**Boreal forest understory plant communities transform after one fire but demonstrate resilience to continued reburning**

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# Abstract: (250/250)

*Premise*

Reburning in short-intervals (50 years or less between fire events) shifts overstory dominance of forests in Interior Alaska from conifer to deciduous, leading to more open forest structure. While the impacts of short-interval reburning on overstory communities are well-documented, the subsequent effects on understory plant communities remain underexamined. Here, we investigate how multiple short-interval fires alter boreal forest understory plant community composition in black spruce stands in Interior Alaska.

*Methods*

We quantified understory plant community composition and compared estimates of understory plant species richness, and cover within plots distributed across forests that burned once, twice or three times in short-intervals in Interior Alaska. To examine the role of abiotic filters, we used linear regression to determine whether light availability or soil organic layer depth mediate or accelerate the impact of repeat reburning on regenerating understory plant communities.

*Results*

The understory plant community increased in species richness and community diversity following a single fire but there were fewer differences in understory species richness, diversity, or identity when comparing once-burned plots to twice or thrice-burned plots. We did not observe an effect of light availability or soil organic layer depth on understory plant species richness or plant community diversity.

*Conclusions*

While a single fire altered the understory plant community, continued reburning did not lead to subsequent differences in richness, diversity or identity. This work informs our ability to predict and manage impacts of repeat burning in boreal Interior Alaska forests and expands on our understanding of the resilience of understory plant communities to increasing disturbance.

Disturbances play a key role in structuring vegetative communities (Seidl et al., 2016; Rodman et al., 2022)by selecting for traits that confer resilience to the broader disturbance regime (Miller and Safford, 2020). For example, tree species in ecosystems that experience frequent fire may have thick bark and highly flammable leaf litter to help trees survive surface fires (Stevens et al., 2020). Changes in the characteristics of a disturbance regime, such as a shift in severity or frequency of events beyond historic norms can lead to changes in post-disturbance species composition and dominance (Fornwalt et al., 2018). Similarly, interactions between individual disturbance events can lead to novel and compound effects wherein the impact of the interaction is greater than that of either individual event (Buma, 2015). Whether through shifts in characteristics or interactions or both, changes in disturbance regimes complicate our ability to anticipate the response of plant communities (Fraterrigo et al., 2020).

One such system experiencing a shift in disturbance regime is the boreal forests of Interior Alaska. Rapidly warming temperatures in high-latitudes have led to an increase in the frequency and extent of fires across the boreal forests of interior Alaska (Hayes and Buma, 2021), a system with historically infrequent fire (Hoecker and Higuera, 2019; Hoecker et al., 2020). Warming temperatures and drying conditions have shrunk fire return intervals in some forests to 50 years or less (Buma et al., 2019). Multiple short-interval fires lead to compound effects on overstory plant communities, driving shifts in dominance from conifer to deciduous species (Hayes and Buma, 2021). However, the corresponding direct and indirect impacts of multiple short-interval fires on the understory plant community remains undocumented.

Understory plant communities in boreal forests regulate several key ecosystem functions, including plant diversity, nutrient cycling, wildlife habitat and forest recruitment. Understory plant communities are the primary source of plant species diversity in the boreal: typical plant communities in the boreal consist of 39 - 77 species, many of which are nonvascular plants (Hart and Chen, 2006). In addition, understory species in the boreal can bypass nitrogen mineralization and uptake organic nitrogen (Näsholm et al., 1998) which is retained by nonvascular species (Weber and Van Cleve, 1981), thus aiding in the cycling of nitrogen in an ecosystem otherwise limited by low nitrogen availability (Du et al., 2020). Furthermore, understory species are a large component of moose and snowshoe hare forage (Hodson et al., 2011; Shively et al., 2019) and provide needed habitat for migratory birds in the spring migration (Leffler et al., 2019). Finally, understory vegetation can decrease light availability (Messier et al., 1998), limiting immediate postfire overstory recruitment (Hart and Chen, 2006), important in a system where initial recruitment of overstory species strongly control subsequent forest composition and densities (Johnstone et al., 2020).

We have a strong mechanistic understanding of how individual fires alter boreal understory plant communities (Hart and Chen, 2006; Frelich et al., 2017; Whitman et al., 2018; Anyomi et al., 2022). Mature black spruce forests are associated with relatively species-poor understory communities (39 - 77 species on average;Hart and Chen, 2006), limited primarily by light availability. Black spruce are well-adapted to an infrequent, high severity fire regime (Baltzer et al., 2021) and can experience high mortality even in relatively low severity fire (Greene et al., 1999). High black spruce mortality enables dramatic declines in canopy cover after a fire, altering understory microclimates and increasing light availability (Pham et al., 2004). In addition, fires combust soil organic layers, increasing soil nutrient availability and pH (Hart and Chen, 2006). The combination of increased light availability and soil organic layer combustion creates plant understory communities post-fire that are more species rich and diverse compared to mature stands (average species turnover after one fire is 40%; Rees and Juday, 2002).

Continued reburning enables further transformations of the overstory of black spruce forests – an additional fire occurring within 30-50 years of an initial event can extirpate black spruce by combusting black spruce seedlings and seedbanks, allowing for dominance of deciduous species like birch (*Betula neoalaskana*) and aspen (*Populus tremuloides*). Continued reburning (3 short interval fires) continues to enforce deciduous dominance, leading towards more open stand structure. In addition, multiple-short interval fires combust soil organic layers more deeply (on occasion, removing soil organic layer entirely, Hayes and Buma, 2021). Thus, reburning may impact understory plant communities both directly through mortality and indirectly, through subsequent shifts in abiotic filters like light availability and soil organic layer depth (Rees and Juday, 2002).

To characterize the understory plant community associated with multiple short-interval fires and to examine how abiotic filters (including light availability as measured by solar irradiance and soil organic layer depth) shape community assembly within reburned forests, we ask the following research questions:

1. How does understory plant community identity, plant species richness, plant community diversity, and plant community composition vary along a gradient of burn and reburn history?
2. What are the effects of abiotic filters, namely light availability and soil organic layer depth, on understory plant species richness and understory community diversity within burned and reburned stands?

We predict that the once-burned understory plant community will exhibit higher species richness and community diversity compared to unburned communities following the expectations provided by Hart and Chen (2006) and others, but that richness and diversity will be lower in reburned stands as many understory plant species (predominantly mosses and lichens in the boreal) will not be able to persist due to a disparity between life history strategies and the post reburn environment (Cedrés-Perdomo et al., 2024). As such, we anticipate a turnover in species commonly found in the unburned forest (mostly moss and lichen species) towards more forb and graminoid species which might more rapidly colonize available habitat, leading to greater dominance in reburned forests. Alternatively, shrub species may become the most dominant after a single burn because underground root structures may help species survive and compete for resources more quickly (Hart and Chen, 2006), but shrub cover will be lower in areas with continued reburning as underground resources become depleted. We also predict light availability, an important abiotic constraint to boreal understory plant communities (Hedwall et al., 2021), will likely be an important predictors of understory plant species richness and community diversity within burned sites (Hart and Chen, 2006).

# MATERIALS AND METHODS

#### Study design –

To examine the effects of short-interval disturbances on plant communities, we established 26 plots in Interior Alaska within a mosaic of unburned, burned, and reburned upland stands that were dominated by mature black spruce prior to the first burn (Fig. 1). We determined fire perimeters, severities and years using a combination of aerial photography, remote sensing, and ground truthing (Hayes and Buma, 2021). Fires occurred within 14-38 years of one another (fire names and years in Table S1), well within the regional definition of a short-interval (50 years, Johnstone et al., 2010), and each fire led to full canopy mortality, as confirmed by coring existing overstory trees to check for survivors.

#### Field sampling –

##### Understory community –

We measured understory plant communities within 5, 1 m2 subsamples within each plot (evenly spaced at each of the plot corners and center) and identified species according to regional guides (Hultén, 1968; MacKinnon et al., 2004; Laursen and Seppelt, 2010), focusing on the lowest identifiable species level (and defaulting to genus when needed). We recorded percent cover in classes of 10%, also recording percent cover of bare ground or rocks where needed. We used five categories of functional groups, following the example set by existing understory research in boreal Alaskan forests: lichen and mosses, graminoids, forbs, seedless vascular plants, and shrubs (Chapin et al., 2006).

##### Abiotic filters –

We measured soil organic layer depth in centimeters in the four corners and the center of each plot after measuring understory cover and averaged measurements to the plot level. To represent light availability, we used solar radiance, a measurement of incoming solar radiation, which we calculated using plot locations, aspect and slope in ArcGIS (Fu, 1999).

#### Data analysis –

##### Understory community response –

To understand how unburned, burned, and reburned plant communities vary, we utilized multiple multivariate approaches to measure the difference between communities. First, we used a Non-Metric Multidimensional Scaling (NMDS) ordination, which compresses multivariate data (e.g., plant species richness and cover measurements) into two axes of variation to visualize the differences between categorical groups (Shipley, 2021). We used the *vegan* package in R (Oksanen et al., 2020) to calculate the NMDS ordination. We used the 95% confidence ellipsoids associated with our ordination to visualize the uncertainty of our grouping estimate. To understand the inherently multivariate nature of understory plant communities, we calculated a Bray-Curtis dissimilarity value for each plot (Beals, 1984). Bray-Curtis dissimilarity values represent the pairwise similarity of two points: values closer to one represent higher dissimilarity between the two points and values closer to zero represent lower dissimilarity between two points. To capture variation within fire history, we calculated the pairwise dissimilarity of plots within the same fire history category. Finally, to compare the variation of within group dissimilarity, we used an analysis of variation (ANOVA) to determine if any of the groups were statistically different and if so, used associated post-hoc TukeyHSD test to understand the pairwise differences between groups (Bolker, 2008).

We quantified understory community diversity using the Simpson’s diversity index, which accounts for both the recorded plant species richness of a plot, as well as their evenness or distributions of cover within a plot. To analyze understory species richness and understory plant community diversity, we employed an ANOVA and post-hoc TukeyHSD framework similar to the analysis of plant community identity described above. To describe understory community composition across unburned, burned, and reburned communities, we constructed rank abundance curves for both the understory plant species, and for the functional groups present in the understory plant community. Finally, we calculated the species turnover rate between fire histories using the following equation:

*Effects of abiotic filters on plant communities –*

To test our hypothesis that light availability, and soil organic layer depth are important abiotic filters of boreal community assembly in postfire understory plant communities, we fit generalized linear regression models to estimate understory plant species richness and understory community diversity, as measured by Simpson’s diversity index, using the covariates for potential abiotic filters as explanatory variables. We used a Poisson error structure to model understory plant species richness due to the discrete nature of species richness data (Bolker, 2008), and a Gaussian error structure to model understory plant diversity because the assumptions of a normal distribution were not violated (Bolker, 2008). We include all environmental covariates (light availability and soil organic layer depth) in a global model to evaluate the potential partial effects of each covariate. We performed all data analysis in R version 4.2.1 (R Core Team, 2022).

# RESULTS

### How does understory plant community identity, plant species richness, plant community diversity, and plant community composition vary along a gradient of burn and reburn history?**–**

Understory plant communities in burned and reburned plots were broadly different from those in unburned plots, demonstrating higher species richness and Simpson’s diversity. In addition, understory plant communities in burned stands demonstrated key differences in species composition and identity across number of fires: we observed different species in once-, twice-, and thrice-burned plots, though again, the greatest differences remained between unburned and burned overall. Our NMDS ordination grouped the unburned understory community separately along the first axis of variation compared to the burned understory communities with no overlap in the 95% confidence ellipsoid. The once-burned community showed no overlap with the twice- or thrice-burned communities, which do overlap on our NMDS ordination (Fig 2A). The burned understory communities were clustered along the first axis of variation but were partitioned among the second axis of variation. These differences are further illustrated with the Bray-Curtis dissimilarity analysis (F = 27.4, df = 3, P less than 0.001): on average, dissimilarity between plots within the unburned category was low (0.19 ± 0.05, mean dissimilarity ± 95% CI), compared to the dissimilarity between plots within the once-burned (0.57 ± 0.03), twice-burned (0.67 ± 0.06), and thrice-burned (0.58 ± 0.05) categories (Fig 2B).

On average, there were 12 species (± 2 species, 95% CI) present in the understory in unburned plots. In plots that experienced a single burn, there were an average 9 additional species present than in unburned plots. Twice-burned plots had 5 fewer species on average than once-burned plots. Plant species richness in the twice-burned communities was comparable to both the unburned and the thrice-burned plant communities, with an average of 18 species (Fig. 3A). Understory plant community diversity, as measured by the Simpson's diversity index showed similar differentiation of the unburned plant community to the burned plant communities (F = 34.2, df = 3, P less than 0.001). Understory plant community diversity was lowest in the unburned community (0.45 ± 0.14, 95% CI) and differed significantly from understory plant community diversity in all burned communities (Fig. 3B).

We observed high turnover in species assemblages between unburned and burned / reburned understory plant communities (61% between unburned to once-burned, 66% between unburned and twice- and 60% between unburned to thrice-), but less turnover between burned and reburned communities. The turnover rate between once-burned to twice-burned communities was 40%, similar to the turnover rate between twice-burned to thrice-burned communities (35%) and once-burned to thrice-burned (35%). Mosses generally maintained the highest average cover across all burn categories (95% ± 8% unburned, 24% ± 9% once-burned, 44% ± 21% twice-burned, & 50% ± 10% thrice-burned, Fig. 4, Table S2) with the exception of the once-burned community which was dominated by shrubs (48% ± 11%, Fig. 4, Table S2). Aside from mosses, all functional groups (shrubs, lichens, graminoids, forbs, and seedless vascular plants) had higher average cover in the once-burned community than the unburned community (Table S2). Average cover of all functional groups except mosses and seedless vascular plants was lower in the reburned communities than the once-burned community (Table S2). Across all plots, mosses comprised the most species diversity in the understory plant community, making up 30% of the unique species observed (number of species = 20), followed by shrubs (22%, n = 15), lichens (21%, n = 14), forbs (15%, n = 10), graminoids (7%, n = 5), and finally seedless vascular species (4%, n = 3). We observed a total of 67 unique species across 41 genera of plants (including mosses and lichens; Table S3), across all plots and number of fires (n = 26).

### What are the effects of abiotic filters on understory plant species richness and understory community diversity within burned and reburned stands?**–**

While solar irradiance and soilr organic layer depth varied across unburned, burned and reburned plots (Table S4), we observed no statistically significant effect (P < 0.05) of either on plant species richness or understory diversity (Table 1). A post-hoc power analysis determined that with our small sample size (n of burned and reburned plots = 21), degrees of freedom (df = 19) and significance threshold (alpha = 0.05), we were only able to detect an effect on the intercept as small as 1.32.

# DISCUSSION

Capturing the impact of short-interval fire on understory plant communities is critical to understanding how boreal forests will continue to change with increasing fire frequency and severity (Buma et al., 2022). Though understory plant communities play an important role in boreal forest diversity **,** their response to reburning has not been investigated previously. We observed that understory plant communities differed greatly between unburned and burned / reburned plots, which aligns with previous research in both the boreal and other forested ecosystems (Hart and Chen, 2006; Laughlin and Fulé, 2008; Cedrés-Perdomo et al., 2024).

Our hypothesis that plant species richness and understory plant community diversity would increase following fire was met. We anticipated that forb and graminoid species would dominate the understory in once-burned plots. We provide evidence that shrub species dominated the once-burned plots and mosses dominated the twice- and thrice-burned plots. Forb, graminoid, and shrub species all have higher average cover in the once-burned plots as compared to unburned plots; however, average cover of these three functional groups was lower in twice- and thrice- burned communities than in the once-burned community. Shrub species with root structures that promote rapid growth after fire such as *Vaccinium spp.* and *Salix spp.* were some of the most frequent species in the once-burned community (Fig 4c). These species may have a lower abundance in the twice- and thrice- burned community due to a depletion of stored resources in belowground structures.

Plots with multiple burns were similar in identity (Fig. 2a), plant species richness (Fig. 3a), plant community diversity (Fig. 3b), and composition (Fig. 4) to plots that only experienced one burn. The similarities of reburned communities to the once-burned community and lower rates of species turnover between burned communities provides evidence that the understory plant community is resilient to further departures from the unburned reference community. When comparing once-burned to twice- and thrice-burned plots, the average cover of functional groups remained consistent. Interestingly, the average moss cover was higher in the twice-burned and thrice-burned plots than the once-burned plots, although cover was still lower than the unburned reference community. This result is unexpected considering the observed decline in moss species after one fire, which is thought to be caused by mosses being outcompeted by more fast-growing forbs and graminoids that can rapidly take advantage of increases in light availability. There was high variability in multivariate plant community identity within all burned categories (Fig. 2b), which is likely caused by more species being present in these communities (Fig. 3a) with slight differences in assemblages (Fig. 4).

The loss of *Hylocomium splendens* from the understory plant community following fire may be of potential concern for nitrogen retention in this system (Weber and Van Cleve, 1981). *H. spendens* has been observed to buffer nitrogen storage as well as other nutrients. The absence of *H. spendens* from burned and reburned plant communities may have implications for nutrient flux. The understory community following burns and reburns appears to have large amounts of variability, as presented by the range of Bray-Curtis dissimilarity values in burned plots being greater than unburned plots. The difference in understory plant community diversity found across burned and reburned plots will likely increase the fine-scale heterogeneity across the landscape, which may have implications for animal habitat, and future forest regeneration.

Neither of the abiotic filters (organic layer depth, or solar irradiance) that have been observed as important for the initial release of the understory plant community following one fire were statistically significant predictors for understory plant species richness or plant community diversity when evaluating their importance exclusively within burn and reburn categories. The lack of an observed effect from any of our covariates that represent the abiotic environment suggests that light and other resources that have been documented to limit plant species richness and plant community diversity prior to fire (Hart and Chen, 2006; Hedwall et al., 2021)are either not as important following an increasing number of reburns, or (more likely) that plant communities in burned and reburned areas employ a variety of strategies to acquire resources that we did not have the statistical power to detect. There are likely many alternative strategies that plant species employ to take advantage of resource availability following multiple disturbance events. Some species might resprout following fire, while others may disperse into the burned area to take advantage of available resources. Future research will need to quantify the functional traits associated with the understory plant community to elucidate the mechanisms responsible for the resilience in the understory plant community observed.

**CONCLUSIONS**

In summary, we provide evidence that understory plant communities remain resilient to further change in the face of continued reburning. The resilience of the understory plant community may provide nitrogen cycling, animal habitat and forage, and help structure the overstory plant community in the absence of continued reburning; however, future research will need to elucidate these relationships. Neither light availability nor soil organic layer depth were statistically significant predictors of plant species richness and understory community diversity when comparing plots that were once-, twice-, or thrice- burned. The potential mechanisms that promote the resilience of the understory plant community with continued reburns remains unknown. Understanding the response of the understory plant community helps inform 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.

# Data Availability

All code used in the analyses of this paper are publicly available as a repository on Github (https://github.com/k8hayes/Community-Regen) and datasets are available on Zenodo (doi).

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## REFERENCES

Anyomi, K. A., B. Neary, J. Chen, and S. J. Mayor. 2022. A critical review of successional dynamics in boreal forests of North America. *Environmental Reviews* 30: 563–594.

Baltzer, J. L., N. J. Day, X. J. Walker, D. Greene, M. C. Mack, H. D. Alexander, D. Arseneault, et al. 2021. Increasing fire and the decline of fire adapted black spruce in the boreal forest. *Proceedings of the National Academy of Sciences* 118: e2024872118.

Beals, E. W. 1984. Bray-curtis ordination: An effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14: 1–55.

Bolker, B. M. 2008. Ecological Models and Data in R. Princeton University Press.

Buma, B. 2015. Disturbance interactions: Characterization, prediction, and the potential for cascading effects. *Ecosphere* 6: 1–15.

Buma, B., B. J. Harvey, D. G. Gavin, R. Kelly, T. Loboda, B. E. McNeil, J. R. Marlon, et al. 2019. The value of linking paleoecological and neoecological perspectives to understand spatially-explicit ecosystem resilience. *Landscape Ecology* 34: 17–33.

Buma, B., K. Hayes, S. Weiss, and M. Lucash. 2022. Short-interval fires increasing in the Alaskan boreal forest as fire self-regulation decays across forest types. *Scientific Reports* 12: 4901.

Cedrés-Perdomo, R. D., J. J. García-Alvarado, Á. Mallorquín, J. Leal, and J. M. González-Mancebo. 2024. Exploring the effects of fire on bryophyte functional groups along an elevational gradient on an oceanic island. *Forest Ecology and Management* 567: 122074.

Chapin, F. S., M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla. 2006. Alaska’s Changing Boreal Forest. Oxford University Press.

Du, E., C. Terrer, A. F. A. Pellegrini, A. Ahlström, C. J. Van Lissa, X. Zhao, N. Xia, et al. 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience* 13: 221–226.

Fornwalt, P., C. Stevens-Rumann, and B. Collins. 2018. Overstory Structure and Surface Cover Dynamics in the Decade Following the Hayman Fire, Colorado. *Forests* 9: 152.

Fraterrigo, J. M., A. B. Langille, and J. A. Rusak. 2020. Stochastic disturbance regimes alter patterns of ecosystem variability and recovery R. Martinez-Garcia [ed.],. *PLOS ONE* 15: e0229927.

Frelich, L. E., P. B. Reich, and D. W. Peterson. 2017. The changing role of fire in mediating the relationships among oaks, grasslands, mesic temperate forests, and boreal forests in the Lake States. *Journal of Sustainable Forestry* 36: 421–432.

Fu, P. 1999. Design and Implementation of the Solar Analyst: an ArcView Extension for Modeling Solar Radiation at Landscape Scales. *Proceedings of the Nineteenth Annual ESRI User Conference*.

Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Can. J. For. Res.* 29: 824–839.

Hart, S. A., and H. Y. H. Chen. 2006. Understory Vegetation Dynamics of North American Boreal Forests. *Critical Reviews in Plant Sciences* 25: 381–397.

Hayes, K., and B. Buma. 2021. Effects of short-interval disturbances continue to accumulate , overwhelming variability in local resilience. *Ecosphere* 12.

Hedwall, P.-O., J. Uria-Diez, J. Brunet, L. Gustafsson, A.-L. Axelsson, and J. Strengbom. 2021. Interactions between local and global drivers determine long-term trends in boreal forest understorey vegetation. *Global Ecology and Biogeography* 30: 1765–1780.

Hensgens, G., H. Laudon, M. Peichl, I. A. Gil, Q. Zhou, and M. Berggren. 2020. The role of the understory in litter DOC and nutrient leaching in boreal forests. *Biogeochemistry* 149: 87–103.

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

Hoecker, T. J., and P. E. Higuera. 2019. Forest succession and climate variability interacted to control fire activity over the last four centuries in an Alaskan boreal landscape. *Landsc. Ecol.* 34: 227–241.

Hoecker, T. J., P. E. Higuera, R. Kelly, and F. S. Hu. 2020. Arctic and boreal paleofire records reveal drivers of fire activity and departures from Holocene variability. *Ecology* 101.

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

Johnstone, J. F., G. Celis, F. S. Chapin, T. N. Hollingsworth, M. Jean, and M. C. Mack. 2020. Factors shaping alternate successional trajectories in burned black spruce forests of Alaska. *Ecosphere* 11: e03129.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16: 1281–1295.

Laughlin, D. C., and P. Z. Fulé. 2008. Wildland fire effects on understory plant communities in two fire-prone forests. *Canadian Journal of Forest Research* 38: 133–142.

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

Leffler, A. J., K. H. Beard, K. C. Kelsey, R. T. Choi, J. A. Schmutz, and J. M. Welker. 2019. Delayed herbivory by migratory geese increases summer‐long CO2 uptake in coastal western Alaska. *Global Change Biology* 25: 277–289.

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

Messier, C., S. Parent, and Y. Bergeron. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science* 9: 511–520.

Miller, J. E. D., and H. D. Safford. 2020. Are plant community responses to wildfire contingent upon historical disturbance regimes? B. Poulter [ed.],. *Global Ecology and Biogeography* 29: 1621–1633.

Näsholm, T., A. Ekblad, A. Nordin, R. Giesler, M. Högberg, and P. Högberg. 1998. Boreal forest plants take up organic nitrogen. *Nature* 392: 914–916.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2020. vegan: community ecology package.

Pham, A. T., L. D. Grandpré, S. Gauthier, and Y. Bergeron. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. *Canadian Journal of Forest Research* 34: 353–364.

R Core Team. 2022. R: A language and environment for statistical computing.

Rees, D. C., and G. P. Juday. 2002. Plant species diversity on logged versus burned sites in central Alaska. *Forest Ecology and Management* 155: 291–302.

Rodman, K. C., R. A. Andrus, A. R. Carlson, T. A. Carter, T. B. Chapman, J. D. Coop, P. J. Fornwalt, et al. 2022. Rocky Mountain forests are poised to recover following bark beetle outbreaks, but with altered composition. *Journal of Ecology*: 1–21.

Seidl, R., T. A. Spies, D. L. Peterson, S. L. Stephens, and J. A. Hicke. 2016. Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology* 53.

Shipley, B. 2021. Ordination methods for biologists: a non-mathematical introduction using R. BS Publishing, Sherbrooke, Quebec.

Shively, R. D., J. A. Crouse, D. P. Thompson, and P. S. Barboza. 2019. Is summer food intake a limiting factor for boreal browsers? Diet, temperature, and reproduction as drivers of consumption in female moose N. Righini [ed.],. *PLOS ONE* 14: e0223617.

Stevens, J. T., M. M. Kling, D. W. Schwilk, J. M. Varner, and J. M. Kane. 2020. Biogeography of fire regimes in western U.S. conifer forests: A trait‐based approach T. Gillespie [ed.],. *Global Ecology and Biogeography* 29: 944–955.

Weber, M. G., and K. Van Cleve. 1981. Nitrogen dynamics in the forest floor of interior Alaska black spruce ecosystems. *Canadian Journal of Forest Research* 11: 743–751.

Whitman, E., M.-A. Parisien, D. Thompson, and M. Flannigan. 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: 151.

**Tables and Figures**

A collage of different types of trees

Description automatically generated**Fig. 1**. (a) Map of plot locations and fire perimeters located in the interior of Alaska, USA. Photos of unburned (b), once-burned (c), twice-burned (d), and thrice-burned (e) plots.

A comparison of a number of objects

Description automatically generated

**Fig. 2**. (a) Non-Metric Dimensional Scaling (NMDS) ordination illustrating the grouping of plots that experienced no fire (yellow), 1 fire (orange), 2 fires (purple), or 3 fires (dark blue) in multivariate space. Points represent plots while open circles represent the 95% confidence ellipsoids. (b) Bray-Curtis dissimilarity (y-axis) analysis for the pairwise comparison of plots within the same burn category (x-axis). Letters at the top of the figure are from a post-hoc TukeyHSD test to determine similarity between burn categories. Burn categories that share the same letter are statistically similar (p > 0.05). The colors used for each burn category are the same as panel (a).

A comparison of a number of fine and a number of fine

Description automatically generated**Fig. 3.** Understory plant species richness (a) and understory community diversity as measured by the Simpson’s diversity index (b) as a function of number of fires each plot experienced. Letters at the top of each panel represent the results of a post-hoc TukeyHSD test; groups that share a letter are not statistically different.

Several different types of graphs

Description automatically generated with medium confidence**Fig. 4.** Percent average cover the functional groups in unburned, once-burned, twice-burned, and thrice-burned communities ordered by the average percent cover of the functional group in the unburned community (a). Pairwise comparisons of average cover (%) for the 10 most abundant species in a community to communities with one additional fire for the unburned community (b), once-burned community (c), and twice-burned community (d). Error bars represent the 95% confidence interval of each species or functional group.

**Table 1.** Results for the generalized linear models that included plant species richness (top half of table) or plant community diversity as measured by Simpson’s diversity index (bottom half of table) as a function of potentially important covariates.

|  |
| --- |
| *Richness ~ Solar Irradiance + Organic Layer Depth (N =21) – R2 = 0.165* |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Coefficient | Estimate | SE | *z-*value | *P*-value |
| Intercept | 14.7 | 7.33 | 2.01 | 0.044 |
| Solar Irradiance ( w/m2) | -1.97 × 10-5 | 1.21 × 10-5 | -1.62 | 0.105 |
| Organic Layer Depth (cm) | 5.70 × 10-4 | 0.020 | 0.029 | 0.977 |
| *Diversity ~ Solar Irradiance + Organic Layer Depth (N =21) – R2 = 0.077* | | | | |
| Coefficient | Estimate | SE | *z*-value | *P*-value |
| Intercept | 3.11 | 1.81 | 1.72 | 0.103 |
| Solar Irradiance (unit) | -3.77 × 10-6 | 3.00 × 10-6 | -1.26 | 0.224 |
| Organic Layer Depth (cm) | -9.79 × 10-4 | 0.005 | -0.203 | 0.841 |

**Appendix**

**Table S1.** Fire history of plots included in this study. Time since fire (TSF) was measured as the years between the most recent fire and sampling in 2018.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Number of fires | Number of plots | Plot ID | Fire Names | Year | TSF at time of sampling |
| 1 | 7 | 12, 41, 48, 50, 52, 64, 65 | Fish Creek | 2005 | 13 |
| 1 | 42 | Erickson | 2003 | 15 |
| 2 | 6 | 56, 57, 47, 16, 8, 39 | Rogers | 1967 | 13 |
| Fish Creek | 2005 |
| 2 | 32, 40 | Rogers | 1967 | 15 |
| Erickson | 2003 |
| 3 | 5 | 7, 14, 15, 54, 55 | Rogers | 1967 | 15 |
| Unnamed fire #132 | 1991 |
| Fish Creek | 2005 |

**Table S2.** Functional group cover and associated 95% confidence interval for each burn category.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | **Moss** | **Shrubs** | **Lichen** | **Graminoid** | **Seedless Vascular** | **Forb** |
| **No Fire** | 95.5 (± 8.02) | 30.6 (± 17.5) | 3.25 (± 1.36) | 0.063 (± 0.123) | 0.813 (± 0.543) | 0.563 (± 0.946) |
| **1 Fire** | 24.5 (± 9.20) | 48.3 (± 10.6) | 8.25 (± 4.42) | 17.2 (± 10.4) | 14.4 (± 8.56) | 8.91 (± 4.02) |
| **2 Fires** | 44.0 (± 21.0) | 21.5 (± 13.7) | 3.34 (± 1.75) | 14.1 (± 18.2) | 28.1 (± 16.3) | 2.13 (± 0.607) |
| **3 Fires** | 50.5 (± 10.3) | 8.67 (± 12.0) | 12.5 (± 4.83) | 10.0 (± 11.2) | 14.9 (± 5.58) | 1.75 (± 1.37) |

**Table S3.** Species list for the species observed across all plots included in the study. We report the functional group and the number of fires that the plot experienced where the species was observed. If a species was observed in plots with varying fire history, multiple numbers are provided.



**Table S4.** Average and standard deviation of organic layer depth and solar radiation covariates across the burn histories

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Burn History | Organic Layer Depth (cm) | | Solar Radiation (w/m2) | |
| *Mean* | *SD* | *Mean* | *SD* |
| 1 | 5.78 | 2.89 | 600755 | 5048 |
| 2 | 3.07 | 2.13 | 605349 | 3931 |
| 3 | 1.82 | 0.782 | 604147 | 1782 |