**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.

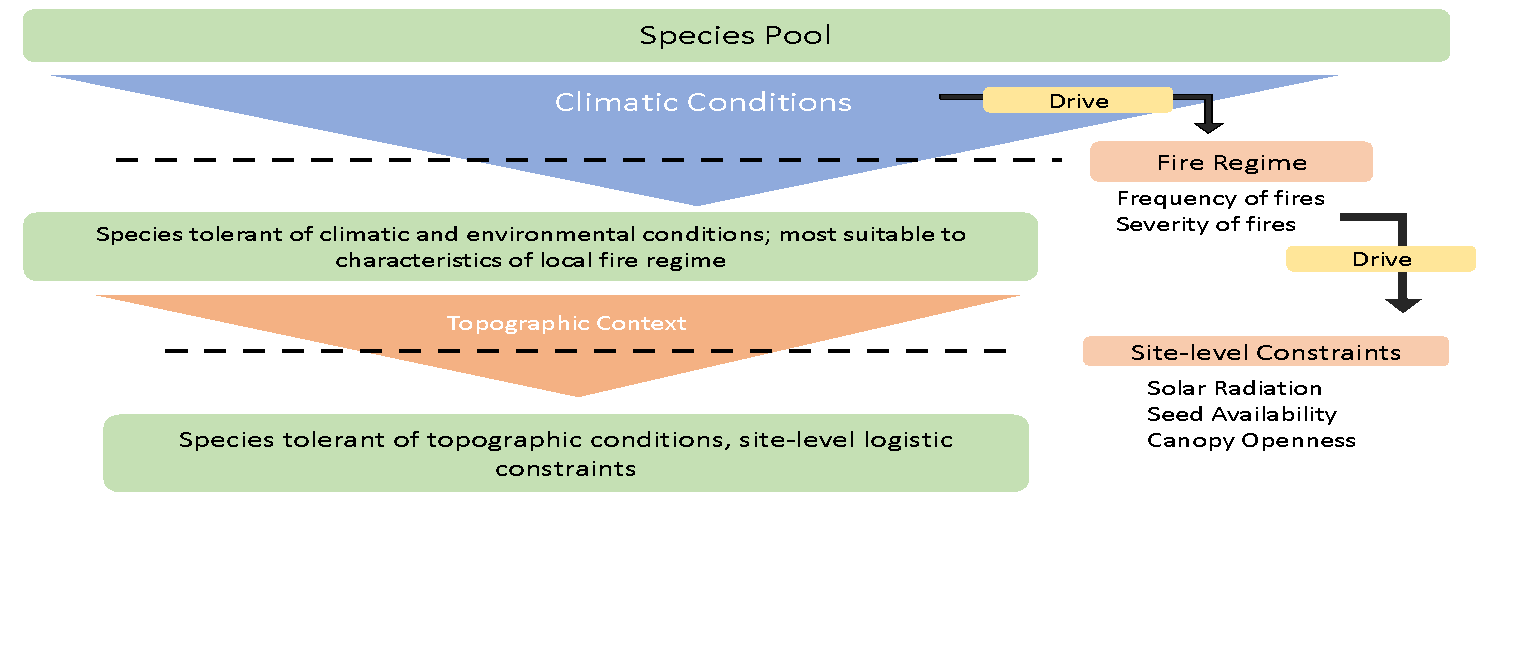
## Introduction

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 has demonstrated 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 on disturbance regime change in systems like the boreal focus 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 boreal plant species are highly adapted to infrequent fire and possess traits enforcing dominance across fire intervals, which promote “ecological legacies” at landscape-scales (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 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 a 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 underlying site 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 strategies: 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, shortly after fire, allowing black spruce to maintain dominance after low or moderate severity fires (Johnstone et al. 2006). Deciduous species may regeneration either sexually via either wind-borne 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 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. To characterize community structure and drivers of that community structure, we compare understory plant species diversity, understory community composition and abundance of regeneration traits across varying fire histories and between two topographic positions with differing underlying drainage conditions. We ask the following research questions: 1) Does fire history or site conditions drive overall diversity, community evenness and richness in reburned stands, and does that effect differ by location? And 2) Do similar understory plant communities emerge in reburned stands, regardless of location? 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 location. 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, independent of location.

## 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. We sampled two locations: an upland region with well-drained soils and a lowland region with flatter topography and poorly drained soils.

Figure X. Map of study locations.

#### Field sampling

We sampled understory and overstory communities in field campaigns during the summer of 2018, 2019 and 2021. We counted vegetation above diameter breast height (DBH, 1.37 m) in 400-m2 sample spaces within each plot, though in denser stands, sample spaces were limited to 100m2 or 200 m2 randomly selected subsamples. For each individual above DBH, we recorded species, diameter at breast height (cm), canopy health (%) and the dominant corresponding understory species. We recorded seedlings and shrubs below DBH in 10 1-m2 subsets at each plot, and classified individuals above DBH but under 2.5 mm in diameter 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 5 1-meter2 subsamples within each plot in the upland site, and across 10 0.5-meter2 sub samples in the lowland. 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, we describe all moss data at the genus level.

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 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 and lowland plant communities according to reburn history using the ‘vegan’ package in R (Oskanen et al. 2017). This index provides a measure of diversity that considers 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 compare the effect sizes and confidence intervals of the 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 a distribution of differences created from comparing each twice-burned plot index to the pool of once-burned plots. That distribution of differences is 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

## Discussion

## Acknowledgements

## References

Balshi, M.S., McGUIRE, A.D., Duffy, P., Flannigan, M., Walsh, J. and Melillo, J., 2009. Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. *Global Change Biology*, *15*(3), pp.578-600.

Castorani, M.C., Reed, D.C. and Miller, R.J., 2018. Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities. *Ecology*, *99*(11), pp.2442-2454.

Chapin, F.S., Oswood, M.W., Van Cleve, K., Viereck, L.A. and Verbyla, D.L. eds., 2006. *Alaska's changing boreal forest*. Oxford University Press.

Fraterrigo, Jennifer M., Aaron B. Langille, and James A. Rusak. 2020. Stochastic disturbance regimes alter patterns of ecosystem variability and recovery. *PloS one* 15(3): e0229927.

Frazer, G.W., Canham, C.D., and Lertzman, K.P. 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright © 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

Gill, N.S., Jarvis, D., Rogan, J. and Kulakowski, D., 2020. Disturbance history modulates how litter and herbaceous cover influence conifer regeneration after fire. *International Journal of Wildland Fire*.

Gimaret‐Carpentier C, Pélissier R, Pascal JP, Houllier F. Sampling strategies for the assessment of tree species diversity. Journal of Vegetation Science. 1998 Apr;9(2):161-72.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. and Simard, M.J., 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*, *29*(6), pp.824-839.

Hughes, A., Byrnes, J.E., Kimbro, D.L. and Stachowicz, J.J., 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology letters*, *10*(9), pp.849-864.

Hultén, E., 1968. *Flora of Alaska and neighboring territories: a manual of the vascular plants* (Vol. 2193). Stanford University Press.

Hodson, J., Fortin, D. and Bélanger, L., 2011. Changes in relative abundance of snowshoe hares (Lepus americanus) across a 265-year gradient of boreal forest succession. *Canadian Journal of Zoology*, *89*(10), pp.908-920.

Hollingsworth, T.N., Johnstone, J.F., Bernhardt, E.L. and Chapin III, F.S., 2013. Fire severity filters regeneration traits to shape community assembly in Alaska’s boreal forest. PloS one, 8(2), p.e56033.

Howard, Janet L. 1996. Populus tremuloides. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer).

Johnstone, J.F. and Chapin, F.S., 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. Ecosystems, 9(2), pp.268-277.

Johnstone, J.F., Hollingsworth, T.N., CHAPIN III, F.S. and Mack, M.C., 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology*, *16*(4), pp.1281-1295.

Johnstone, J.F., Rupp, T.S., Olson, M. and Verbyla, D., 2011. Modeling impacts of fire severity on successional trajectories and future fire behavior in Alaskan boreal forests. *Landscape Ecology*, *26*(4), pp.487-500.

Kasischke, E.S., Rupp, T.S. and Verbyla, D.L., 2006. Fire trends in the Alaskan boreal forest. *Alaska’s changing Boreal forest*, pp.285-301.

Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire*, *18*(1), pp.116-126.

Laursen, G.A. and Seppelt, R.D., 2010. *Common Interior Alaska Cryptogams: Fungi, Lichenicolous Fungi, Lichenized Fungi, Slime Molds, Mosses, and Liverworts*. University of Alaska Press.

MacKinnon, A., Pojar, J. and Alaback, P.B., 2004. *Plants of the Pacific Northwest coast*. Lone Pine Pub.

Magurran, A.E., 2013. *Measuring biological diversity*. John Wiley & Sons.

Oskanen, J., Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O’Hara, R., Simpson, G. and Solymos, P., 2017. vegan: Community ecology package, Version 2.4-3.

Roland, C.A., Schmidt, J.H. and Nicklen, E.F., 2013. Landscape‐scale patterns in tree occupancy and abundance in subarctic Alaska. *Ecological Monographs*, *83*(1), pp.19-48.

Thom, D., Rammer, W., Dirnböck, T., Müller, J., Kobler, J., Katzensteiner, K., Helm, N. and Seidl, R., 2017. The impacts of climate change and disturbance on spatio‐temporal trajectories of biodiversity in a temperate forest landscape. *Journal of Applied Ecology*, *54*(1), pp.28-38.

Turetsky, M.R., Kane, E.S., Harden, J.W., Ottmar, R.D., Manies, K.L., Hoy, E. and Kasischke, E.S., 2011. Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nature Geoscience*, *4*(1), pp.27-31.

Van Cleve, K., Dyrness, C.T., Viereck, L.A., Fox, J., Chapin III, F.S. and Oechel, W., 1983. Taiga ecosystems in interior Alaska. *Bioscience*, *33*(1), pp.39-44.

Viereck, L.A., 1973. Wildfire in the taiga of Alaska. *Quaternary Research*, *3*(3), pp.465-495.

Wirth, C., 2005. Fire regime and tree diversity in boreal forests: implications for the carbon cycle. In *Forest diversity and function* (pp. 309-344). Springer, Berlin, Heidelberg.

|  |
| --- |
|  |

Whitman, E., Parisien, M.A., Thompson, D.K. and Flannigan, M.D., 2018. Topoedaphic and forest controls on post-fire vegetation assemblies are modified by fire history and burn severity in the northwestern Canadian boreal forest. *Forests*, *9*(3), p.151.

Whitman, E., Parisien, M.A., Thompson, D.K. and Flannigan, M.D., 2019. Short-interval wildfire and drought overwhelm boreal forest resilience. *Scientific Reports*, *9*(1), pp.1-12.