**Title:** The effect of multiple short interval fires on community and functional trait-based regeneration in boreal Alaska

**Abstract:** (193/250 words, from AAG)

Fire is a major driver of forest structure, composition and age in boreal landscapes across spatial and temporal scales. Repeat short-interval fires in Interior Alaska (occurring within 50 years or less) are a departure from historic norms of fire intervals and drive ecological transitions from conifer-dominated to deciduous-dominated forests. However, uncertainty remains regarding how short-interval reburning alters boreal forest communities beyond the effects on tree regeneration. Specifically, the effects of repeat short-interval fires on understory plant communities and functional trait regeneration remain unknown. Here, we investigate how multiple short-interval fires alter community structure and functional trait assemblages in two sites of regenerating stands in boreal Interior Alaska. Each site contains a mosaic of burn perimeters from fires burning once, twice or three times in short-intervals (>30 years). We report initial results of understory community composition, overall species richness and differences in regeneration traits, and examine the role of local site conditions in mediating the impact of repeat reburning on regenerating plant communities. This work informs our ability to predict and manage impacts of repeat burning in boreal Interior Alaska forests and expands on our understanding of disturbance-driven ecological change in high-latitude boreal environments.

## Introduction

Disturbances alter ecosystems by changing biodiversity across communities and scales. Theory suggests frequency and severity of disturbances differ in their effects on ecological diversity (Fraterrigo et al. 2020), leading to uncertainty about how ecological communities may respond to changing disturbance regimes. Empirical research indicates the importance of examining interactive effects between frequency and severity of disturbance (i.e., Thom et al. 2017, Hughes et al. 2007, Castorani et al. 2018). However, the bulk of research into disturbance regime change in systems like the boreal focuses primarily on either severity or frequency effects individually (i.e., Hollingsworth et al. 2013, Johnstone et al. 2011). Understanding how diversity and community structure will change with changing disturbance regimes requires investigating the interactive effects of disturbance frequency and severity on biological communities.

Here, we use fires in the boreal as a model system, to examine how changing disturbance frequency and severity interact to alter community and functional trait assemblages. The boreal ecoregion is adapted to infrequent severe fires, occurring every 100 or more years under historic norms (Viereck 1973). Dominant plant species are highly adapted to infrequent fire and possess traits enforcing dominance across fire intervals, promoting “ecological legacies” across the landscape (Johnstone et al 2010). Rapidly warming temperatures across high latitudes have led to an increase in the frequency and severity of wildfires (Balshi et al. 2009), amplifying short-interval fires across the region (Buma et al. 2021, *in prep*). Fire severity in the boreal is strongly linked to patterns of community composition and plant functional traits, but the role of fire frequency in shaping community dynamics remains unclear (Whitman et al. 2018). Furthermore, wetter topographic contexts in the boreal may mediate increases in fire severity while still succumbing to increases in fire frequency (Hayes and Buma 2021). This would suggest that the effects of fire on ecological communities may differ according to fire severity, but not fire frequency.

To better understand the effects of multiple-short interval fires on ecosystem processes of modern boreal forest systems, it is necessary to 1) characterize the structure, composition and functional traits of regenerating overstory and understory communities in reburned areas and 2) determine whether reburned areas support understory plant communities that differ significantly from similar vegetation communities regenerating in regions with different fire histories. Examining the success of specific functional traits within given community assemblages occurring after multiple short-interval fires builds on our mechanistic understanding of the drivers of successional divergence in boreal Interior Alaska. Here, we investigate community regeneration in two reburned stands with comparable burn histories (1, 2 or 3 fires in <30 years) but differing cumulative severity effects. Fire severity in most systems is often measured as a metric of canopy or overstory mortality; however, even moderate severity fires in the boreal can cause full canopy mortality (Kasischke et al. 2006). Substrate consumption, or the amount of soil consumed during fire, is often used as a more sensitive alternative (i.e., Turetsky et al. 2011). Not only does organic layer consumption as a metric of burn severity capture higher severity events, it also allows for the possibility of resilience mechanisms inbuilt in topographic contexts that may mediate or negate the effects of fire. Specifically, poor drainage and generally higher soil moisture characteristic of lowland topographies indicates two fires in different topographic positions may produce different levels of organic soil consumption, culminating in ultimately different fire severity in terms of effects. Here, we use the term “cumulative severity” to indicate not the severity of individual events, but the difference in severity observed more generally between topographic position due to underlying drainage conditions.

Community assemblies in the boreal are driven primarily by the interaction between disturbance history, topographic context and site conditions (Hollingsworth et al. 2013, Roland et al. 2013). This interaction occurs across regional, stand and site-level scales (Fig. 1). Out of all species climatically and environmentally tolerant of boreal conditions, local fire regimes select for those with traits most suitable to survive and reproduce through infrequent, severe fires, while topographic conditions like aspect, slope and elevation influence both species distributions and fire occurrence at various scales. At a site-level, solar radiation, seed availability and canopy openness drive diversity in understory communities. Investigating ecological communities in the boreal requires acknowledging the role of complex interacting drivers across the appropriate scale.



**Fig. 1. Conceptual diagram of factors driving overstory and understory community composition in the boreal.**

### Regeneration strategies in the Boreal

One dominant functional trait shaping communities in the boreal is regeneration strategy: tree species in the boreal regenerate either sexually or asexually (Greene et al. 1999). Sexual reproduction occurs via serotinous or wind-born dispersal strategies, while asexual reproduction is achieved through sprouting (Greene et al. 1999). Both traits involve adaptations to infrequent fire. Conifers like black spruce typically regenerate sexually via semi-serotinous seedbanks (Viereck 1973). This strategy allows for a large input of relatively heavy seeds, usually shortly after fire, allowing black spruce to maintain dominance after low or even moderate severity fires (Johnstone et al. 2006). Deciduous species may regeneration either sexually via either wind-born seed establishment or asexually via sprouting (Chapin et al. 2006). Species like birch and aspen have lightweight seeds that can be carried by wind over great distances (Van Cleve et al. 1983). Greater dispersal distance capability means that many broadleaf boreal species are not as meaningfully constrained by local seed availability post-fire as black spruce (Johnstone and Chapin 2006, Gill et al. 2017, Whitman et al. 2019). Finally, species like aspen, poplar and birch often regenerate by resprouting (often vigorously) after fire (Greene et al. 1999). Aspen in particular can reproduce from seed, sprout in genetically identical clumps of stems, or sprout individually (Howard 1996). Patterns of sexual vs asexual reproduction across the boreal landscape influence ecosystem process like the distribution of aboveground carbon storage, genetic diversity and the connectivity of fuel loads.

This study evaluates the patterns of plant community and functional trait regeneration across a gradient of reburns to investigate post-fire community regeneration and successional trends following multiple short-interval fires. This study characterizes both community structure and drivers of that community structure in reburned stands and examine similarity between community assemblages across burn history in uplands and lowlands in boreal Interior Alaska. We compare understory plant species diversity, understory community composition and abundance of regeneration traits across varying fire histories and between two topographic positions with varying cumulative disturbance severity. We ask the following research questions: 1) Does the abundance of asexual or sexual reproduction in tree species differ according to reburn history?, 2) Does fire history or site conditions drive overall diversity, community evenness and richness in reburned stands, and does that effect differ by cumulative disturbance severity? And 3)Do similar understory plant communities emerge in reburned stands, regardless of cumulative disturbance severity?

We hypothesize serotinous species will be specifically disadvantaged by repeat short interval fires, leading to a greater presence of asexual reproduction in reburned stands. We hypothesize that fire history will have the largest effect on diversity in reburned stands, overwhelming the effects of site conditions like canopy openness, topography and solar radiation. Furthermore, we anticipate that single fires or reburns may lead to an initial increase in diversity in understory plant communities, but that communities will become less diverse with additional reburning, regardless of cumulative burn severity. Finally, we hypothesize understory communities emerging in reburned stands will become more dissimilar to communities regenerating after single fires, and that communities will continue to become more dissimilar with additional reburns, regardless of cumulative burn severity.

### Methods

#### Study design

To examine the effects of short-interval disturbances on plant communities, we established a network of 50 plots in two topographic positions in Interior Alaska that contain a mosaic of unburned, burned and reburned stands. The two locations we sampled were an upland region with well-drained soils and a lowland region with flatter topography and poorly drained soils. Burn severity is primarily measured through organic layer consumption in Alaska (Keeley 2009), and poorly drained soils in lowland topographies may mediate initial severity by preventing full combustion. To evaluate the effects of both fire frequency and fire severity, we sampled in locations with comparable fire histories (1, 2 or 3 fires within a 70-year time period), but with probable differences in fire severity due to local soil drainage conditions. Here, we use soil organic layer depth as a proxy for severity and infer accordingly that the lowland site experienced milder burn severity since less soil was consumed during each fire (Hayes and Buma 2021).

#### Field sampling

Sampling of understory and overstory communities took place in field campaigns during the summer of 2018 and 2019. Vegetation above diameter breast height (DBH, 1.37 m) was counted in 400-m2 sample spaces within each plot, though in denser stands, sample spaces were limited to 100m2 or 200 m2 randomly selected subsamples. We recorded species, diameter at breast height (cm), canopy health (%) and dominant corresponding understory species for each live or dead individual within the sample space. Seedlings below 1.4 meters in height were recorded in 10 1-m2 subsets at each plot. Individuals above DBH but under 2.5 mm in diameter were classified as saplings. Given the sensitivity of biodiversity metrics to sample size (Maurregan 2013), sample size was constrained specifically to a maximum of 400 m2  sub-samples of overstory vegetation and 100 m2 of understory vegetation.

We recorded species present and percent cover of understory vegetation within 10 1-meter2 subsamples within each plot in the upland site. Species were identified according to regional guides (Mackinnon et al. 2004, Laursen and Seppelt 2010, Hulten 1968). When individuals were unidentifiable to the species level, the genus level was used. Due to difficulties in identifying moss species consistently across plots, all moss data will be described at the genus level. To maximize time during the field sampling season of 2018, understory composition in lowland plots was recorded at the scale percent cover of functional groups, not species. I intend to complete this dataset by collecting species-level data at the lowland site during the next available field season.

Regeneration strategy was distinguished based on rooting style: individual stems were categorized as sexual reproduction, while clumps of stems were recorded as an initial single sexual reproduction event, and each stem thereafter recorded as asexual reproduction. Relative abundance of each strategy was determined by dividing the abundance of a given trait by the total number of stems on a plot.

To capture canopy openness as it relates to light availability, we took skyward hemispherical photographs at the center of each plot. Pixels were classified as “sky” or “non-sky” using Gap Light Analyzer (GLA) software, which was then used to quantity canopy openness (Frazer et al. 1999).

#### Data analysis

~~To investigate the prevalence of different regeneration strategies in post-fire communities across the reburn sequence, we intend to use a permutation test to create a null distribution in which the relative abundance of asexual reproducers is distributed randomly across reburn history and topographic position. This approach will allow us to quantify the difference between the null distribution of randomly distributed asexual reproducers and the observed distribution of asexual reproducers across reburn history, essentially comparing between the mean across all samples, and the means of each reburn history (0, 1, 2 and 3). A p-value of mean difference between the pooled sampled mean and means of each reburn category will be calculating using a two-tailed t-test.~~ [Not doing anymore, need to revise]

To examine the specific drivers of community diversity in understories of upland reburned stands, we use multivariate regression models with Simpson’s diversity index as a dependent variable, and number of fires, organic layer depth (as a metric of disturbance severity), solar insolation, slope, and canopy openness as independent variables. Simpson’s index was calculated for upland plant communities according to reburn history using the ‘vegan’ package in R (Oskanen et al. 2017). This index provides a measure of diversity that takes into account both species richness and evenness of abundance by measuring the probability that two individuals randomly selected from an area will belong to the same species (Magurran 2013). Simpson’s diversity index was selected over the commonly used Shannon diversity index due to the stability of Simpson’s index at lower sample sizes (Magurran 2013, Gimaret-Carpentier et al. 1998). This model was used to compared the effect sizes and confidence intervals of the aforementioned independent variables to evaluate the main drivers of diversity between a predefined set of frequency, severity and topographic characteristics.

To evaluate how plant communities in reburned stands differ according to reburn history or topographic context, we used presence/absence data of individual species to calculate Jaccard’s similarity index. Jaccard’s index uses the size of intersection and the size of the union of two finite sample sets to evaluate similarity (Magurran 2013). Once-burned species communities will be pooled and treated as one community. Jaccard’s index on its own is often a descriptive metric: to provide a quantitative estimate of community difference across reburns, we calculated Jaccard’s index comparing each plot experiencing either 2 or 3 fires to the pooled one-burn community. This approach produced distribution of differences created from comparing each twice-burned plot index to the pool of once-burned plots. That distribution of differences wasthen be compared between 1-burn vs 2-burn and 1-burn vs 3-burn, providing a specific quantitative measure of whether additional reburns drives converging or diverging communities.

### Preliminary Results

#### Regeneration strategies

Presence of asexual reproducers appears to increase across increasing reburns (Fig. 2).

Chart, scatter chart

Description automatically generated

**Fig. 2. Relative abundance of regeneration strategies across reburn history.**

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