (PCoA) on species presence/absence data using Jaccard distance as the dissimilarity metric. We defined "plant community" as all overstory and understory vascular plants, along with understory moss, liverwort, and lichen groups (e.g., feathermoss, reindeer lichens). Ordinations used the full range of plot ages from 1 to 275 years after fire. Use of all plots for PCoAs was deemed appropriate even though there were limited data over certain age ranges, as ordinations simply visualize similarities/differences in plots, rather than attempting to infer trends over certain poorly sampled age ranges.

We identified seven covariates expected to be associated with plant community composition (Appendix S1): time after fire (years), soil moisture class (dry, mesic, wet), average growing degree-days (number of days), SOL depth (in centimeters), SPD (in centimeters), stem density (in stems per square meter—trees and selected shrubs), and the presence or absence of ground ice (binary factor). As soil moisture can influence fire severity and, consequently, site resilience (Day et al., 2020; Johnstone et al., 2016), the interaction between time after fire and soil moisture class was included (Walker, Baltzer, et al., 2018; Walker et al., 2017). The presence/absence of ground ice was hypothesized to influence plant recovery following fire due to the contribution of permafrost and seasonal ice to site structure, hydrology, and soil temperature, so the interaction between time after fire and presence/absence of near-surface ground ice was also

included (Connon et al., 2014; Osterkamp et al., 2000; Young-Robertson et al., 2017). Average growing degree-days were calculated as the number of days exceeding 5°C for the full 24 h annually averaged over a 30-year period (1980–2010) using gridded data from Climate North America (Wang et al., 2016).

We assessed the importance of our predictor variables (time after fire, average growing degree-days, organic soil depth, SPD, stem density, soil moisture, presence/absence of ground ice) on vegetation community composition using permutational multivariate analysis of variance (PERMANOVA), specifying Jaccard distances as the dissimilarity measure on species presence/absence. A species was considered present if it occurred in at least one of the five vegetation quadrats for each sampling plot. p values were estimated from 999 permutations using the function adonis in package vegan (Oksanen et al., 2019). Permutations were restricted within study sites to account for spatial autocorrelation due to the nested sampling design (2–3 plots nested within each site).

Influence of time after fire and environmental variables on individual species

To assess the influence of time after fire and other environmental variables on the relative abundance of individual plant and lichen species, 24 generalized linear mixed effects models (GLMMs) of individual species or species groups (e.g., sedges) were developed using the glmmTMB package (Brooks et al., 2017): 14 for the Plains and 10 for the Shield. Site was used as a random effect in all models to account for the nested structure of our data. Data were filtered to exclude plots older than 130 and 100 years for the Plains and Shield, respectively, as data availability was limited above these ages. The use of generalized additive mixed effects models or splines was considered to model trends more complicated than a logistic curve. However, model fit was notably worse for these techniques than for the logistic GLMMs.

We modeled the probability of species occurrence at the plot level using the binomial error family and logit link function. The observational data were coded as the numbers of quadrats where the species was present per plot (0–5). Probability of occurrence versus probability of absence (adding to 1) was the binomial response variable. Count models were also fit for paper birch, trembling aspen, and black spruce seedlings/saplings. The dependent variable was the number of seedlings and saplings <1.3 m tall per plot, calculated as the sum of quadrat-level counts. Models using both the Poisson and negative binomial families were fit to the count data and compared in terms of Akaike information criterion (AIC). Package DHARMa

(Hartig, 2020) was used to evaluate the suitability of model family and test for zero inflation. The negative binomial family can be used to correct overdispersion in Poisson models (Zuur, 2009), and was ultimately chosen for all seedling/sapling counts as the negative binomial models had lower AIC scores and less zero inflation.

We initially assessed the distribution of model covariates using R base function qqnorm(). As all appeared to violate the assumption of normality, Kendall's Tau was used to quantify pairwise correlations. Pairs with correlations of 0.5 or greater were considered overly collinear (as suggested by Zuur, 2009). In the Plains, no correlation scores exceeded this threshold, so all covariates (time after fire, average growing degree-days, organic soil depth, SPD, stem density, soil moisture, presence/absence of ground ice) and the interactions between the presence/absence of ground ice and soil moisture with time after fire were included in models. On the Shield, only time after fire, average growing degree-days, stem density, soil moisture, and the interaction of soil moisture with time after fire were included.

To determine influential variables for each species, manual backwards stepwise elimination was performed on all models until the AIC was minimized. At each step, function check_model() in package performance (Lüdecke et al., 2020) was used to estimate the variance inflation factor (VIF) for each covariate and to assess the normality of random effects. Variables with a VIF of 5 or greater were considered overly collinear and the variable among these having the highest VIF was dropped. For all models, marginal R^2 was used as an estimate of percent variation explained by fixed effects and conditional R^2 as percent variation explained by the entire model. Due to the large number of tests performed on a single dataset, a Bonferroni correction was applied to account for type I error inflation (Cabin & Mitchell, 2000). The Bonferroni-corrected critical values were estimated as $\alpha = 0.05/10 = 0.005$ for the Shield, and $\alpha = 0.05/14 = 0.0036$ for the Plains.

RESULTS

Caveat regarding study data

Though sampling site selection (using GPS layers) was intended to cover a full range of ages from 1-year postfire to mature forest for this project, tree ring analysis indicated that none of our plots fell between 5 and 30 years after fire. This may be partially due to the fact that earlier research involving this dataset focused on sampling sites where lichen species of interest were expected to occur (see Greuel et al., 2021, for more details). However, the amount of early and later successional data used for this analysis still offers useful insights into general recovery patterns and the

influence of environmental conditions on both full plant community and individual plant and lichen species.

Full plant community

A total of 233 species (and nonvascular functional groups) were found on the Plains and 116 on the Shield. After removal of rare species and those causing anomalies (e.g., plants that could only be identified to the genus level in the first few years after fire, but to the species in older plots leading to greater apparent separation in vegetation communities over time than likely existed), 148 and 80 species were used for analyses in the Plains and Shield, respectively. The first two axes of the PCoAs explained 21.2% of total variation in plant community composition on the Plains, and 28.7% on the Shield (Figure 2). The Shield plot displayed an arch that proved difficult to remove through data transformations and the use of different distance measures. This suggests that the arch may be due to a significant gradient in species richness across Shield plots (Podani & Miklós, 2002), likely driven by the fairly distinct plant communities in wetland versus nonwetland locations, and is not a concern for our ordinations. In both the Plains and the Shield, very young plots (1–4 years after fire) clearly separate from the rest, but there was substantial mixing across the remaining range of time after fire. Although the identities of the species vary, lichens, feathermoss, and *Acrocarpus* mosses were strongly associated with longer times after fire in both regions. Fire moss (*Ceratodon/Pohlia* spp.) and forbs were associated with younger plots. Grasses and broadleaved trees/shrubs such as aspen also tended to be more strongly associated with recent fires than older areas. In terms of moisture, jack pine, deciduous trees (paper birch, aspen), and various forbs and shrubs (e.g., bearberry, *Arctostaphylos uva-ursi* (L.) Spreng.; corydalis, *Corydalis* spp.) tended to be associated with dry plots, and wet plots with Labrador tea (*Rhododendron groenlandicum* (Oeder) K.A. Kron & W.S. Judd), horsetails (*Equisetum* spp.), sedges (*Cyperaceae* spp.), and peatmoss (*Sphagnum* spp.), among others. Ordination plots colored by moisture class can be found in Appendix S2.

PERMANOVA results indicated that all predictor variables and the interaction of time after fire and soil moisture explained a significant amount of variation in vegetation community composition on the Plains, while the interaction between time after fire and presence/absence of ground ice was not significant (Table 1). On the Shield, all predictors and interactions explained a significant amount of variation (Table 2). Time after fire explained the most variation in plant community composition in both the Plains and the Shield. Soil moisture was also important; on the Plains, it explained 6% of variation, and on the Shield, it explained approximately the same amount of variation as time after fire (11%), followed by growing degree-days (5%).

Individual species

Time after fire and/or an interaction between time after fire and soil moisture significantly influenced the

TABLE 1 Results from permutational multivariate analysis of variance to test the variation explained by predictor variables on plant community composition in the Taiga Plains ecoregion of the Northwest Territories, Canada.[a]

Variable	Variation explained (%)	df	SS	MS	Pseudo F	p
Time after fire	11.3	1	0.184	0.184	53.0	**0.001**
Moisture class	6.7	1	0.109	0.109	31.4	**0.001**
Growing degree-days	3.6	1	0.059	0.059	17.1	**0.001**
Stem density	3.4	1	0.055	0.055	15.8	**0.001**
Soil permeability depth	2.1	1	0.034	0.034	9.8	**0.02**
Organic soil depth	1.1	1	0.018	0.018	5.3	**0.029**
Pres/abs ground ice	0.7	1	0.012	0.012	3.4	**0.031**
Time after fire × moisture class	0.5	1	0.008	0.008	2.4	**0.002**
Time after fire × pres/abs ground ice	0.2	1	0.003	0.003	1.0	0.546
Residuals	70.3	330	1.147	0.003		
Total	100	339	1.631			

Note: Bold values indicate that the predictor variable has a significant influence on vegetation community composition (α < 0.05).
Abbreviation: MS, mean squares.
[a]Nine hundred and ninety-nine permutations were performed on a distance matrix of species presence/absence (pres/abs) data using Jaccard distance—permutations restricted within study site (α = 0.05).
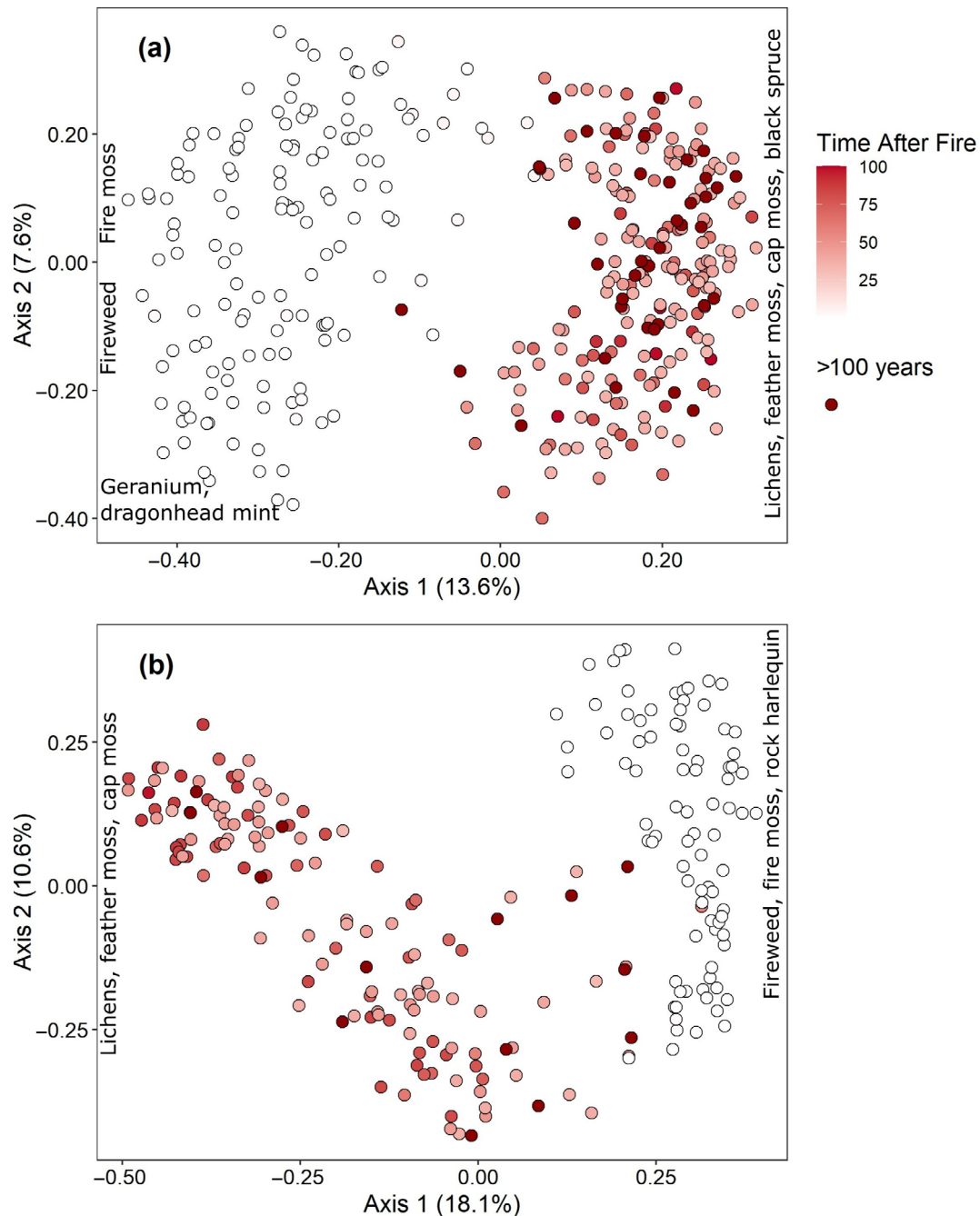
FIGURE 2 Plot scores for principal coordinates analysis of plant community composition based on species presence/absence data using Jaccard distance in (a) the Taiga Plains and (b) the Taiga Shield ecoregions of the Northwest Territories, Canada. White points indicate plots where time after fire is <5 years. Plots cover a total range of 1–275 years after fire. Species names indicate notable species with relatively high loadings in the area they are located: fireweed, *Chamaenerion angustifolium*; fire moss, *Ceratodon/Pohlia* spp.; cap moss, *Acrocarpus* spp.; geranium, *Geranium bicknellii*; dragonhead mint, *Dracocephalum parviflorum*; black spruce, *Picea mariana*; rock harlequin, *Corydalis sempervirens*. Values in brackets indicate the proportion of total variation in plant community explained by each axis.

probability of occurrence for most species modeled (18 of 24 models, 75%; Table 3). However, the strength and direction of these effects varied greatly among species (Figure 3), with birch, aspen, and grasses (*Poaceae* spp.) tending to decrease with time after fire while most others increased at varying rates. In addition, all seedling/sapling count models indicated decreasing abundance over time after fire (Figure 4). Soil moisture mediated the rate and shape of abundance changes over time after fire for several species, most commonly either speeding the rate that abundance increased or switching the direction of abundance change over time in wetter areas

TABLE 2 Results from permutational multivariate analysis of variance to test the variation explained by predictor variables on plant community composition in the Taiga Shield ecoregion of the Northwest Territories, Canada.[a]

Variable	Variation explained (%)	df	SS	MS	Pseudo F	p
Time after fire	11.3	1	7.2	7.2	36.0	**0.001**
Moisture class	11.1	1	7.0	7.0	35.2	**0.001**
Growing degree-days	5.0	1	3.2	3.2	16.0	**0.001**
Soil permeability depth	3.0	1	1.9	1.9	9.4	**0.001**
Stem density	1.8	1	1.1	1.1	5.7	**0.001**
Time after fire × moisture class	1.8	1	1.1	1.1	5.6	**0.001**
Organic soil depth	1.7	1	1.1	1.1	5.3	**0.001**
Pres/abs ground ice	0.7	1	0.5	0.5	2.4	**0.037**
Time after fire × pres/abs ground ice	0.7	1	0.4	0.4	2.1	**0.037**
Residuals	63.0	200	39.8	0.2		
Total	100	209	63.1			

Note: Bold values indicate that the predictor variable has a significant influence on vegetation community composition (α < 0.05).
Abbreviation: MS, mean squares.
[a]Nine hundred and ninety-nine permutations were performed on a distance matrix of species presence/absence (pres/abs) data using Jaccard distance—permutations restricted within study site (α = 0.05).

(Figure 5). In addition, soil moisture class independently was the most commonly significant variable over all models (67% of models) followed by stem density (54%; Table 3). The amount of variation in probability of occurrence explained by each model varied greatly by both species and ecoregion (marginal R^2 ranging from 0.108 to 0.687, conditional R^2 from 0.275 to 0.882; Appendix S3).

DISCUSSION

In general, our results indicate that, while time after fire is an important driver of boreal plant community composition and abundance, local environmental conditions, particularly soil moisture, are also highly influential. Time after fire had a significant influence on both full vegetation community and most of the individual species examined. However, no clear successional patterns in vegetation community composition were identifiable after the first few years following fire, suggesting that environmental variation can mask autogenic changes in community composition over time. The pattern and speed of vegetation recovery, in terms of abundance on site over time after fire, varied greatly by species and was often mediated by soil moisture. Soil moisture itself was one of the most influential variables for both plant community composition and individual species occurrence following fire, emphasizing the importance of environmental conditions on boreal vegetation recovery and composition. Our results provide information on recovery patterns and the influence of fire and a range of environmental variables on both common boreal plant and lichen species and vegetation community composition in the northwestern boreal forests of North America. They also add support to previous literature describing the influence of fire and moisture on boreal plant community (Day et al., 2020; Echiverri & Macdonald, 2019; Johnstone et al., 2020).

Influence of time after fire and environmental conditions on plant community

PCoAs displayed clear compositional differences between recent burns (1–4 years post-fire) and older burns, but no other trends in plant community over time after fire were evident. Recent burns tended to be associated with fire moss as well as fast-growing forbs such as fireweed, grasses, and deciduous species such as paper birch and aspen/poplar (*Populus* spp.), consistent with previous research (Black & Bliss, 1978; Hammond et al., 2019; Markham & Essery, 2015). The separation between the recent burns and more mature stands captures the large difference in plant communities dominated by fast-growing or short-lived species in the first few years following fire. Immediately after fire, young stands are more likely to have higher light availability due to changes in canopy structure and density and abundant exposed soil, creating favorable conditions for species establishment (Hart & Chen, 2006). Within a few years, vegetation will recolonize areas left bare, and plants will start competing for space and light, to the detriment of sun-loving species such as fireweed and bluejoint (*Calamagrostis canadensis* (Michx.) P. Beauv),

TABLE 3　Summary of output from generalized linear mixed effects models of the probability of species occurrence or seedlings/sapling counts over time after fire in the Taiga Plains and Taiga Shield ecoregions of the Northwest Territories, Canada (for full model results, see Appendix S3).

| Species	Time after fire	Soil moisture	Stem density	Growing degree-days	SOL depth	SPD	Pres/abs ground ice	Fire × moisture	Fire × ice
Plains									
Trees									
Picea mariana	POS	ns	ns	ns	ns	ns	POS	POS	NEG
Populus tremuloides	NEG	NEG	ns	ns	ns	ns	ns	ns	ns
Tree seedlings/saplings									
Picea mariana	ns	ns	ns	ns	ns	ns	ns	ns	ns
Populus tremuloides	NEG	ns	ns	ns	ns	ns	ns	ns	ns
Shrubs									
Betula spp.	ns	POS	POS	ns	ns	POS	ns	NEG	ns
Salix spp.	POS	POS	POS	ns	ns	POS	ns	ns	ns
Shepherdia canadensis	POS	NEG	ns	POS	ns	ns	ns	ns	ns
Vaccinium uliginosum	ns	POS	ns	NEG	ns	ns	ns	ns	ns
Vaccinium vitis-idaea	POS	POS	NEG	NEG	ns	ns	ns	POS	NEG
Graminoids									
Cyperaceae spp.	POS	POS	POS	ns	ns	POS	ns	NEG	ns
Poaceae spp.	ns	ns	NEG	ns	ns	ns	ns	ns	NEG
Calamagrostis spp.	NEG	POS	ns	NEG	ns	ns	ns	ns	ns
Forbs									
Equisetum spp.	ns	POS	POS	ns	ns	POS	ns	VAR	ns
Nonvasculars									
Reindeer lichen	POS	ns	ns	ns	ns	ns	ns	ns	ns
Shield									
Trees									
Picea mariana	POS	POS	POS	ns	x	x	x	POS	x
Tree seedlings/saplings									
Picea mariana	NEG	POS	ns	ns	x	x	x	ns	x
Betula papyrifera	NEG	NEG	ns	ns	x	x	x	ns	x
Shrubs									
Alnus crispa	ns	ns	POS	ns	x	x	x	ns	x
Betula spp.	NEG	ns	POS	ns	x	x	x	ns	x
Salix spp.		POS	ns	ns	x	x	x	ns	x
Vaccinium vitis-idaea	ns	POS	POS	ns	x	x	x	ns	x
Graminoids									
Poaceae spp.	ns	ns	POS	ns	x	x	x	NEG	x
Forbs									
Equisetum spp.	ns	POS	POS	ns	x	x	x	NEG	x
Nonvasculars									
Reindeer lichen	POS	NEG	NEG	ns	x	x	x	ns	x

Abbreviations: NEG, significant negative effect (Shield: $p < 0.005$, Plains: $p < 0.0036$); ns, not significant; POS, significant positive effect (Shield: $p < 0.005$, Plains: $p < 0.0036$); Pres/abs, presence/absence; SOL depth, soil organic layer depth; SPD, soil permeability depth; VAR, significant—direction of effect depends on plot moisture (mesic vs. wet); x, variable not included in Shield models.
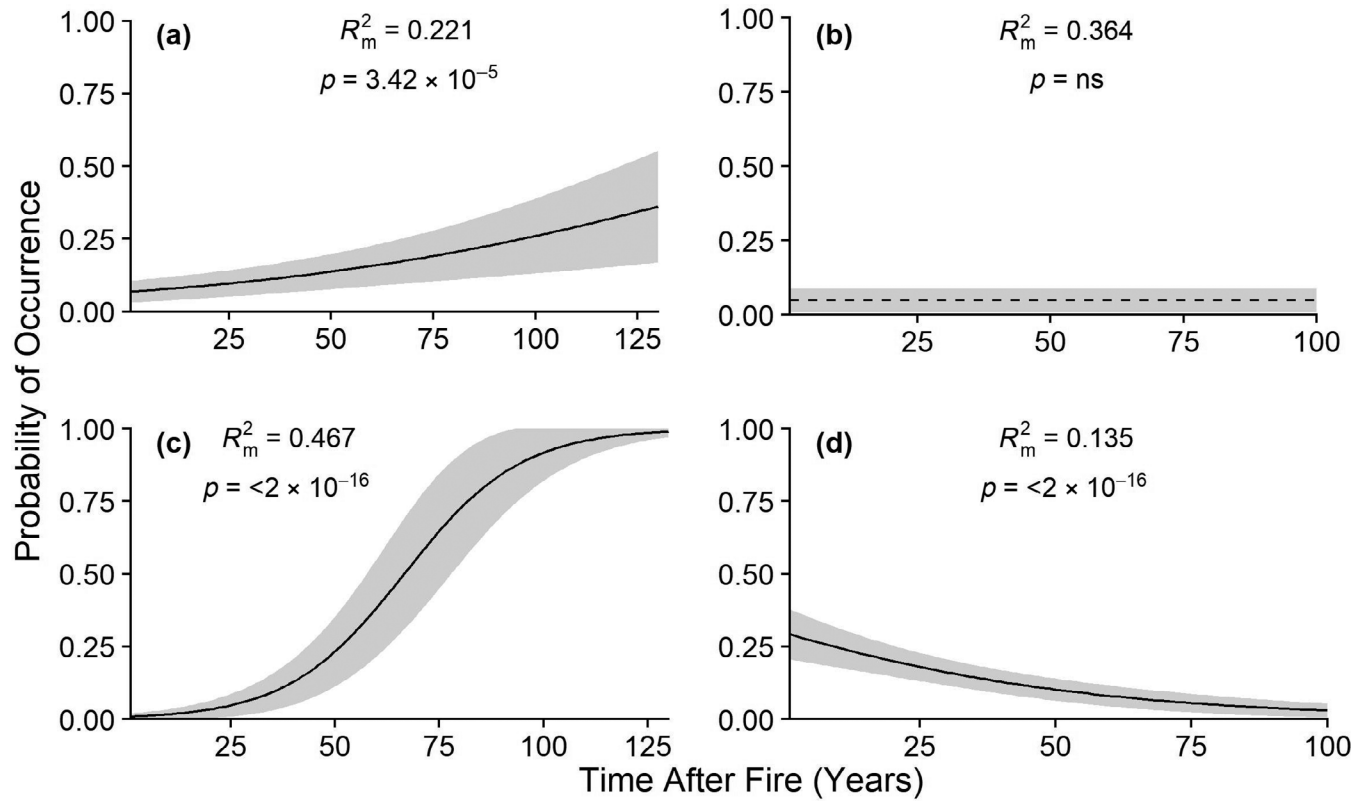
FIGURE 3   Plots displaying trends in the probability of occurrence over time after fire for various forage species in the Taiga Plains ($n = 323$) and Taiga Shield ($n = 198$) ecoregions of the Northwest Territories, Canada: (a) soapberry (*Shepherdia canadensis*)—Plains, (b) willow (*Salix* spp.)—Shield, (c) reindeer lichen (*Cladonia* spp.)—Plains, (d) birch (*Betula* spp.)—Shield. These species were chosen for display because they illustrate a range of local recovery patterns. Predictions from binomial generalized linear mixed effects models with logit link. All covariates other than time after fire held constant at the median value, with soil moisture (categorical) fixed at the intermediate level. Ribbons indicate 95% CIs. $R_m^2 = $ marginal R^2.
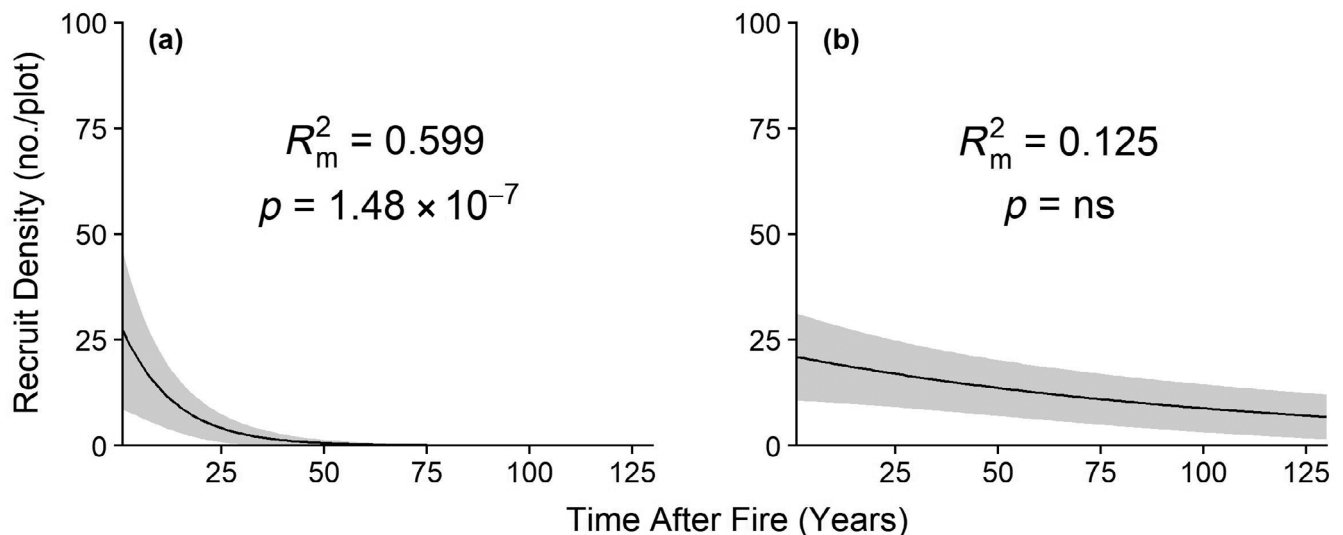
FIGURE 4   Predicted count of (a) trembling aspen (*Populus tremuloides*) and (b) black spruce (*Picea mariana*) seedlings/saplings (<1.3 m) per plot over time after fire in the Taiga Plains ecoregion of the Northwest Territories, Canada. Predictions from negative binomial generalized linear mixed effects model with log link ($n = 305$), all covariates other than time after fire held constant at the median value with soil moisture (categorical) fixed at the intermediate level. Ribbons indicate 95% CIs. $R_m^2 = $ marginal R^2.
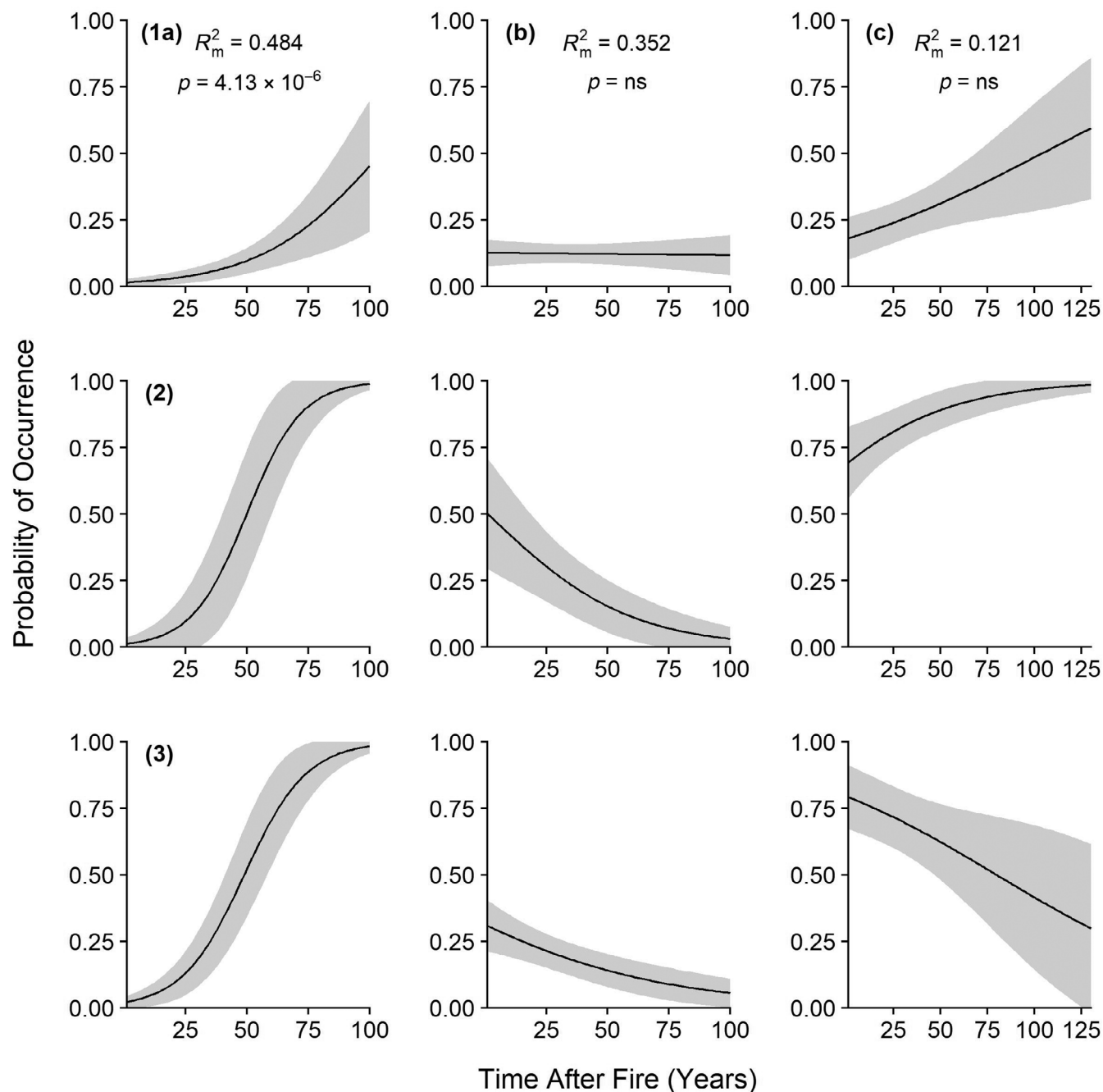
FIGURE 5 Predicted probability of occurrence of (a) black spruce (*Picea mariana*) in the Taiga Shield ($n = 198$), (b) grasses (*Poaceae* spp.) in the Taiga Shield ($n = 198$), and (c) horsetails (*Equisetum* spp.) in the Taiga Plains ($n = 323$) ecoregion, at (1) dry, (2) mesic, and (3) wet plots in the Northwest Territories, Canada. Predictions from binomial generalized linear mixed effects model with logit link—all covariates other than time after fire held constant at the median value. Ribbons indicate 95% CIs. R^2_m = marginal R^2.

likely resulting in their decreased abundance over time (Lieffers & Stadt, 1994; Macdonald & Lieffers, 1993).

Our analyses did not identify clear successional trajectories associated with time after fire after the first few years, but instead established that environmental factors, particularly soil moisture, influenced composition to shape plant communities. Previous studies that have identified distinct successional patterns using multivariate analyses have usually restricted samples to a single tree canopy type (e.g., Hollingsworth et al., 2006) or narrow geographic region (e.g., Taiga Shield; Day et al., 2017). Here we aimed to explore broad variations in composition across the wide spatial scales and environmental conditions present in boreal North America, and thus incorporated substantial variation in soils and vegetation type. Within this context, time after fire

explained the greatest amount of variation in plant community composition in both the Plains and Shield (though soil moisture was effectively equal to time after fire in the latter). However, nearly all variables and interactions examined significantly influenced plant community composition in both ecoregions, particularly soil moisture. The importance of soil moisture in both regions suggests that future work identifying successional changes in vegetation requires incorporation of soil moisture variation independently from time after fire in sampling design. This finding is consistent with previous studies demonstrating the importance of moisture on both overstory and understory composition, abundance, richness, and diversity in boreal North America (Day et al., 2020; Echiverri & Macdonald, 2019; Mallon et al., 2016; Taylor & Chen, 2011).

Influence of time after fire and environmental conditions on individual species

Time after fire or its interaction with soil moisture was significant in 75% of models, but the rate and pattern of recovery varied considerably among species. The influence of time after fire may be explained by a combination of individual plant and lichen species following differing growth and reproductive strategies, and systematic changes in biotic and abiotic site conditions over time such as alterations to the soil fungal community and decreased light, pH, and nutrient availability as the site recovers (Brais et al., 1995; Day et al., 2019; Lavoie & Mack, 2012; Simard et al., 2001). The influence of changing site conditions, specifically light availability, is supported by our finding that stem density, our proxy for both cover and light availability, was the second most commonly significant single variable in our models (54%, 13 of 24 models).

The rate and pattern of species recovery after fire were regulated by soil moisture class in 33% of models (significant time after fire × soil moisture interaction). Soil moisture is an important determinant of SOL combustion during fire, which influences tree and understory vegetation recovery, with greater combustion often favoring the regeneration of deciduous species over spruce (Baltzer et al., 2021; Day et al., 2020; Hollingsworth et al., 2013; Walker, Baltzer, et al., 2018). Wetter sites experience lower proportional SOL combustion, meaning that the residual postfire seedbed is organic (Walker, Baltzer, et al., 2018; Walker et al., 2017). Hence, these sites would be expected to have greater proportions of resprouters and plants that rely on survival in residual patches (Day et al., 2020; Hollingsworth et al., 2013; Tsuyuzaki et al., 2013). Soil moisture can also affect vegetation both

through its direct impact on plant available water and its association with factors such as nutrient availability, temperature, and decomposition, with moister sites often having cooler conditions and slower decomposition rates (Araya et al., 2013; Gundale et al., 2009; Holden et al., 2016; Sierra et al., 2017). The interaction between time after fire and soil moisture may also simply be explained by plants having differing adaptations to moisture, affecting growth and competition. Soil moisture alone was the most commonly significant variable in our models, consistent with our PERMANOVA results supporting its role as one of the most influential determinants of plant community composition in both ecoregions.

Time after fire was associated with decreasing abundance of seedlings and saplings for all three species modeled (paper birch, aspen, and black spruce). Birch and aspen seedling/sapling counts decrease sharply within the first few years, then more steadily over the longer term. This pattern is likely due to a combination of natural thinning, reduced light availability over time, and fast growth, meaning that these species rapidly transition out of the seedling/sapling stage.

It is important to note that there are some limits to the chronosequence approach used in this study. Chronosequence modeling of species recovery effectively assumes that all plots, young and old, started with the same conditions, and does not take factors like alternate successional trajectories or differing disturbance severity into account. However, the use of a chronosequence allowed us to examine vegetation recovery over a much longer time period than would be feasible for time series data.

CONCLUSION: IMPLICATIONS OF CLIMATE CHANGE FOR WILDLIFE FORAGE AND SUGGESTIONS FOR FUTURE RESEARCH

Climate change is causing the size and frequency of fires to increase and altering precipitation patterns across boreal North America (Price et al., 2013; Veraverbeke et al., 2017; Walker et al., 2020). In western North America where drought is becoming more common (Price et al., 2013), this may shift plant communities toward greater dominance of species adapted to dry conditions, such as grasses, and to those most able to recover rapidly following fire. Such changes have implications for the wildlife that rely on boreal ecosystems for food and habitat. Though we only modeled a limited number of plant and lichen species (Appendix S3), we can venture certain generalizations about the impact of climate change on the abundance of different plants within the study region, and what this might mean for forage

availability for northern wildlife such as wood bison (*Bison bison athabascae* Rhoads, 1898), woodland caribou (*Rangifer tarandus caribou* Gmelin, 1788), moose (*Alces alces* Linnaeus, 1758), and snowshoe hare (*Lepus americanus* Erxleben, 1777). Therefore, we offer some suggestions on the potential consequences of climate warming on wildlife.

More frequent fire may increase forage for wood bison, which often consume large amounts of graminoids (Jung et al., 2015; Larter, 1988; Species at Risk Committee, 2016), as grasses tend to be most abundant shortly after fires, while sedges generally recover relatively quickly given adequate soil moisture. Forage availability for woodland caribou, in the form of reindeer lichen (Fischer & Gates, 2005; Thompson et al., 2015; Webber et al., 2022), will likely decrease as these species take many years to become abundant after a fire. Deciduous trees and shrubs, which are often favored by moose and snowshoe hare (Bryant & Kuropat, 1980; Hodges, 2000; Renecker & Schwartz, 2007), tend to be most common within the first few years after fire (aspen, birch), or increase in abundance relatively rapidly after burns (willow; *Salix* spp.), likely due to their resprouting ability. However, the impact of increased fire on forage availability is anticipated to vary seasonally. Caribou tend to consume higher levels of deciduous species and graminoids during summer (Webber et al., 2022), suggesting that the availability of caribou summer forage may actually increase. On the other hand, snowshoe hare may experience winter food stress in some areas, as slow-to-recover spruce may make up more than half of their winter diet (Alaska: Elliott, 1998; Wolff, 1978). Consideration of the drier conditions predicted for the western boreal under climate change further complicates any preliminary assessment of future forage availability. All deciduous species examined, other than aspen, tended to be more common in mesic or wet than dry areas, suggesting that moose, hare, and caribou in summer may experience greater declines in forage availability than would be expected from changes in fire frequency alone. Bison will likely still benefit from increased grass availability; however, they may also lose forage in the form of sedges in drying areas. It is unclear whether this trade-off will benefit, harm, or have a negligible influence on bison.

Given the large number of conditions that can influence boreal vegetation communities and the range of recovery patterns observed, we suggest that further research is required on the postfire recovery of boreal vegetation under differing environmental conditions, particularly over the first 30 years, to help anticipate the influence of climate change on the distribution of different species and ecosystem types. We also suggest that

northern communities and land managers monitor both local forage availability and wildlife diet to help detect unexpected future changes due to factors such as the invasion of more southern species (both plants and animals) into the northwest boreal region, which was not covered in this study.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data (Jorgensen et al., 2023) are available from Borealis: https://doi.org/10.5683/SP3/F45UGZ.

ORCID
Alexis Gardiner Jorgensen https://orcid.org/0000-0002-4690-7201
Geneviève Éliane Degré-Timmons https://orcid.org/0000-0002-1121-4659
Jill F. Johnstone https://orcid.org/0000-0001-6131-9339
Xanthe J. Walker https://orcid.org/0000-0002-2448-691X
Jennifer L. Baltzer https://orcid.org/0000-0001-7476-5928

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.