**Title:** *Repeat short-interval fires continue to transform boreal forests beyond a modeled simple conifer to deciduous transitions*

**Abstract:**

Warming temperatures in the boreal have increased the frequency and severity of wildfires, causing time intervals between fires in areas to decrease to 10-15 years within the last several decades. Shortening fire intervals drive changes in successional pathways in boreal forests, but the extent of those changes and the interaction between topography and fire remains unclear. While post-fire succession in upland boreal black spruce forests is well understood, the effect of varying topography on the impact of multiple short-interval fires remains unclear. To investigate how increasing short-interval fires impact both conifer and deciduous post-fire regeneration, and to examine whether landscape variability alters that impact, we established 50 plots across a mosaic of fire histories (1-3 fires in 70 years) in two Interior Alaska sites with differing hydrology. We compared regeneration of conifers, deciduous trees/shrubs, and graminoids in an upland site (drier) and a lowland site (wetter). All stands were originally dominated by black spruce (*Picea mariana*), and at both sites, black spruce regeneration was significantly lower following three fires, compared to unburned stands and stands burned once. In the wetter lowland site, less organic soil was consumed by fire and presence of black spruce persisted until two fires, indicating local topography may initially drive successional divergence via differences in substrate consumption. Deciduous regeneration differed between two sites after three fires, with Alaskan birch (*Betula neoalaskana*) dominating in upland plots and willow (*Salix spp.)* and aspen (*Populus tremuloides*) in lowlands. Results of this study offer strong empirical evidence of the divergence of boreal successional trajectories from previous historic norms and indicate the importance of examining the role of spatial heterogeneity on the impact of multiple disturbances.

**I. Introduction**

An increase in the frequency and intensity of wildfires in northern latitudes driven by warming temperatures has sparked concern that short-interval fires will drive changes in forest composition and structure via altered successional trajectories (Young et al. 2017). Fire is the primary initiator of secondary succession in boreal systems (Kurkowski et al. 2008), but typically occurs within return intervals of ~ 100 years in Interior Alaska (Yarie 1981, Viereck 1983, Johnstone et al. 2010). Across the last six decades, an increasing rate of fire return intervals of 20 years or less has raised concerns that shortening fire intervals may disrupt historic successional trajectories and lead to landscape-level shifts in forest composition and structure (Kasischke et al. 2010, Brown & Johnstone et al. 2012, Johnstone & Chapin 2006a, Johnstone & Chapin 2006b, Mann et al. 2012).

The predominant successional pathway in boreal Interior Alaska is self-replacement (Kurkowski et al. 2008). Black spruce (*Picea mariana*) typically self-replaces via large canopy seedbanks after fire, remaining the dominant canopy cover before and after disturbance. Its semi-serotinous cones enable dense regeneration within 10 years after fire (Kurkowski et al. 2008, Johnstone et al. 2004, Johnstone et al. 2010), allowing the species to maintain persistent canopy cover under historic fire return intervals (Johnstone et al. 2010). However, serotinous regeneration strategies are more vulnerable under increasing short-interval fires in boreal and other systems. Short-interval fires can consume local serotinous seedbanks, extirpating local populations and allowing for rapid forest type conversion (Buma et al. 2014). The majority of *P. mariana* seeds disperse within distances of 30 meters (move up citation). In the boreal specifically, the consumption of *P. mariana* seedbanks via short fire intervals promotes an increase in deciduous trees and shrubs which have larger dispersal distances, allowing them to recolonize from outside burn perimeters (Brown and Johnstone 2012, looking for dispersal distance citation). Modeling results suggest that an increase in area reburned in short intervals will lead to a shift in forest community composition from conifer-dominated stands to deciduous forest (Mann et al. 2012, Roland et al. 2019) or grassland (Brooks et al. 2004, Rupp et al. 2011) via a disfavoring of serotinous regeneration.

Under shortening fire intervals, *P. mariana* self-replacement may be further disfavored by the interactive effect of substrate consumption and deciduous seed characteristics (Brown & Johnstone 2012, Johnstone et al. 2004, Hollingsworth et al. 2013, Johnstone & Chapin 2006a, Johnstone et al. 2009). Mature *P. mariana* stands have deep soil organic layers, which strongly control trends in regeneration: the large seeds of *P. mariana* can withstand extreme fluctuations in temperature and moisture experienced during time spent in surface organic layers, allowing them to outlast the smaller seeds of deciduous species like aspen (*Populus tremuloides)* and birch (*Betula neoalaskana)* (Greene and Johnson 1999, Viereck 1983, Johnstone et al. 2010). Short-interval fires may consume deep soil organic layers entirely, exposing mineral soil surface and promoting deciduous dominance (Whitman et al. 2018, Johnstone et al. 2010). Theremoval of soil organic layers by repeated fire negates the establishment advantage of *P. mariana* seeds and favors *B. neoalaskana* and *P. tremuloides* which produce large quantities of small wind-borne seeds that germinate directly on mineral soil surfaces (Roland et al. 2013, Barrett et al. 2016, Johnstone et al. 2010A). (a majority of *P. mariana* seeds fall within 30 m of seed source) (McCaughey et al. 1985)Finally, increasing frequency of short-interval fires may prevent the redevelopment of organic layers (which typically re-establish in conjunction with *P. mariana* communities) (Johnstone et al. 2010), further favoring competitive establishment of deciduous species and cementing the possibility of rapid ecological change in the boreal.

Signs indicate deciduous species-replacement post-fire successional pathways have already become more common under shortening fire intervals: the transition of dominance from *P. mariana* to *B. neoalaskana* and other deciduous species following two consecutive fires has been well documented in Interior Alaska (Johnstone et al. 2004), the Yukon Territory (Brown et al. 2015, Whitman et al. 2018), Eastern Canada (Bergeron et al. 2012) and Northern Minnesota (Camill & Clark 2000, Frelich et al. 2017). The effect of single reburns in *P. mariana* stands is well documented in boreal Interior Alaska, but primarily in gently sloped upland environments (Gibson et al. 2016, Houle et al. 2017). Successional trends in flatter and wetter lowland topographies remain underexamined, though they represent 42% of boreal Interior Alaska (Douglas et al. 2014, Jorgensen and Shur 2007). The under-examination of reburns in lowlands in comparison to uplands may be in part because of the historic unlikelihood of lowlands burning (Le Goff and Sirois 2004, Whitman et al. 2019). Higher soil moisture in lowlands may have an important role in mediating the effects of fire on successional pathways in lowland environment (Houle et al. 2017): the importance of substrate consumption in driving post-fire successional trajectories suggests that *P. mariana* stands in lowland environments may be more resilient or resistant to change. Given the trend towards warmer and drier summers, lowland environments may begin burning more frequently, making it crucial to understand post-fire successional trajectories in lowlands, particularly if their wetter site conditions are more resistant to the effects of shortening fire intervals. Wetter site conditions may limit consumption of substrate during fire events, therefore limiting the mechanism disfavoring conifer regeneration.

Prior research on shortening fire intervals has been limited to single reburn events (2 fires in sequence) in conifer stands, and in Interior Alaska, primarily upland *P. mariana* stands. This limits our ability to make inferences regarding future boreal forest community composition for two reasons: One, the cumulative effects of three or more fires on *P. mariana* stands remains unknown, though we can expect to see fire sequences of that magnitude in the future. Secondly, research on short-interval fires has almost entirely focused on conifer resilience, limiting our understanding of the effects of short-interval fires on emerging deciduous stands. An increase in fire frequency means an increase in repeated short-interval events in both *P. mariana* stands and potential emerging deciduous communities. Given the increasing evidence that reburning leads to stands dominated by deciduous trees and shrubs (Johnstone et al. 2011, Brooks et al. 2004), understanding the effects of multiple short-interval fires on emerging deciduous-dominated stands will be essential to understanding and predicting the impact of ongoing environmental and climatic change in high-latitude environments.

This study characterizes post-fire regeneration of tree species in upland and lowland stands across a gradient of 0-3 fires occurring via a rapid increase in fire frequency from the 1940’s to present in boreal Interior Alaska. We ask the following research questions:

1. What is the impact of repeat short-interval fires on conifer and deciduous post-fire tree regeneration?

2. Does local topography (site type) mediate the effect of repeat short-interval fires on tree regeneration of either conifer and deciduous populations?

3. What is the impact of post-fire soil characteristics on post-fire tree regeneration, and does it differ according to site type?

We hypothesize the following: repeat, short-interval fires will reduce conifer regeneration and favor an increase in deciduous tree regeneration in stands previously dominated by *P. mariana*. We anticipate that plots in the well-drained, sloped upland sites may be less resistant to this switch from conifer to deciduous, given the proposed effect of underlying drainage conditions on substrate consumption during fire. Finally, we hypothesize that repeat subsequent burning (3 fires in sequence in short intervals) in newly transitioned or emerging deciduous stands will cement successional trends in favor of broadleaf species.

We test these hypotheses by A) documenting patterns of post-fire regeneration across a range of fire histories within a single pre-fire forest type in upland and lowland sites and by B) comparing the effect of fires on post-fire conifer and deciduous regeneration within each site. Finally, we investigate the subsequent roles of topographic and soil characteristics in cementing trends in post-fire conifer and deciduous tree regeneration.

**II. Methods**

**Figure 1. Map of Study Sites. [need to add scale bar]**

**A close up of a map

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**Site Selection**

We established a total of 50 individual 20x20m plots in the summers of 2018 and 2019 between an upland and lowland location in Interior Alaska in natural mosaics of *P. mariana* pre-fire forest types differing in reburn sequence (Figure 1). Using burn history identified with historic aerial photographs from the Alaska Large Fire Database (https://www.frames.gov/catalog/10465) and modern remotely sensed fire perimeters from MTBS (https://www.mtbs.gov), we identified plots of pre-fire mature *P. mariana* stands that have experienced between one to three fires in the last 60 years, with the final burn in 2004, 2005 or 2006 (Table S1 and S2). Eight plots were established in unburned mature *P. mariana* stands as controls (total n=50). For the earliest fires, pre-fire composition and complete aboveground mortality at a plot was inferred via the historical photographs described above and verified via wood anatomy/tree ages where possible. We sampled plots representing four specific stages of reburn history: 1) mature unburned *P. mariana* forest stands (Fig. 2A), 2) once-burned *P. mariana* forest recovering from a single short-interval fire (~15 years ago, Fig. 2B), 3) twice-burned *P. mariana* forest recovering from two short-interval fires (one ~ 30 years ago, and the second ~15 years ago, Fig. 2C), and 4) thrice-burned *P. mariana* forest, burned once ~45 years ago, a second time ~30 years ago and finally a third ~15 years ago (Figure 2D). Time between fires was constrained to 10-15 years, and all plots last burned 15 to 16 years ago.

Fires were of comparable size and severity (Table S1 and S2). All plots experienced full canopy mortality during each fire, as identified by aerial photography and remotely sensed fire perimeters described above. To verify, we aged snags to ensure no survivors existed from prior events.

To infer initial site conditions, we also surveyed unburned stands in both sites (n = 4 each) (Fig. 4A). Surveying in unburned *P. mariana* stands helped determine whether meaningful differences in forest structure characteristics existed between the upland and lowland site prior to fire.

*Site Locations and History*

Plots were randomly placed within various burn histories, with a minimum of 50 meters spacing and a minimum of 100 meters away from unburned legacies to control for *P. mariana* dispersal distances. Plots were stratified evenly between an upland and lowland location. The upland site (n = 26) represents well-drained, gently sloped (slope 3-13 degrees) boreal forest topographies; the lowland (n = 24) a flatter (slope = 0.3-2.6 degrees), more poorly drained location (Table SX). Plots were climatically similar: (data obtained from the Western Regional Climate Center database: <https://wrcc.dri.edu/wraws/akF.html>). Both are on the northern edge of the discontinuous permafrost zone and nearby unburned *P. mariana* communities have shallow permafrost in both locations (data not shown). All plots were dominated by *P. mariana* before the first fire with occasional individual *B. neoalaskana* or *Salix spp*.

**Figure 2. Pictures of study sites. A) Unburned mature black spruce stand. B) Once-burned former black spruce stand, 15 years since last fire C) Twice-burned former black spruce stand, 15 years since last fire. D) Thrice-burned former black spruce stand, 16 years since last fire.**

A view of a forest

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*Field Sampling*

To determine the impact of repeat short-interval fires on conifer and deciduous post-fire regeneration, we surveyed density, basal area and composition of each plot. For all individual trees above diameter at breast height (DBH or 1.37 meters), we recorded species, DBH and condition (live or dead). Where density precluded counting over the entire 400m2, a randomly selected subset (100 or 200 m2) was counted and then scaled accordingly. We recorded presence, species and condition of seedlings that fell below 1.37 meters across ten 1-meter sections randomly placed on each plot. For asexual reproducers such as *Salix* and *P. tremuloides*, each individual stem in a given clump was counted and then clumps and their characteristics (including basal area) were pooled and treated as individuals in order to avoid overestimating abundance of regeneration.

To characterize post-fire soil characteristics in each site, we evaluated organic layer depth, percent cover of exposed mineral soil and adventitious roots. Distance from adventitious roots to current soil surface was measured where snags with such roots were available to sample to infer soil consumption in the most recent fire (Walker et al. 2018). Current organic layer depth was measured at the center and at each corner of each plot. Presence and abundance of organic and exposed mineral soil surfaces were estimated across 1-meter subplots at each corner of each site.

**Data Analysis**

To characterize post-fire patterns of tree regeneration, we examined patterns in three metrics of regeneration amongst tree species: 1) the relative presence or proportion of species within a plot, 2) density (number of stems per hectare), and 3) basal area (square centimeters per hectare). The drivers and implications of changes in tree density, tree basal area and tree proportion are distinct and meaningful. Stem density is used to represent post-fire stand structure. Basal area is used here as an indication of biomass, representing stand-level trends in aboveground carbon. We use the proportion of tree species present on a plot here to investigate stand-level patterns in post-fire tree community composition. Using all three metrics allows us to distinguish accordingly.

To characterize patterns in post-fire tree regeneration according to number of reburns, differences in patterns of tree regeneration across reburn history and between site type were evaluated using Kruskal-Wallis tests, followed by pairwise comparisons using Dunn’s test with Bonferroni corrected p-values.

To investigate whether site type plays a role in mediating the effects of repeat short-interval reburns on conifer and deciduous tree regeneration, we used generalized linear mixed effect models (GLMEs) to evaluate the effects of both while accounting for the random effect of plot. We tested whether the effects of fire interacted with the effect of site type by allowing for interactive effects between the two. Plot ID number was included as a random effect to account for unmodeled variance between individual plots. We modeled two metrics of conifer and deciduous tree communities (density and basal area) and one metrics of conifer and deciduous seedling communities (density).

To examine the specific effects of both topographic and soil characteristics on trends in post-fire regeneration, we tested generalized linear mixed effect models containing those attributes as fixed effects. We accounted for the variation explained by fire and site type by treating number of fires as a random slope that varied as a function of site, allowing us to focus on the remaining effects of topography and soil characteristics. Fixed effects included the following topographic and soil characteristics: slope, total annual solar radiation, average organic layer depth, and average exposed mineral soil. Slope and solar radiation for each site were calculated using IFSAR digital elevation models from the Alaska mapping initiative (USGS 2019). Elevation, while an important factor driving tree community composition in Alaska, was not included as a variable since it did not vary meaningfully either between sites or within sites (Table SX). All fixed effect variables were standardized (mean zero, SD 1) using the ‘effectsize’ package in R to allow for comparison of effect sizes (Makowski et al. 2019). Overall model fit was evaluated using AIC.

All analysis, model fit, and selection were performed in R version 1.2.1335 (R Development Core Team, 2018) and reported means include one standard deviation. Generalized mixed models were conducted using ‘lme4’ (Bates et al. 2019). Figures were created through ‘ggplot2’ (Wickham 2016) and ‘cowplot’ (Wilkes et al. 2019). Because our plots are clustered by design to take advantage of natural experimental conditions, spatial autocorrelation among plots was assessed using Moran’s I. We found evidence of spatial autocorrelation within tree data of lowland plots (Table S3) but accounted for the grouping of plots in sites by including site as a random effect in GLMEs. No spatial autocorrelation was found within seedling densities at either site.

**III. Results**

Paragraph - Initial conditions [insert unburned figures basal / density] Overall tree basal area was highest in unburned plots of both sites (117 cm2/ha, SD 294) (Figure 5). Upland plots had consistently higher basal area than lowland plots across all fire histories, even in unburned controls.

**Patterns of regeneration across reburns**

*Patterns in species presence: Current canopy individuals*

Individuals above DBH represent current canopy composition conditions: 6 plots had no individuals large enough to qualify as trees (2 once-burned upland plots, 2 once-burned lowland plots, and 2 twice-burned lowland plots). Only unburned plots contained canopies dominated in abundance by conifers: the overstories of all burned sites were predominantly composed of deciduous species. Trends in deciduous species presence diverged between upland and lowland plots by the third fire: twice-burned plots of both sites contained high proportions of *B. neoalaskana*, that proportion declined in thrice-burned lowland plots, and *P. tremuloides* became the most present overstory species on average (Table 1).

*Patterns in species presence: seedlings*

*P. mariana* seedlings were most abundant in unburned plots in both the upland (average proportion present 86.7%, standard deviation 11.4%) and lowland site (98.2% SD 3.5%). *P. mariana* seedling presence persisted into thrice-burned plots of both sites, but in very low relative quantities (uplands 2.3% and lowlands 4.9%). The proportion of deciduous seedlings present increased across reburn sequence in both upland and lowland plots: *B. neoalaskana* and *Salix* seedlings increased between once-, twice- and thrice-burned upland plots while lowland plots were characterized by increasing presence in *Salix* and *P. tremuloides* seedlings. *Salix* spp. were the most present seedling in twice- and thrice-burned lowland plots, though *B. neoalaskana* and *P. tremuloides* were the most present tree species in the canopy.

**Figure 3. Average proportion of species of all growth forms present on a plot across reburn sequence between upland and lowland plots. Error bars represent standard deviations.**

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**Figure 4. Conifer and deciduous tree density across reburn sequence and between site types. Results from Dunn’s multiple pairwise comparison test shown where differences were significant. Only sequential comparison results presented. Significance of effect indicated as follows: \*\*\* p ≤ 0.001, \*\* p ≤ 0.01, \* p ≤ 0.05.**

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*Patterns in density*

Total tree density was highest in unburned plots in both the upland and lowland site (mean 584 stems per ha, SD 913 in uplands and 245 stems per ha, SD 636 in lowlands) and declined with continued reburning in both sites (Figure 4). Pairwise Dunn’s tests between groups showed that conifer tree densities only differed significantly between unburned and once-burned plots in both sites (Dunn’s test, upland p-value = <0.001, lowland p-value = <0.001). Patterns in deciduous tree densities differed according to site: deciduous tree density in upland plots was only significantly different between once- and twice-burned plots (p = <0.001), while lowland deciduous tree density different significantly between unburned and once-burned plots (p = <0.001) and twice and thrice-burned plots (p=<0.001) (Figure S1).

Total seedling density increased significantly in both sites after one fire (Dunn’s test, upland p = <0.001, lowland p = <0.001), but site-level trends diverged after subsequent fires (Figure 4). Conifer seedling density was significantly different between all reburns in upland plots (0 vs 1 p = <0.001, 1 vs 2 p = <0.001, 2 vs 3 p = <0.001). Density of conifer seedlings was only significantly different between unburned and once-burned plots (p = <0.001) and twice- and thrice-burned plots (p = <0.001). Deciduous seedling density increased significantly after one fire in both sites (upland p = <0.001, lowland p = <0.001), and continued to increase significantly with additional reburns in lowland plots (1 vs 2 p = <0.001, 2 vs 3 p = <0.001) but was not significantly different in reburned upland plots (1 vs 2 p = 0.07, 2 vs 3 p = 1) (Figure S3).

*Patterns in Basal Area*

Similar to densities, summed conifer tree basal area only differed significantly between unburned and once-burned plots in both sites (Dunn’s test, upland p = <0.001, lowland p = <0.001). Upland deciduous basal area differed significantly between unburned and once-burned plots (p = <0.001) and once- and twice-burned plots (p = <0.001), while lowland deciduous basal area differed significantly between all fire histories (0 vs 1 p= <0.001, 1 vs 2 p = <0.001, 2 vs 3 p = <0.001) (Figure S2).

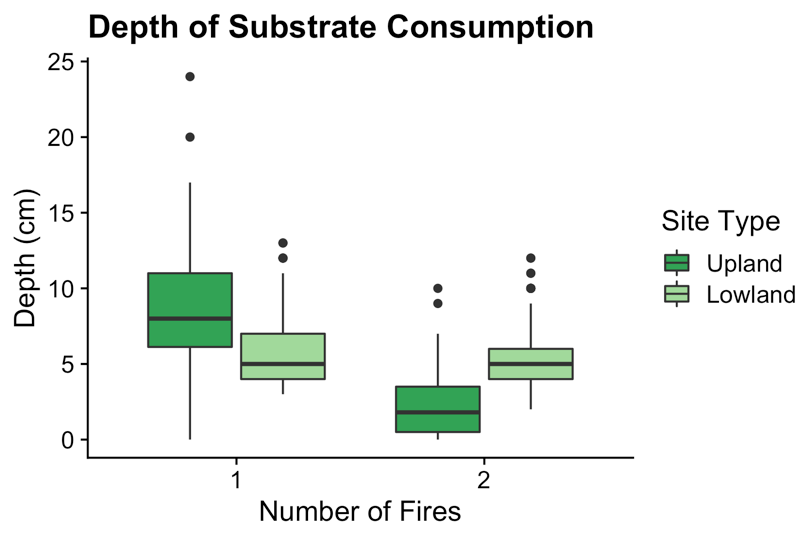
**Figure 5. Conifer and deciduous tree basal area (cm2/Ha) across reburn sequence and between site types. Results from Dunn’s multiple pairwise comparison test shown where differences were significant. Only sequential comparison results presented. Significance of effect indicated as follows: \*\*\*\* p ≤ 0.0001, \*\* p ≤ 0.01, \* p ≤ 0.05.**

**A screenshot of a cell phone

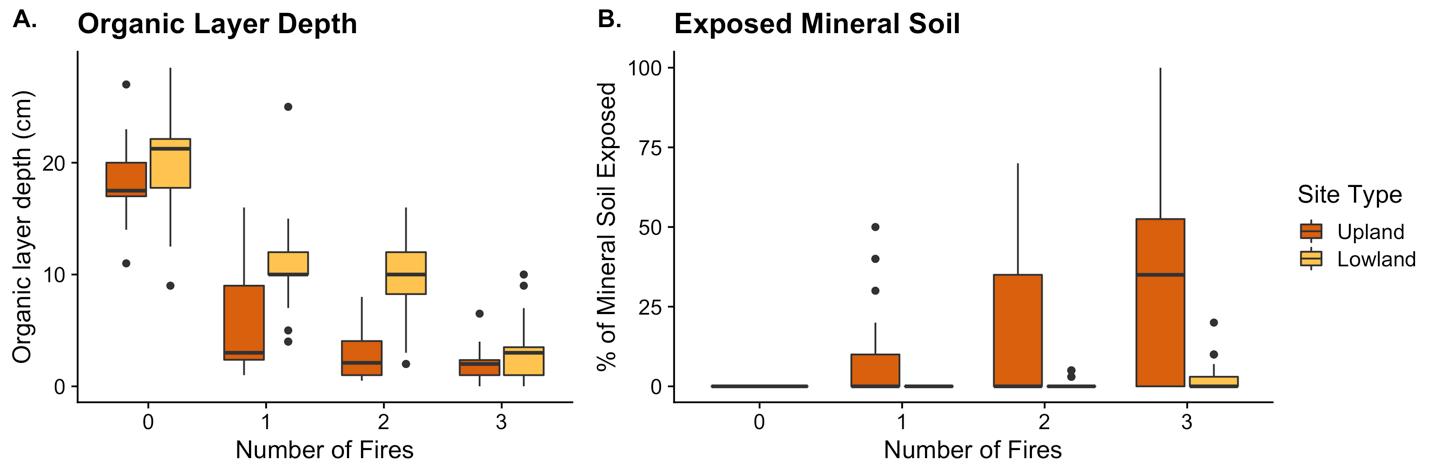
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**Patterns of post-fire soil characteristics across reburns**

**Figure 6. Inferred substrate consumption: distance in centimeters between highest adventitious *P. mariana* roots to soil surface across reburn sequence.**



**Figure 7. A) Depth of Organic Layer (cm) in upland and lowland plots according to reburn sequence. B) Percent cover of exposed mineral soil in upland and lowland plots across reburn sequence.**



Adventitious roots were only available to sample in once- and twice-burned plots, as three burn plots had no *P. mariana* to assess (Figure 6). Depth from adventitious root to current soil surface ranged from 0 to 24 cm in once-burned upland plots, and 3 to 7 cm in once-burned lowland plots. Average adventitious root depth in upland plots shrank between once- and twice-burned plots by a factor of 2.4. Adventitious root depth in lowland plots did not differ significantly (Dunn’s test, p-value = 0.17) between once-burned and twice-burned plots.

Lowland organic-layers were thicker than upland layers regardless of number of reburns by a factor of 1.6, and the difference between the two sites was largest in twice-burned plots where lowland organic-layers were larger by a factor of 3.2. The decline in organic layer depth occurs faster in upland plots than in lowland plots: organic layers were reduced by a factor of 3.2 after one fire in upland plots, but only by a factor of 1.8 in lowland plots (Figure 7A). Similar trends exist for exposed mineral soil: upland plots had no exposed mineral soil in unburned plots but saw an increased in the amount of exposed mineral soil, up to 100% in some thrice-burned plots (Figure 7B).

**Impact of repeat fires and topography on tree regeneration**

Site type did not appear to play a role in mediating the effects of repeat short-interval fires on tree regeneration across the 3-burn sequence. In every case, model fit improved when number of fires and site type were held as separate fixed effects (fire + site), rather than interactive effects (fire\*site). The lack of interaction indicates that 3 short-interval fires had the same effect on deciduous and conifer post-fire regeneration in both the upland and lowland site. In both sites, increasing numbers of reburns reduced both conifer tree density and conifer basal area. Increasing short-interval fires lead to greater deciduous density and basal area in both upland and lowland stands (Figure 2A).

**Table 2. Parameters of fire-regen models (regen = fires + site + (1 | plot ID number) with CI, df and p-values based on Wald approximation.**

**Table 2A. Effects of fire and site on post-fire density and basal area of conifer and deciduous trees.**

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Metric** | **Division** | **Effect** | **Coeff.** | **SE** | **95% CI** | **z** | **df** | **p** |
| Density | **Conifer** | Intercept | - 9.37 | 3.33 | (-15.91, -2.84) | - 2.81 | 496 | .005 |
| Fire # | - 0.39 | 1.43 | (-3.19, 2.41) | - 0.27 | 496 | .784 |
| Site | - 0.23 | 2.24 | (-4.63, 4.17) | - 0.10 | 496 | 0.919 |
| **Decid.** | Intercept | 4.82 | 0.41 | (4.01, 5.63) | 11.66 | 496 | <.001 |
| Fire # | 0.83 | 0.19 | (0.46, 1.2) | 4.44 | 496 | <.001 |
| Site | - 0.48 | 0.31 | (-1.08, 0.12) | -1.55 | 496 | 0.12 |
| Basal Area | **Conifer** | Intercept | 6.01 | 3.95 | (-1.73, 13.75) | 1.52 | 495 | 0.128 |
| Fire # | -2.73 | 1.78 | (-4.05, -1.91) | -1.53 | 495 | 0.126 |
| Site | 2.48 | 2.91 | (-3.22, 8.18) | 0.85 | 495 | 0.394 |
| **Decid.** | Intercept | 66.19 | 53.09 | (-37.86, 170.24) | 1.25 | 495 | 0.212 |
| Fire # | 38.08 | 23.95 | (-8.86, 85.02) | 1.59 | 495 | 0.112 |
| Site | -111.15 | 39.09 | (-187.76, -34.54) | -2.84 | 495 | 0.004 |

**Impact of topographic and post-fire soil characteristics on tree regeneration**

To further investigate the potential differences between tree regeneration in our upland and lowland sites, we examined the effect of specific topographic and post-fire soil characteristics. After accounting for the variation explained by reburn sequence, the primary factors driving post-fire tree density of conifers in order of effect sizes were solar radiation (+), slope (+) and average organic layer depth (-) (Table 3). Post-fire conifer basal area was controlled by the same effects, though average organic layer depth had a slightly larger effect than slope (- 6.28 compared to 5.98 respectively) (Table 4A). Deciduous tree density was similarly driven by solar radiation (-), elevation (+), average organic layer depth (-) and exposed mineral soil (-) while basal area of post-fire deciduous trees was controlled primarily by average organic layer depth (-) (Table 3 and 4B). Seedling densities were similarly driven (Table 3 and 4A).

**Table 3. Best fitting multivariate linear mixed-effect models describing post-fire stem density, stem proportion and basal area for conifer and deciduous regeneration across growth forms.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  |  | Metric | Model | Df |
| **Tree** | **Conifer** | Density | SLOPE + OL\_AV + (1 + FIRE | SITE) | 9 |
| BA | SLOPE + (1 + FIRE | SITE) | 9 |
| **Deciduous** | Density | SOLAR + ELEV + OL\_AV + EXP\_MIN + (1 + FIRE | SITE) | 9 |
| BA | OL\_AV + (1 + FIRE | SITE) | 6 |
| **Seedling** | **Conifer** | Density | SLOPE + SOLAR + ELEV + OL\_AV + EXP\_MIN + (1 + FIRE | SITE) | 10 |
| **Deciduous** | Density | SLOPE + SOLAR + ELEV + EXP\_MIN + (1 + FIRE | SITE) | 8 |

**Table 4. Direction and significance of effect sizes of topographic and soil attributes on regeneration of conifer and deciduous seedlings and trees. Significance of effect indicated as follows: \*\*\* p ≤ 0.001, \*\* p ≤ 0.01, \* p ≤ 0.05. Stem densities represented by stems/Ha, basal area by cm2/ha**

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Covariate | | **Tree and Seedling Density** | | **Tree Basal Area** | |
| *Conifer* | *Decid.* | *Conifer* | *Decid.* |
| **Topographic Attrib.** | Slope | + 14.66 \*\* |  |  |  |
| Solar Radiation |  | - 3023.31 \*\*\* |  |  |
| **Soil Attrib.** | Av. OL Depth | - 20.33 \*\*\* | - 533.15 \*\*\* |  |  |
| Av. Exp. Min. Soil |  | - 471.27 \*\*\* |  |  |

**IV. Discussion**

Our two primary objectives were to 1) characterize post-fire tree regeneration in sites that experienced up to three short-interval fires, and 2) investigate whether the effect of fire differed according to site type (via differences in local topographic and soil characteristics). Reburned stands in this study were predominantly composed of deciduous species, though the specific assemblages of species differed between the upland and lowland site. Conifer populations declined later in the reburn sequence in the lowland site, suggesting that local site conditions may allow conifers to persist for longer under repeated short-interval fires. However, after three fires, conifer tree populations in the lowland site declined to the same level as the upland counterparts, indicating a possible threshold of resistance to the conifer-deciduous transition had been crossed.

Patterns of burn severity differed between sites as predicted: upland plots had substantially thinner organic layers and significantly more exposed mineral soil than lowland equivalents. Given the role of burn severity in altering circumstances of competitive standing between coniferous and deciduous species, this variation between sites indicates that heterogeneity in hydrology via local topography may facilitate resilience or resistance in *P. mariana* stands experiencing increasing short-interval fires. Local soil moisture may act as a mechanism of resistance to short fire intervals only up until a given threshold of fire exposure, ~~given that the organic layers in thrice-burned lowland plots did become statistically similar to those found in thrice-burned upland plots.~~

A divergence in species-level trends in tree occupation, density and abundance between upland and lowland sites indicates that site-level differences in drainage conditions and fire severity effects play an important role in determining species successional outcomes in boreal Interior Alaska. Upland reburned plots were composed of *Salix* and *B. neoalaskana* in higher abundance and densities than comparable lowland plots and experienced a decline in *P. mariana* earlier in the sequence of reburns. *P. mariana* populations declined slower in lowland plots and were replaced by *P. tremuloides* and *Salix* after three fires. Furthermore, reburned lowland plots contained consistently lower densities and basal area of trees than upland counterparts. Results from linear mixed effect models indicate that post-fire substrate conditions play an important role in controlling post-fire tree occupation, density and basal area conditions. However, number of fires did not interact with site type significantly to improve model fit, indicating the interaction between site type and reburn history did not better explain subsequent patterns of regeneration, forest structure and biomass.

Stand characteristics differed across reburn sequence and between sites. Our upland plots showed consistently higher tree density and basal area than lowland counterparts, but in both sites, both basal area and tree density never returned to pre-fire levels. Changes in stand density imply a change in stand structure, which has implications for landscape characteristics like aboveground carbon storage and landscape flammability. Given that fuel will play a central role in ongoing boreal fire regime change, understanding the influence of decreasing stand density on local fuel loads and structure will be crucial to managing and predicting future fire behavior in reburned stands (Higuera et al. 008). Furthermore, an overall decline in basal area with increasing fire implies a similar decline in aboveground carbon stocks, particularly aboveground storage of carbon by trees.

Paragraph addressing divergence between tree and seedling patterns: If you just look at trees, the trend is different

The extent, both spatially and temporally, of a trend towards a deciduous-dominated boreal remains unknown: a boreal transition towards deciduous communities appears to be spatially constrained to site- or fire-level effects (Roland et al. 2019). However, results from this study contribute to the growing body of evidence of site-level successional trajectory disruption caused by short-interval reburns. Furthermore, our results specifically indicate a disruption of self-replacement trajectories occurring even in a wetter lowland sites, previously thought to be more resistant or resilient to transition.

Our work presents several key inferences suggesting repeat reburning in Alaskan boreal *P. mariana* stands leads to an untethering of successional trends via consumption of substrate, regardless of site type. First, we found that in both sites in this study, deciduous communities emerged after multiple repeat short-interval fires, replacing original *P. mariana* communities entirely. While the specifics of species composition, structure and regeneration of those communities differed according to site type, both upland and lowland thrice-burned plots were predominantly composed of deciduous species of all growth forms. Second, the low quantities of *P. mariana* seedlings in twice- and thrice-burned plots suggests a potential local extirpation of *P. mariana* seed sources. Finally, organic soil layers in both sites were consumed during each reburn, even in the wetter lowland site, leading to increased exposure of mineral soil surfaces. No organic layer in reburned plots of either site has recovered to inferred pre-fire depth, even 15 years post-fire. Together, these patterns suggest that repeat burning leads to a meaningful disruption of existing successional trends despite proposed local resiliency via poorly drained lowland conditions, and that repeat burning in emerging deciduous post-fire communities cement successional trends towards dominance of deciduous trees and shrubs via removal of organic soil layers and surfaces.

**V. Conclusions**

Observed trends in tree regeneration indicate a boreal forest successional trajectory untethered from regional legacy conditions. Low abundance of *P. mariana* in burned plots suggests the prevention of self-replacement as a future successional pathway in our specific sites. Furthermore, deciduous species are emerging in assemblage’s novel to Interior Alaska boreal forests: the strong presence of *Salix* and *P. tremuloides* in particular indicate the emergence of not only a species-replacement successional trajectory, but a species-replacement successional trajectory much more in line with primary successional trends than secondary. Furthermore, the composition of emerging deciduous communities appears to differ according to local drainage conditions and therefore fire severity effects. Wetter lowland forests are initially more resistant to a transition to deciduous communities, given the mitigating effects of soil moisture, but that resilience appears to be overcome by subsequent fires. Results from this study indicate the importance of investigating the varying effects of multiple reburn events in different topographic contexts. Reburning can lead to local degradation of permafrost through changes in aboveground insolation, and so moving forward, investigating how changes to drainage induced by changing permafrost further influences fire behavior and successional trends will be critical to understanding future environmental change in the boreal.

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**VI. Supplemental Materials:**

**Table S1. Fire sequence, history and size across upland plots.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Plot ID #** | **# of Fires** | **Fire** | **Year** | **Fire Size** |
| 64, 65 | 1 | Missing Value |  |  |
| 12, 52, 41, 48, 50 | 1 | Fish Creek | 2005 |  |
| 42 | 1 | Erickson | 2003 |  |
| 56, 57, 47, 16, 8 | 2 | Rogers | 1967 |  |
| Fish Creek | 2005 |  |
| 39 | 2 | Missing Value |  |  |
| Fish Creek | 2005 |  |
| 32, 40 | 2 | Rogers | 1967 |  |
| Erickson | 2003 |  |
| 15, 54 | 3 | Missing Value |  |  |
| Rogers | 1967 |  |
| Fish Creek | 2005 |  |
| 55, 14, 7 | 3 | Missing Value |  |  |
| Rogers | 1967 |  |
| Missing Value |  |  |

**Table S2. Fire sequence, history and size across lowland plots.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Plot ID #** | **# of Fires** | **Fire** | **Year** | **Fire Size** |
| 33, 29, 28, 18, 5 | 1 | Boglen Creek | 2004 |  |
| 20, 36 | 1 | Graveyard Creek | 2006 |  |
| 26, 27, 4, 3, 19 | 2 | Crazy Mountain | 1953 |  |
| Boglen Creek | 2004 |  |
| 34 | 2 | Central W-10 | 1957 |  |
| Boglen Creek | 2004 |  |
| 22, 17, 25, 35, 24, 23, 2 | 3 | Central W-10 | 1957 |  |
| Albert Creek | 1974 |  |
| Boglen Creek | 2004 |  |

**Table S3.** Plots ranged in elevation from 245 m to 442 m above sea level and slope ranged from flat to 13 degrees. On average, upland plots received between 594,486 and 610,390 W/m2 of annual solar radiation, while lowland plots received 610,0880 to 618011 W/m2. Upland plots range from X-X degrees in winter and X-X degrees in summer, while lowland plots fall between X\_X and X\_X respectively, indicating the two sites are generally similar climatically. Upland plots receive an average of XX inches of rainfall per year, while lowland plots receive XX.

**Table S3. Results from Moran’s I for spatial autocorrelation in density (stem count per hectare) and basal area (square centimeters per hectare) of growth forms within upland and lowland sites.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Growth Form | Comparison | Variable | Observed | Expected | P-value | sd |
| Tree | Upland | Density | -0.02012 | -0.00775 | **0.03** | 0.005 |
| Basal Area | -0.02543 | -0.00775 | **> 0.01** | 0.005 |
| Lowland | Density | -0.00704 | -0.00598 | 0.79 | 0.004 |
| Basal Area | -0.00788 | -0.00598 | 0.64 | 0.004 |
| Seedling | Upland | Density | -0.05960 | -0.00483 | **>0.01** | 0.003 |
| Lowland | Density | -0.05379 | -0.00388 | **>0.01** | 0.004 |

**Table S5. Current composition of canopy and understory. Average relative proportion of trees and seedlings of all species between sites and across reburn sequence. Species not present at a given site not included. Bolded numbers represent species most present on average within site and number of fires.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Fires | Site | Species | Tree % | Tree SD (%) | Seedling % | Seed SD (%) |
| 0 | Upland | *B. neoalaskana* | 2.8 | 2.1 | 0.7 | 1.4 |
| ***P. mariana*** | **91.7** | **2.7** | **86.8** | **11.5** |
| *Salix* | 5.4 | 3.3 | 12.5 | 10.2 |
| Lowland | ***P. mariana*** | **99** | **0.7** | **98.1** | **3.8** |
| *Salix* | 0.9 | 0.7 | 1.9 | 3.8 |
| 1 | Upland | *A. crispa* | 14.4 | 11.5 | 7.6 | 16 |
| ***B. neoalaskana*** | **22.6** | **30.8** | 13.7 | 16.6 |
| *P. mariana* | 6.5 | 10.6 | **51.8** | **37.6** |
| *Salix* | 13.1 | 21.4 |  |  |
| Lowland | *A. crispa* | 14 | 21.9 | 0.4 | 1 |
| *B. glandulosa* | 5 | 11.2 |  |  |
| *B. neoalaskana* | 25 | 43.3 | 3.9 | 4.3 |
| *P. mariana* | 16 | 35.8 | **62.4** | **18.9** |
| *P. tremuloides* |  |  | 2.7 | 4.04 |
| ***Salix*** | **40** | **54.8** | 30.6 | 15.8 |
| 2 | Upland | *A. crispa* | 15 | 26.4 | 6.7 | 13.8 |
| ***B. neoalaskana*** | **62.2** | **24.7** | 8 | 10.8 |
| *P. glauca* |  |  | 7.3 | 20.5 |
| *P. mariana* |  |  | 29 | 23.3 |
| *P. tremuloides* | 0.8 | 2.5 | 12 | 31.5 |
| *Salix* | 21.9 | 17.8 | **36.9** | **30** |
| Lowland | *A. crispa* | 25 | 50 | 0.3 | 0.5 |
| *B. glandulosa* |  |  | 0.8 | 1.4 |
| ***B. neoalaskana*** | **50** | **40.8** | 3.7 | 1.4 |
| *P. mariana* |  |  | 33.8 | 12.3 |
| *P. tremuloides* |  |  | 6.3 | 3.1 |
| *Salix* | 25 | 28.9 | **55** | **12.5** |
| 3 | Upland | *A. crispa* | 21 | 26.5 | 4.8 | 6.19 |
| ***B. neoalaskana*** | **50** | **35.7** | **57.9** | **30.8** |
| *P. mariana* |  |  | 2.3 | 3.2 |
| *P. tremuloides* |  |  | 0.2 | 0.4 |
| *Salix* | 29 | 17.5 | 34.7 | 29 |
| Lowland | *A. crispa* |  |  | 0.3 | 0.5 |
| *B. glandulosa* | 3.4 | 8.9 | 2.8 | 3.5 |
| *B. neoalaskana* | 6.4 | 6.4 | 11.6 | 11 |
| *P. balsamifera* | 0.8 | 2.2 |  |  |
| *P. mariana* |  |  | 4.9 | 5.6 |
| ***P. tremuloides*** | **49** | **31.4** | 21.1 | 18 |
| *Salix* | 40.3 | 24.1 | **59.3** | **21.9** |

**Table S4. Results from comparison of conifer and deciduous tree basal area (cm2/Ha) and densities of conifer and deciduous tree and seedling densities (stem/ha) across reburn sequence and between site types using Dunn’s multiple pairwise comparison test. P-values adjusted with Holm-Bonferonni correction. Only sequential comparison results presented. Significance of effect indicated as follows\*\*\* p ≤ 1e-04, \*\* p ≤ 0.01, \* p ≤ 0.05.**

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Metric** | **Division** | **Site** | **Comparison** | **n1** | **n2** | **statistic** | **p** | **Adjust. p** | **Sig** |
| Density | Conifer | Upland | 1 vs 2 | 208 | 208 | -4.14 | 3.5e-5 | 3.5e-5 | \*\*\* |
| 2 vs 3 | 208 | 156 | -5.16 | 2.47e-7 | 4.93e-7 | \*\*\* |
| Lowland | 1 vs 2 | 210 | 180 | 0.0885 | 0.929 | 0.929 |  |
| 2 vs 3 | 180 | 210 | -4.74 | 1.29e-6 | 3.88e-6 | \*\*\* |
| Deciduous | Upland | 1 vs 2 | 208 | 208 | -0.744 | 0.457 | 1 |  |
| 2 vs 3 | 208 | 156 | 0.865 | 0.393 | 1 |  |
| Lowland | 1 vs 2 | 210 | 180 | 4.68 | 2.81e-6 | 5.61e-6 | \*\*\* |
| 2 vs 3 | 180 | 210 | -0.0196 | 0.984 | 0.984 |  |
| Basal Area | Conifer | Upland | 1 vs 2 | 80 | 80 | -3.72 | 0.0002 | 0.0004 | \*\*\* |
| 2 vs 3 | 80 | 60 | -1.15 | 0.251 | 0.251 |  |
| Lowland | 1 vs 2 | 98 | 84 | -1.58 | 0.115 | 0.23 |  |
| 2 vs 3 | 84 | 98 | 2.55 | 0.0109 | 0.0327 | \* |
| Deciduous | Upland | 1 vs 2 | 80 | 80 | 8.26 | 1.44e-16 | 4.31e-16 | \*\*\* |
| 2 vs 3 | 80 | 60 | -2.14 | 3.26e-2 | 3.26e-2 | \* |
| Lowland | 1 vs 2 | 98 | 84 | -2.82 | 4.81e-3 | 4.812-3 | \*\* |
| 2 vs 3 | 84 | 98 | 11.2 | 5.54e-29 | 1.66e-28 | \*\*\* |