Tree seedling regeneration in Canada's southern Rocky Mountains: contrasting recently burned and unburned areas

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Abstract

To predict patterns of forest regeneration following wildfires, we must determine the factors that affect tree seedling establishment. We tested the relative influence of abiotic, biotic, and landscape factors on the probability of tree seedling presence in Waterton Lakes National Park, Alberta, Canada. We recorded the presence of seedlings in 98 plots that were first surveyed 25 years before the 2017 Kenow Wildfire, 53 of which burned in the fire. We included plots that did not burn to test the effect of the wildfire on seedling occurrence, and whether the importance of other factors varied in burned versus unburned plots. Lodgepole pine seedlings occurred in about 25% of burned plots, but only 2% of unburned plots. Seedlings of poplars, subalpine fir, and Engelmann spruce occurred in 7.5% or less of the burned plots and 20% to 48% of unburned plots. After accounting for burn status, pine seedlings were more likely to occur in plots with higher herbaceous plant cover, while spruce seedling occurrence declined with elevation. After burn status, past presence of the tree species in a plot was the strongest predictor of seedling occurrence. However, seedlings of spruce and fir are still mostly absent from burned areas. Long-term monitoring of these plots will reveal whether these species can successfully recolonize burned areas, and how long it will take.

Keywords: forest, forest fire, succession, recovery, resurvey

Introduction

Globally, wildfires are becoming more common, and they are capable of dramatically changing the landscapes they impact. By the end of the century, the area burned annually in Canada could be 100% greater than the annual amount burned at the end of the 20th century (Flannigan et al. 2005). It is important to study how forests respond following severe wildfires to understand the effects that wildfires will have on forest-dependent species and on ecosystem services (i.e. the timber and recreation industries). Tree seedling establishment immediately post-wildfire is an early indicator of the degree of forest resilience (Donato et al. 2009, Hansen and Turner 2019).

Regeneration is often influenced by abiotic factors. For example, water availability can affect successful tree regeneration (Casady et al., 2009). Higher elevations tend to receive more precipitation than lower areas, making those areas more favourable for seedling regeneration (Casady et al. 2009). In southern Alberta, north facing slopes have higher soil moisture levels and receive less solar radiation, resulting in reduced evapotranspiration (Lieffers and Larkin-Lieffers 1986). Rother and Veblen (2016) found that conifer regeneration was greatest at higher elevations and on north facing slopes following severe wildfires in Colorado, due to greater water availability for seedlings. Soil drainage can also influence tree regeneration. Roy et al. (1999) found that black spruce (*Picea mariana* Kuntze) seedlings in better-drained soils had increased foliar concentrations of both carbon and nitrogen, resulting in increased growth. Well-drained soils may also have greater nutrient availability due to having more oxygen available for the decomposition of organic material (Perry et al. 2008).

Another factor that can influence seedling regeneration is slope steepness. Stevens-Rumman and Morgan (2019) found that steeper slopes have shallower soil beds, resulting in reduced sapling regeneration density on steeper slopes following wildfires across the western United States. This contrasts with the findings of Franklin and Bergman (2011) who found that slope steepness had little influence on occurrence of Coulter pine (*Pinus coulteri* D.Don) seedlings. Interestingly, Tsuyuzaki et al. (2013) determined that poplars (*Populus* spp.) were more likely to regenerate on steeper slopes, suggesting that steep or concave slopes acted as traps for wind-dispersed seeds. Therefore, seedling occurrence may vary with slope steepness, particularly for species with long-range wind dispersal.

Biotic factors can also influence seedling establishment. For example, the abundance of understorey vegetation can affect tree seedling establishment and growth. Thick understorey vegetation may hinder tree regeneration due to competition with seedlings for both nutrients and sunlight (Bonnet et al. 2005). In contrast, Chambers et al. (2016) found that understorey vegetation cover was positively correlated with the density of Douglas-fir (*Pseudotsuga menziesii*) seedlings. This effect was attributed to herbaceous understorey vegetation shielding the light-sensitive Douglas-fir from excessive sunlight. However, the same study found no effect of understorey vegetation cover on the regeneration of ponderosa pine (*Pinus ponderosa* Douglas ex Loudon). After studying the regeneration of whitebark pine (*Pinus albicaulis* Engelm.) following wildfires in Montana, Leirfallom et al. (2015) found that seedling presence was positively correlated with understorey vegetation up to 30% cover, with this facilitation of seedling survival being due to the partial shade provided, but probability of seedling presence decreased above that point due to increased competition for light. Therefore, the cover of understorey vegetation may have a positive, negative, or no effect, and this may vary for different tree species.

The patchwork of unburned refugia surrounding a burned site can influence patterns of regeneration for wind-dispersed tree species. Wind rarely disperses conifer seeds more than 250 meters from seed sources, which reduces the probability of finding wind-dispersed tree seedlings far from a viable seed source (Greene and Johnson 1996; Kemp et al. 2015; Peeler and Smithwick 2020). For example, Kemp et al. (2015) found that for Douglas-fir, ponderosa pine, and grand fir (*Abies grandis* Hook.), distance to a live seed source was the most important predictor of tree sapling densities following wildfires in the Idaho and Montana Rocky Mountains. However, the distance beyond which seedling establishment is limited may exceed a few hundred metres. For example, Donato et al. (2009) found high conifer seedling densities up to 400m away from the edge of a burn, suggesting that actual dispersal distances may be underestimated. In any case, for species that are primarily wind dispersed, distance to an unburned seed reservoir may be the most important predictor of seedling presence in burned areas.

However, distance to unburned refugia may not influence regeneration for all species. Lodgepole pine (*Pinus contorta* Bol.) has serotinous cones which can withstand wildfire, allowing regeneration from on-site seeds rather than relying on seeds dispersing from unburned areas (Lyon and Stickney, 1976). While these seeds are able to maintain germination viability only up to 100°C when exposed, when protected within the cone they are able to survive much higher temperatures (Knapp and Anderson 1980). As a result, viable seeds can survive fire and begin regeneration regardless of distance to an unburned seed reservoir (Kemp et al. 2015). Other species rely on resprouting as their primary method of regeneration, producing sprouts from underground rootstock. For these species the survival of belowground tissues is critical, and therefore burn severity may be the most important predictor of regeneration post-fire. For example, Moreno and Oechel (1994) found that high severity burns could damage subterranean roots and rhizomes of chaparral shrubs, preventing resprouting and slowing regeneration in areas of high burn severity. Trembling aspen (*Populus tremuloides* Michx.) generally regenerates by resprouting, with only occasional establishment from seed (Kay 1993). Therefore, burn status may be the most important predictor of seedling presence for lodgepole pine and poplars, with lodgepole pine more likely in burned areas and poplars more likely in unburned sites.

Several studies have examined tree regeneration after wildfire in the US Rocky Mountains (e.g. Doyle et al. 1998, Kemp et al. 2015, Chambers et al. 2016, Harvey et al. 2016, Stevens-Rumann and Morgan 2019) and in Canada's boreal forest (e.g. Jean et al. 2020). However, we found no studies that examined tree regeneration following wildfire events in the Canadian Rocky Mountains. In addition, most studies of tree regeneration do not compare patterns in burned areas to natural regeneration occurring in unburned sites. Forests in the Rocky Mountains are thought to be quite resilient to wildfire, with early-successional species representing many of the same species that dominate late-successional communities (Lyon and Stickney 1976). However, this resilience could be reduced in the context of anthropogenic climate change in which wildfires are now occurring. In this study, we aim to identify what factors affect tree seedling occurrence in the Canadian Rocky Mountains in both recently burned and unburned sites. We test the relative importance of abiotic, biotic, and landscape factors for tree regeneration in Waterton Lakes National Park (WLNP), Alberta, Canada, in both burned and similar but unburned sites 2-3 years after a severe wildfire in 2017. This allows us to contrast regeneration rates and influences in recently burned areas with areas in later stages of succession. We use a unique database of nearly 100 vegetation plots surveyed both in 1994-1999 and in 2019 and 2020, after just over half of them had burned.

Methods

Study Site

WLNP is located in the southwest corner of the Canadian Rocky Mountains and covers about 525 km^2 between 49°00' and 49°12' N, and 113°40' and 114°10' W (Figure 1). There is significant variation in climatic and topographical conditions throughout the park. Elevation ranges from 1280 m above sea level in the foothills (mean annual temperature 3°C, mean growing season precipitation 377mm) to 2940 m above sea level in the high alpine (mean annual temperature -2.4°C, mean growing season precipitation 472 mm; Natural Regions Committee 2006). Located along the Continental Divide, WLNP includes four distinct ecoregions (foothills parkland, montane, subalpine, and alpine). Aspen (*Populus sp.*) groves are distinctive vegetative features of the foothills parkland ecoregion. While aspens are able to disperse seeds long distances, following disturbance they primarily regenerate via resprouting (Frey et al.

2003). Aspen are shade intolerant (USDA 2024). The montane and subalpine ecoregions are characterized by coniferous forests, with vegetation dominated by lodgepole pine and subalpine fir. The lodgepole pine included in this study is notable for its serotinous cones (Lyon and Stickney 1976). Like aspen, lodgepole pine is shade intolerant (USDA 2024). Subalpine forests can also be differentiated by the co-dominance of the shade intermediate Engelmann spruce (*Picea engelmannii* Engelm.; USDA 2024). The alpine ecoregion vegetation is mainly composed of low-laying shrubs (Strong and Leggat 1992). Over half of Alberta's vascular plant species can be found in the park (Achuff et al. 2002). First designated as a national park in 1895, WLNP is a popular area for tourism and recreation, hosting over half a million visitors annually (Parks Canada 2020).

Median fire return intervals in the WLNP region prior to 1948 (when effective fire suppression was implemented) ranged between 26 and 85 years, depending on the ecoregion (Rogeau 2016). In the last hundred years, WLNP has experienced two major wildfire events. The Sofa Mountain Wildfire in September 1998 was limited to the southeast corner of the park, burning approximately 15 km^2. In 2017, a lightning strike in southeastern British Columbia ignited the Kenow Wildifire. The fire reached WLNP by early September and rapidly spread (Greenaway et al. 2018). Although firefighting efforts saved most of the small village within WLNP, 193 km^2 of the park (38%) was affected by fire (Parks Canada 2019). Roughly 50% of vegetated area within the park was burned, with about three quarters of that burning at a high severity (Greenaway et al. 2018). Within high severity areas, less than 10% of the pre-fire canopy cover remained (Key and Benson 2006).

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Data collection

Over the course of three field seasons in 1994, 1995 and 1999, Parks Canada biologists surveyed 330 vegetation plots to classify plant communities and soil types at WLNP (Achuff et al. 2002). Plots varied in size depending on the vegetation type: 20x20m plots for forests/woodlands, 15x15m plots for shrublands, and 10x10m plots for grasslands/herbaceous vegetation. At each plot, surveyors identified and visually estimated percent cover for all vascular plant species present. They also classified vegetation into four different strata: (1) all woody plants greater than 5m tall, (2) woody plants 2-5m tall, (3) all woody plants between 0.5 and 2m tall, (4) woody plants less than 0.5m tall and all herbaceous species regardless of height. They classified soil drainage following the guidelines in the Canadian Soil Information System using the following scale: (1) very rapidly drained, (2) rapidly drained, (3) well drained, (4) moderately well drained, (5) somewhat drained, (6) poorly drained and, (7) very poorly drained (Day 1983, Achuff et al. 2002).

Following the Kenow Wildfire, during the summers of 2019 and 2020, we relocated and resurveyed 98 of the original plots, 53 of which had burned in the Kenow Wildfire (Figure 1). We resurveyed plots following the same protocol established by Parks Canada during the initial surveys. We selected plots to resurvey based on accessibility and maximizing variation in elevation, slope steepness, slope aspect, and vegetation type among both burned and unburned plots. The plots were not permanently marked in the original survey, but the coordinates of each plot were recorded using a handheld GPS unit. We estimate that relocation error ranged from 3-5 m based on the accuracy of the GPS units. Given the relatively large size of the plots (100 - 400 m^2), we consider this a relatively small source of error. Unfortunately, we did not count individual tree seedlings, therefore we do not have an estimate of seedling density. The main aim of our resurvey was to assess shifts in the plant community as a whole (Lloren 2021, Lloren & McCune 2024). However, the presence of a tree species in layer 4 (less than 0.5 m height) indicates the presence of at least one seedling or young sapling. At this early stage of succession, seedlings were never in abundance greater than 1% cover. Because we aimed to record every species present in each plot, regardless of abundance, our surveys were comprehensive, requiring two surveyors up to four hours in unburned sites.

We then compiled data on potential predictors of tree seedling presence. Burn severity was mapped by WLNP workers following the fire in October 2017 using satellite imagery. Burn severity classes were then determined using the Normalized Burn Ratios (NBR) as published by Key and Benson (2006) to delineate five burn severity classes based on a comparison of near-infrared and mid-infrared reflectance of vegetation pre- and post-fire (dNBR). Burn classes ranged from 1 (low severity, dNBR -0.10 to +0.09) to 5 (high severity, dNBR +0.66 to +1.30). The region burned by the Kenow Wildfire was almost all classified as class 4 or 5 (Figure 1), meaning that large trees and the upper canopy were entirely burned, with foliage at all strata being torched. Therefore, we classified each plot as either burned or unburned in the Kenow Wildfire.

We noted the historical presence of trees in each site based on the original survey data from the 1990s. We considered a species to be historically present if it was found in the plot in any strata during the original surveys (i.e. present at *any* height from <0.5 m to > 2m). We acknowledge that because twenty-five years have passed between the original surveys and the wildfire, some species could have disappeared from a plot in the interim (i.e. due to windfall, disease), before the wildfire. However, we think this is unlikely. In unburned areas, all unburned plots still contained the tree species found in the original surveys.

We determined the elevation and aspect of each site using a 25m Digital Elevation Model (DEM) in ArcGIS. The original surveyors measured slope steepness (%) at each plot using a clinometer. To convert aspect in degrees to a linear predictor, and based on evidence that north facing slopes were most likely to have seedling presence (Casady et al. 2009, Rother and Veblen 2016), we calculated an index of 'northness' as follows:

$$northness = \frac{|(aspect\ in\ degrees - 180)|}{180}$$

This results in a continuous value for aspect, with north facing slopes as 1, south as 0, and east or west as 0.5.

We used GIS to measure the distance from the center of each plot to the nearest unburned area bordering line based on burn area data obtained from Parks Canada. The geospatial data used to denote burn area was created by using pre- and post-fire Landsat imagery, using the dBNR index (Key and Benson 2006). Edges were refined by hand using aerial images. All plots that were not burned had a distance to unburned area of zero, by definition. We quantified the total understorey cover in each plot in 2019/2020 by summing the percent cover of all species present in each plot within stratum four (all herbaceous species and woody species <0.5m tall). Due to physical overlap of plants of different species, total understorey cover can be greater than 100%. We used soil drainage values as assessed by the original study (Achuff et al. 2002), but reduced them from 7 to three categories, with drainage values of 2 being classed as moderately drained, 3 as well drained, and 4,5,6 and 7 as poorly drained. None of the resurveyed plots had a soil drainage value of 1 (very rapidly drained).

Statistical Analysis

We used generalized linear models (GLMs) to test the relative influence of each factor on the probability of finding at least one tree seedling. We built five models for seedling presence: one for the presence or absence of seedlings of any species, and one each for the presence or absence of lodgepole pine seedlings, poplar seedlings, subalpine fir seedlings, and Engelmann spruce seedlings. We included both *Populus* species (*P. tremuloides* and *P. balsamifera* Lyall) in the poplar model due to their similar regeneration methods.

Our explanatory variables included burn status (burned vs. unburned), historical presence of trees (any of the five species for the general model, or the species in question for the single-species models), elevation, northness, slope steepness, distance from the site to the unburned area in metres, soil drainage (poor, well, moderate) and the total percent cover of herbaceous understorey species in 2019/2020. We included the interaction between northness and elevation as we expected that the role of slope aspect (northness) on seedling establishment could vary with elevation, with southerly slopes at cooler, higher elevations less prone to drought. We also included the year of the resurvey as a categorical predictor. Differences in seedling frequency between 2019 and 2020 surveys could result from a delay in colonization and/or germination of seedlings in the burned areas. Alternatively, variability in seedling occurrence frequency between years could result from variability in seed production or climatic conditions year to year, which could cause variability in seedling frequency between survey years even in unburned plots (e.g. LaMontagne et al. 2021). In the general model, we also included all pairwise interactions between burn status and the other predictors based on evidence from the literature that the effects of fire on tree regeneration can vary depending on these factors (e.g. Coop et al. 2010, Tsuyuzaki et al. 2013). Models for individual species had insufficient data (i.e. very few occurrences in burned plots) to consider these interactions. We checked for correlations between all explanatory variables, and no pair of predictors had absolute correlation coefficients greater than r=0.62. We log-transformed understorey cover to improve normality.

For each response variable, we built a binomial GLM with a logit link including all the potential explanatory variables. We standardized continuous predictors by rescaling them so that they had a mean of zero and a standard deviation of 0.5. We then used backward stepwise model selection to determine the explanatory variables included in the minimum adequate model based on Akaike's Information Criterion (AIC). Next, we used a 'drop1' test to determine the importance of each explanatory variable, while accounting for all other variables, by comparing the selected minimum adequate model to a model excluding the variable in question. We used spline correlograms to check for spatial autocorrelation in the residuals of each model. We also ensured there was no overdispersion by comparing the dispersion of simulated residuals to the observed residuals.

We visualized the final models using partial regression plots, which hold all other predictors in the model constant while adjusting the focal variable (Breheney and Burchett

2013). Finally, we evaluated the performance of each model by calculating the percent of the null deviance explained by the model, and a measure of classification accuracy: the area under the receiver-operating characteristic curve (AUC; Swets 1988). We carried out all statistical analyses in R version 4.0.3 (R Core Team 2013) and used the following packages: 'arm' to standardize predictors (Gelman et al. 2007), 'ncf' to create spline correlograms (Bjornstad and Cai 2020), 'MASS' for stepwise model selection (Venables and Ripley 2002), 'visreg' to make partial regression plots (Breheney and Burchett 2013), 'rocr' to calculate AUC (Sing et al. 2020), and 'DHARMa' to test for model misspecification problems (Hartig 2020).

Results

Of the 98 resurveyed plots, 53 were burned in the Kenow Wildfire. None of the plots were burned in the 1998 Sofa Mountain Wildfire. Twenty-three plots were located in grasslands/herbaceous vegetation (15 burned), 15 plots were located in shrubland vegetation (7 burned), and 60 plots were located in forest/woodland (31 burned). Elevation ranged from 1,268m to 2,323m, with a median value of 1,712.5m. Of the 98 plots, 50 had at least one seedling in 2019/2020, compared to only 33 plots in the 1990s. The number of plots with Engelmann spruce and subalpine fir seedlings did not change much between the original survey and the 2019/2020 survey, whereas the number of plots having lodgepole pine and poplar seedlings increased (Table 1). Subalpine fir and Engelmann spruce seedlings were very rare in burned plots, occurring in only two and one burned plot, respectively.

The minimum adequate model for the presence of one or more tree seedlings regardless of species included seven individual predictors and three interactions. When all other factors were accounted for, burn status, historical tree presence, survey year, northness, total understory cover, and the interaction between burn status and elevation were significant predictors (Table 2, Figure 2). The probability of tree seedling occurrence was highest in plots that were unburned and that had trees present at the time of the first survey in the mid-1990s (conditional mean probability 77.5% in unburned plots with prior tree presence compared to 2.0% in unburned plots without prior tree presence). After accounting for burn status, the probability of tree seedling presence increased on southerly aspects and with increasing understory plant cover. The probability of seedling presence declined with elevation, but only in burned plots (Figure 2). The model explained 59.7% of the null deviance and AUC was 0.95.

The minimum adequate model for the presence of one or more lodgepole pine seedlings included burn status, historical presence, elevation, slope steepness, northness, distance from unburned refugia, herbaceous cover, and the interaction between elevation and northness. However, only burn status, historical presence of pine trees, and herbaceous cover were important predictors of pine seedling presence once the other factors had been accounted for (Table 3). The probability of lodgepole pine seedling presence was highest in burned plots that had prior presence of lodgepole pine. Burned plots with prior presence of pine trees had a predicted probability of 94.3% of having a pine seedling, compared to 5.4% probability in burned plots without trees prior to the fire (Figure 3). Plots with higher herbaceous plant cover also had higher probability of having pine seedlings present (Figure 3). The model explained 54.0% of the null deviance and AUC was 0.93.

The minimum adequate model for the presence of one or more poplar seedlings included burn status, historical presence of poplar, survey year, and total herbaceous cover. Based on the drop1 test, historical poplar presence and survey year were significant predictors (Table 3). The probability of poplar seedling presence was higher in unburned plots that had a prior poplar presence (predicted probability 26.8%) compared to unburned plots without poplars in the 1990s survey (predicted probability 2.6%) and in plots assessed in 2020 (89.4% if poplars present in the 1990s) compared to plots assessed in 2019 (26.8% if poplars present in the 1990s; Figure 4). The model explained 36.8% of the null deviance and AUC was 0.91.

The minimum adequate model for the presence of one or more subalpine fir seedlings included historical presence of subalpine fir, survey year, and the distance to unburned refugia, and all were significant predictors according to the drop1 test (Table 3). Historical presence of subalpine fir resulted in a higher probability of subalpine fir seedling presence (53.6%) than when fir trees were absent in the plot at the time of the 1990s surveys (2.2%), and plots surveyed in 2020 were more likely to have subalpine fir seedlings, as were those closer to or within unburned areas (Figure 5). The model explained 51.5% of the null deviance and AUC was 0.93.

Finally, the minimum adequate model for the presence of one or more Engelmann spruce seedlings included burn status, historical presence, survey year, elevation, northness, and the interaction between northness and elevation. The drop1 test indicated that burn status, historical presence, survey year, and elevation were significant predictors after accounting for the other predictors in the model (Table 3). The probability of Engelmann spruce seedling presence was highest in plots that did not burn, with Engelmann spruce presence in the original 1990s survey, in 2020, and at lower elevations (Figure 6). For example, in unburned plots at the median elevation, with historical spruce presence, and surveyed in 2020, the predicted probability of seedling occurrence is 57.0%, compared to 5.9% in similar plots that burned. The model explained 46.8% of the null deviance and AUC was 0.93.

Discussion

The ability of tree species to regenerate following wildfire is the key to resilience of forest systems (Donato et al. 2009, Hansen and Turner 2019). If the dominant tree species present before a wildfire are not able to regenerate, there will be a shift to an alternative state (e.g. Johnstone and Chapin 2006). The 'normal' fire regime of our study region is thought to consist of large and severe wildfires (Lyon and Stickney 1976). Post-fire forest regeneration begins with lodgepole pine, which quickly dominates, and a smaller pulse of immediate post-fire spruce seedling establishment – with fir arriving much later (Day 1972). Natural thinning of pines begins about 30 years after the fire, allowing spruce and fir to begin increasing, eventually becoming dominant, but only after more than 100 years without fire (Day 1972). Our results are consistent with the very earliest stages of this long-term process. However, if increased fire frequency or increased temperatures or drought reduce the ability of tree seedlings to establish or survive, this successional pattern could be altered. Therefore, it is important to track tree seedling regeneration after recent wildfires and to understand what factors promote or limit tree seedling establishment.

We studied the relative roles of abiotic, biotic, and landscape factors on the presence of tree seedlings in sites recently burned in the Kenow wildfire and long unburned sites within WLNP across a wide gradient of elevation and vegetation types. We found that the presence of a tree species at a site in the past is a strong predictor of seedling presence. However, seedlings of all species except lodgepole pine were very rare in burned sites 2-3 years following the fire. In fact, among plots that had trees at the time of the 1990s surveys, only 56% of those that burned had tree seedlings present in 2019/2020, compared to 85% of unburned plots. In Glacier National Park, just south of WLNP, post-fire establishment of Engelmann spruce and subalpine fir began right after wildfire but did not peak until 4-6 years afterwards (Harvey et al. 2016). We found increased occurrence of seedlings in 2020 compared to 2019, suggesting we may be in the early stages of seedling establishment of these species in burned areas. However, seedling occurrence frequency increased in 2020 compared to 2019 even for species found mainly in unburned plots (e.g. poplar), suggesting that year-to-year variability in seed availability or climatic conditions – rather than delayed colonization alone – contributed to this pattern. Therefore, continued monitoring is needed to determine to what extent trees will recolonize burned areas in the next few years, and how this will be affected by local or landscape factors.

Abiotic conditions at local sites – in particular, soil moisture levels – are known to be important determinants of tree seedling establishment success in the Rocky Mountains (Casady et al. 2019, Harvey et al. 2016, Hansen and Turner 2019, Peeler and Smithwick 2021). Given that south-facing slopes are much drier in our region, we were surprised to find that seedlings of all species lumped together had a higher probability of occurring on south-facing slopes (northness index closer to 0) than on north-facing slopes. One explanation could be that the presence of trees prior to the wildfire was concentrated on south-facing slopes, and therefore having 1990s tree presence in the models accounted for slope aspect. However, 1990s tree presence was not correlated with aspect. Alternatively, south-facing slopes may be more likely to support seedling establishment where temperature is limiting establishment more than moisture. This may be the case in the montane and sub-alpine ecoregions of WLNP where forest vegetation dominates. Climatic conditions in WLNP from 2018 to 2020 – including annual precipitation and average maximum temperature – were within normal ranges for the previous decade, so seedling establishment was likely not aided by exceptionally favourable growing conditions, or depressed by drought (Alberta Agriculture and Forestry 2022).

Although we expected greater rates of seedling occurrence at higher elevations (where moisture is greater), the probability of finding tree seedlings of all species combined declined with elevation in burned plots. Similarly, Engelmann spruce had a higher likelihood of seedling presence at lower elevations. Redmond and Kelsey (2018) also found Engelmann spruce seedling density to decline with elevation in the Colorado Rockies, suggesting this could result from frost damage or other consequences of lower temperatures at higher elevations. This could be the case also in WLNP. Coop et al. (2010) found that tree regeneration measured about 30 years post-fire at high elevations in Colorado declined with elevation. However, Donato et al. 2009 found elevation to be relatively unimportant for seedling density 2-4 years post-fire in the Klamath-Siskiyou Mountains of Oregon, USA.

The presence of dense herbaceous or shrubby understorey vegetation can either promote or depress tree seedling establishment, depending on the context (e.g. Leirfallom et al. 2015, Chambers et al. 2016). When we pooled all species, seedling occurrence was more likely in plots with higher total cover of understorey vegetation, which is consistent with a facilitative rather than a competitive effect. Pine seedling probability of occurrence was also correlated with increasing understorey cover. Peeler and Smithwick (2021) found understorey vegetation cover to be relatively unimportant as a predictor of tree seedling establishment in the U.S. Rocky Mountains, south of our study area. However, they examined regeneration about two decades post-wildfire, whereas our surveys were only 2-3 years after wildfire. It may be that higher cover of understorey vegetation benefits tree seedlings at earlier stages, but later becomes unimportant, or even a detriment to older saplings, as competition for soil moisture and nutrients intensifies.

Several studies have found that landscape context – in particular the proximity and relative topographic position of living seed trees – is an important predictor of tree regeneration patterns (e.g. Doyle et al. 1998, Donato et al. 2009, Coop et al. 2010, Peeler and Smithwick 2020, 2021). We predicted that distance to an unburned area would be a significant predictor of seedling presence in burned plots for the wind dispersed species, subalpine fir and Engelmann spruce, however this was the case only for subalpine fir. At this stage only 2-3 years post-fire, very few seedlings of spruce or fir were found in burned plots in our surveys. The one spruce seedling found in a burned plot was only 106 m from an unburned area, while the two subalpine fir seedlings found in burned plots were 6.5 m and 156 m distant from unburned refugia. Most likely our surveys were too soon after the burn to detect the influence of proximity to unburned refugia for Engelmann spruce, as practically no spruce has yet been able to establish in burned sites. The significant effect of distance on fir seedling occurrence is likely driven by the fact that the majority of seedlings were in unburned sites (distance = 0m), with the two burned sites being relatively close to the unburned areas – hence distance in this case is effectively a proxy for burn status. The probability of seedling occurrence was far more likely in plots we surveyed in 2020 compared to 2019, but this was true for both burned and unburned plots. It may be that our surveys in 2020 were just capturing the beginning of a rise in tree seedling establishment. Continued monitoring of the plots within the burn will allow us to determine the timing of the peak of seedling establishment, and to measure how strongly the distance from the burn edge predicts seedling presence or density.

Our study has a number of limitations. First, our survey methods recorded the presence of tree seedlings but not their density. Seedling density may be a more sensitive index of tree regeneration. Many studies have found strong relationships between tree seedling density and local or landscape predictors (e.g. Doyle et al. 1998, Donato et al. 2009, Coop et al. 2010, Harvey et al. 2016). Second, the relative importance of abiotic, biotic, and landscape factors for tree regeneration in burned sites likely changes over time, and our study only applies to the very earliest stages post-fire. While lodgepole pine seedlings generally establish in the first two growing seasons after wildfire in our region, establishment of other species may peak a few or several years after fire (Harvey et al. 2016). More detailed data on soil characteristics, in addition to our coarse categorical classification of soil drainage, might also help to explain more of the variation in seedling occurrence in these plots.

Conclusion

In their comprehensive review of post-fire succession in the Rocky Mountains, Lyon and Stickney (1976) suggest that wildfire should be considered "an internal perturbation of a generally stable system". Rather than recovery proceeding by a sequential succession of suites of different species, the early colonizers are the same species that will make up the 'climax' forest; what changes is the relative abundance of these species over time. This aligns with the stand structure study by Day (1972), showing that pine, and then spruce and fir, are able to re-colonize burned sites within a few decades, and only their relative abundance changes as succession proceeds. Similarly, long-term studies following the massive wildfires in Yellowstone National Park, USA, in the late 1980s have found that the plant communities present prior to the fire were re-established within a couple of decades, with few exceptions (Abella and Fornwalt 2015, Romme et al. 2016). Studies in other parts of the Rocky Mountains have also found that the best predictor of post-fire forest composition was pre-fire forest composition (Doyle et al. 1998, Harvey et al. 2016). In WLNP at this early stage post-fire, seedlings occupy only about half of the previously forested plots in the burned sites, and firs and spruce seedlings are very rare. The changing context in which wildfires are now occurring has the potential to disrupt the return to pre-fire tree composition in the burned sites (Coop et al.

2020). Long-term tracking of tree regeneration and plant community composition in WLNP will reveal whether or not these forests will ultimately recover to something like their pre-fire composition.

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TABLE 1. Number of plots with seedling presence pre-fire (1990s) and post-fire (2019/2020). Some plots had more than one tree species present. In each column, the number of plots with an occurrence of trees or tree seedlings is indicated, out of the total number of plots. In the first column, the numbers in brackets show the number of plots out of 53 that would eventually burn in the 2017 wildfire that had trees present in the 1990s. Pre-fire frequency of trees was approximately even among plots which burned and did not burn.

SPECIES	# of plots with trees present 1990s (any height)	# of plots with seedlings present 1990s	# of plots with seedlings present 2019 or 2020	# of burned plots with seedlings present 2019 or 2020	# of unburned plots with seedlings present 2019 or 2020
any	67/98 (33/53)	33/98	50/98	18/53	32/45
lodgepole pine	18/98 (7/53)	2/98	14/98	13/53	1/45
poplars	17/98 (9/53)	2/98	14/98	4/53	10/45
subalpine fir	50/98 (25/53)	26/98	24/98	2/53	22/45
Engelmann spruce	36/98 (16/53)	10/98	10/98	1/53	9/45

TABLE 2. Model coefficients and results of drop1 test for each factor included in the best model for the presence/absence of at least one tree seedling (all species combined). Factors determined to be important predictors based on a drop1 test are in bold. Null deviance 135.82 (df = 97), residual deviance 54.65 (df = 87).

PREDICTOR	coefficient	SE[a]	AIC[b]	p[c]
Intercept	-0.46	0.39	76.65	n/a
burn status (unburned/burned)	**-1.74**	**0.85**	**79.19**	**0.033**
historical presence of trees (no/yes)	**5.13**	**1.35**	**110.81**	**<0.001**
survey year (2019 or 2020)	**4.35**	**1.36**	**94.79**	**<0.001**
elevation	-0.91	1.11	75.32	0.410
slope	1.28	0.93	76.63	0.159
northness index	**-1.68**	**0.92**	**78.59**	**0.047**
cover of understorey vegetation	**2.43**	**1.10**	**80.27**	**0.018**
burn x elevation interaction	**-4.19**	**2.22**	**78.82**	**0.041**
burn x slope interaction	2.65	1.71	77.30	0.103
burn x understory cover interaction	-3.15	2.29	76.69	0.153

[a] standard error

[b] AIC of the model including all factors except the one being tested

[c] p value based on a Chi-squared test comparing the full model with a model excluding the factor

TABLE 3. Model coefficients and results of drop1 test for each factor included in the best model for the presence/absence of at least one seedling for each species separately. Factors determined to be important predictors based on a drop1 test are in bold.

PREDICTOR	coefficient	SE[a]	AIC[b]	p[c]
lodgepole pine (Null deviance 80.38 (df = 97), residual deviance 36.95 (df = 89))				
Intercept	-3.87	0.98	54.95	n/a
burn status (unburned/burned)	**5.09**	**2.30**	**61.22**	**0.004**
historical presence (yes/no)	**5.66**	**1.90**	**73.29**	**<0.001**
elevation	1.90	1.79	54.15	0.273
slope steepness	1.64	1.03	56.53	0.058
northness index	1.75	1.32	54.95	0.158
distance to unburned area (m)	1.67	0.86	56.76	0.051
cover of understorey vegetation	**3.14**	**1.88**	**56.89**	**0.047**
elevation x northness interaction	4.25	2.86	55.43	0.115
poplars (Null deviance 80.38 (df = 97), residual deviance 50.82 (df = 93))				
Intercept	-3.12	0.67	60.82	n/a

burn status (unburned/burned)	-1.25	0.78	61.60	0.095
historical presence (yes/no)	**2.62**	**0.90**	**69.47**	**0.001**
survey year (2019 or 2020)	**3.13**	**0.98**	**73.65**	**<0.001**
cover of understorey vegetation	1.99	1.25	61.77	0.086
subalpine fir (Null deviance 109.1 (df = 97), residual deviance 52.94 (df = 94))				
Intercept	-3.68	1.09	60.94	n/a
historical presence (yes/no)	**3.93**	**1.05**	**87.69**	**<0.001**
survey year (2019 or 2020)	**1.97**	**1.02**	**64.022**	**0.024**
distance to unburned area (m)	**-8.86**	**3.28**	**91.43**	**<0.001**
Engelmann spruce (Null deviance 64.59 (df = 97), residual deviance 34.39 (df = 91))				
Intercept	-4.72	1.21	48.39	n/a
burn status (unburned/burned)	**-3.05**	**1.40**	**54.28**	**0.005**
historical presence (yes/no)	**2.14**	**1.00**	**52.03**	**0.018**
survey year (2019 or 2020)	**2.84**	**1.28**	**52.68**	**0.012**
elevation	**-2.84**	**1.42**	**51.16**	**0.029**
northness index	-1.26	1.21	47.57	0.278
elevation x northness interaction	-5.66	3.23	49.89	0.061

[a] standard error

[b] AIC of the model including all factors except the one being tested

[c] p value based on a Chi-squared test comparing the full model with a model excluding the factor

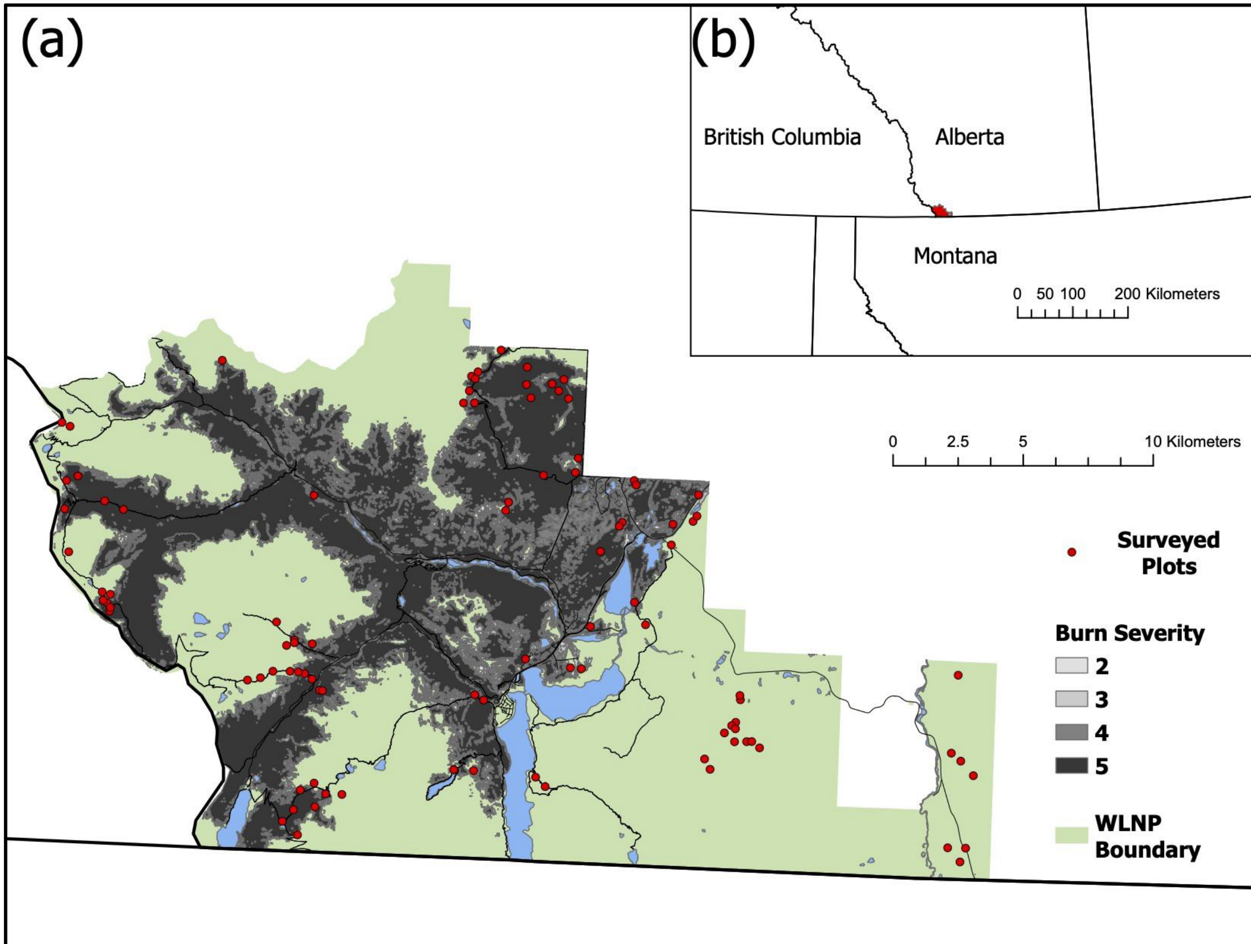

Figure 1. (a) Map outlining the boundaries of Waterton Lakes National Park (WLNP). The area burned in the 2017 Kenow Fire is indicated by grey shading according to burn severity. Red points show the locations of all surveyed plots. (b) The location of Waterton Lakes National Park (red) within the province of Alberta and the surrounding provinces and states.

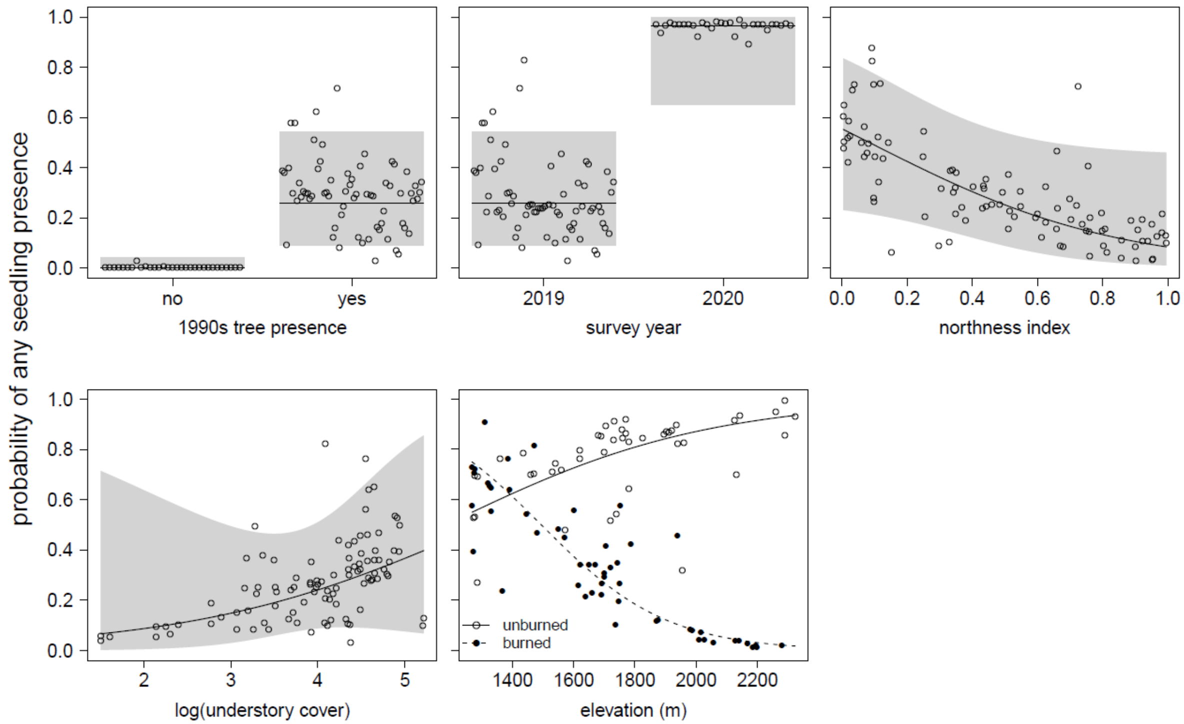

Figure 2. Partial regression plots based on the best model for presence/absence of any species of tree seedling showing the predicted probability of seedling occurrence for historical tree presence, survey year, northness index (1 = northerly aspects, 0 = southerly aspects), total understorey cover, and the interaction between burn status and elevation. In each panel, all other predictors in the model are held constant at their median or the most frequent category. Confidence bands show the 95% confidence interval for the conditional prediction. These bands are omitted in the last panel for clarity.

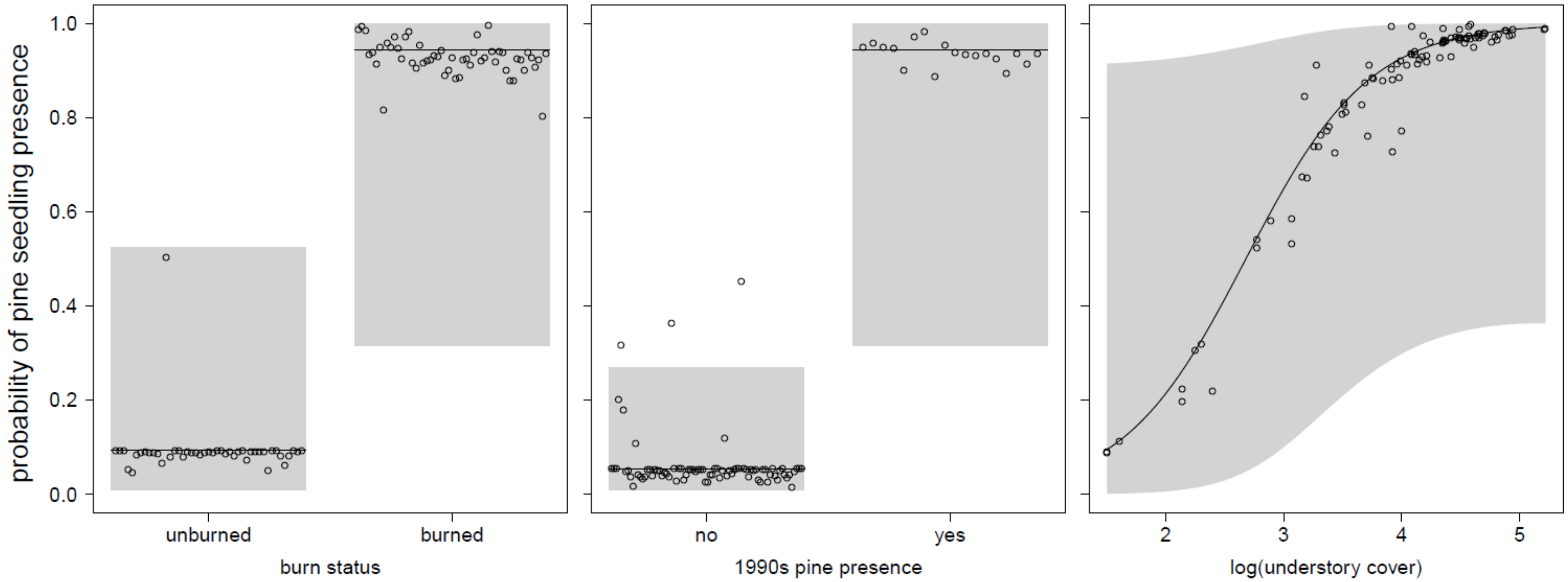

Figure 3. Partial regression plots based on the best model for presence/absence of lodgepole pine seedlings showing the predicted probability of seedling occurrence for burn status, historical tree presence, and total cover of understorey vegetation. In each panel, all other continuous predictors are held constant at their median except historical pine presence was set to 'yes' when not the focal predictor. Confidence bands show the 95% confidence interval for the conditional prediction.

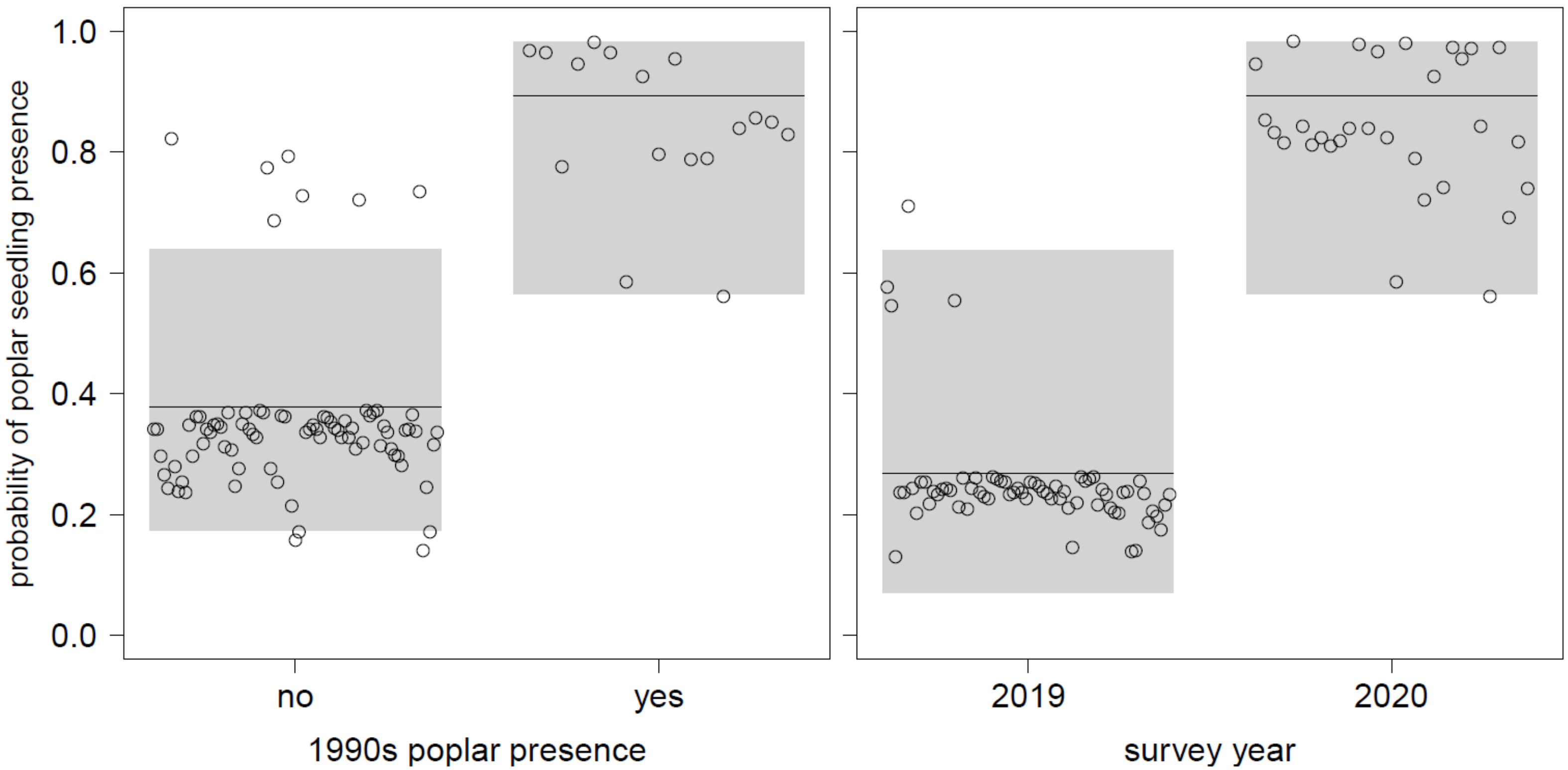

Figure 4. Partial regression plots based on the best model for presence/absence of poplar seedlings showing the predicted probability of seedling occurrence for historical tree presence and survey year. Burn status is set to 'unburned'. In the first panel, survey year is set to 2020. In the second panel, historical poplar presence is set to 'yes'. Confidence bands show the 95% confidence interval for the conditional prediction.

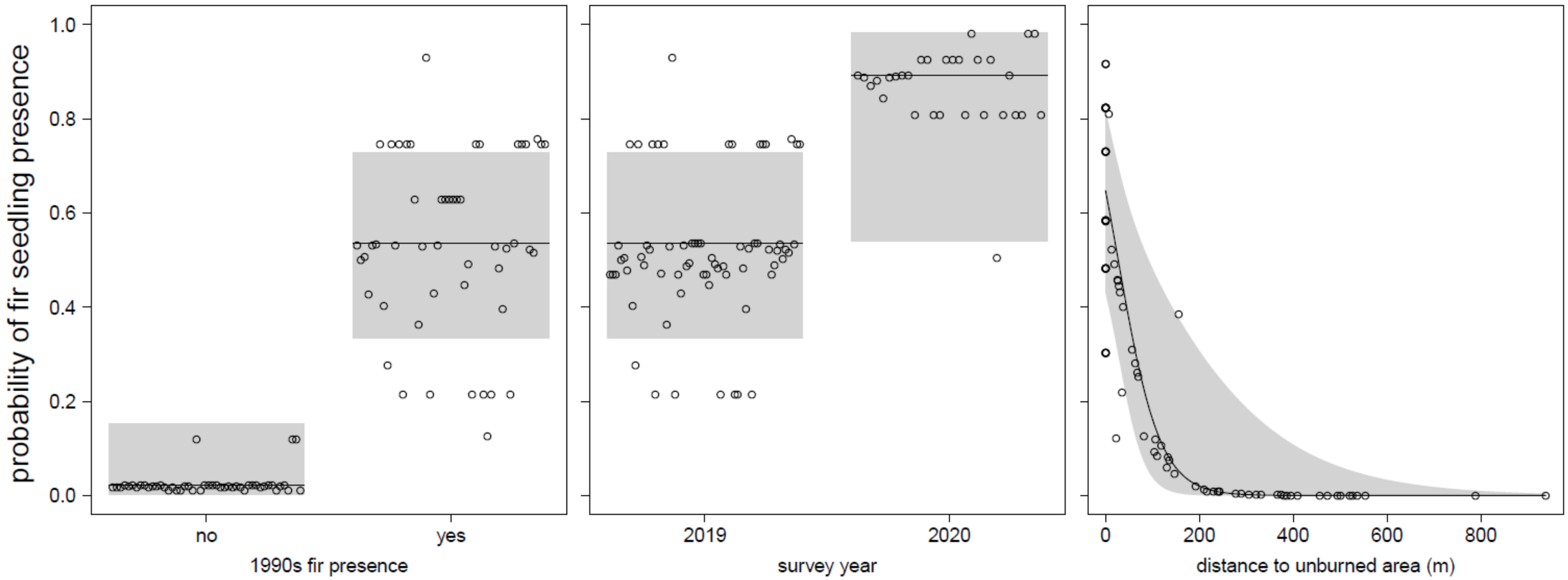

Figure 5. Partial regression plot based on the best model for presence/absence of subalpine fir seedlings showing the predicted probability of seedling occurrence based on historical tree presence, survey year, and distance to unburned area. In each panel other factors are held constant at their median or the most frequent category. Confidence bands show the 95% confidence interval of the conditional prediction.

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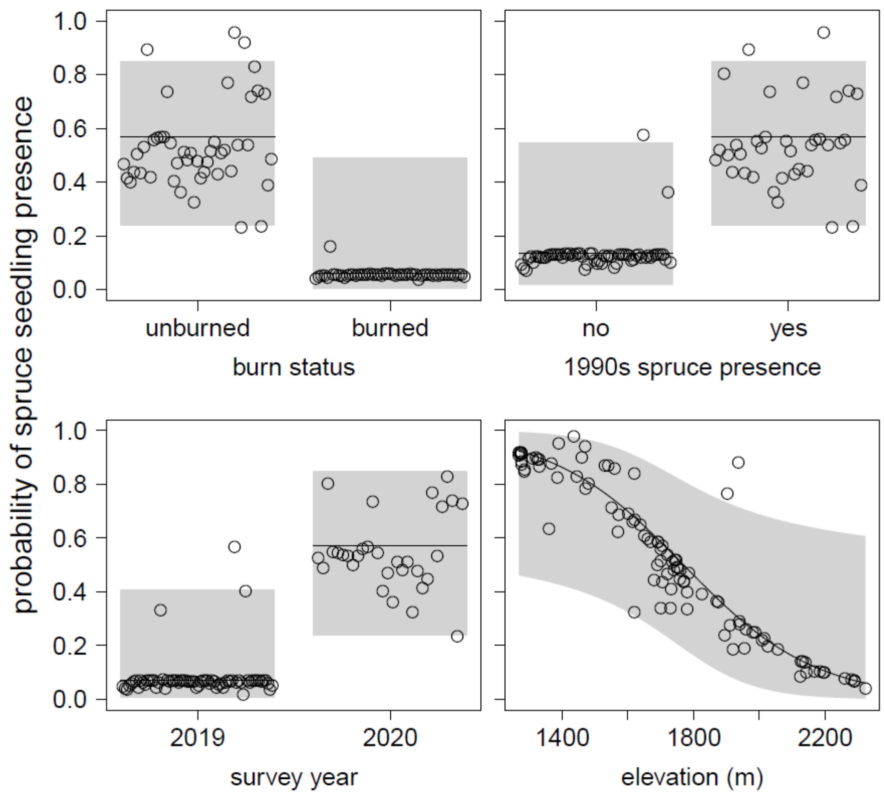

Figure 6. Partial regression plots based on the best model for presence/absence of Engelmann spruce seedlings showing the predicted probability of seedling occurrence for burn status, historical tree presence, survey year, and elevation. Burn status is set to 'unburned', 1990s spruce presence is set to 'yes', and survey year is set to 2020 in the panels in which they are not the focal predictor. Confidence bands show the 95% confidence interval of the conditional prediction.