**Methods**

**Study Site**

This study was conducted within and immediately adjacent to the perimeter of the 2019 Museum Fire, located approximately 1.6 km north of Flagstaff, Arizona, USA (35.252169, -111.634913 WGS84). This fire burned in late July of 2019, with a total of 793.6 hectares burned. The Museum Fire was a mixed-severity fire, with patches of very low-, low-, moderate-, and high-severity patches present (USDA Forest Service, 2019). No post-fire seeding treatments were implemented within the research site.

The canopy is dominated by *Pinus ponderosa* and *Quercus gambelii* with *Juniperus deppeana*, *Pinus strobiformis*, and *Pseudotsuga menziesii* interspersed. Elevations within the burn scar range from approximately 2240 m to approximately 2760 m above sea level. Our research plots were monumented at lower elevations within this range, between 2251 and 2328 m above sea level. All plots were located on slopes with a southeasterly aspect, with slopes between 20 and 30 degrees. Soils are based on mixed igneous parent material, with both Alfisol and Mollisol soil orders.

The precipitation averages 52.17 cm (National Weather Service 2025), with a bimodal precipitation regime. An average of 28% of annual precipitation falls in winter (December to March), while 34% occurs in summer (June to September) due to the southwestern monsoon (Hereford 2007). The thirty-year (1993-2023) average maximum, minimum, and average temperatures are 33.33°C, -20.56°C, and 8.28°C, respectively (National Weather Service 2025). See Appendix S1: Table S1 for annual weather data.

**Plot Establishment**

Plots were established in May of 2020, 10 months following the fire. We established 60 4 m × 4 m research plots across the burn severity gradient, with 20 plots located within unburned (U), low-severity (L), and high-severity (H) burn areas. Unburned plots were located immediately outside of the burn perimeter and no further than 470 m from the edge of the fire perimeter. Burn severity classifications for these research plots were initially derived from the USDA Burned Area Emergency Response (BAER) map, which is based on Burned Area Reflectance Classification remote-sensing data that have been verified by field crews (Parsons et al. 2010; Noll and Malis-Clark 2020). BAER classifications are based on relative change in soil organic matter and soil structure due to fire (Keeley 2009). We confirmed burn severity classifications for each plot by visually assessing first-order fire severity effects in May 2020, including vegetation cover within plots, the presence of bare mineral soil within plots, and overstory mortality within an approximately 25-m radius of the center of each research plot. Indicators of low severity fire included extant understory vegetation, low bole scorch height, and less than 50% overstory mortality. Indicators of high-severity fire included more than 50% bare mineral soil and more than 90% overstory mortality. Each research plot was subdivided into four 1-m2 subplots located 1 m apart. For this study, one 1-m2 subplot was used per plot. See Taber and Mitchell (2023, 2024) for more information on experimental design and concurrent research projects.

**Data collection**

*Community composition*

Community composition and abundance data were collected in the 1-m2 subplots in the second week of September 2024, approximately 5 years post fire. Individuals were identified to the species level and absolute species cover was recorded to the nearest 0.25% using a modified Daubenmire method. Species accounting for less than 0.25% of cover on a given plot were recorded with a value of 0.2% cover. All nomenclature follows the USDA NRCS Plants Database (https://plants.usda.gov/) accessed in 2025. For the purposes of this project, we removed rare species by removing species that only occurred in 5% of the plots or less.

      Three plots were lost over the 5 years of data collection associated with this project: 2 in low-severity, 1 in high-severity. These 3 plots were removed from our data, bringing the total number of plots to n = 57.

*Plant functional traits*

Over the 5 years of data collection associated with this project, we collected three plant traits: SLA (mm2 g−1), LDMC (g g−1), and height (m). Our species pool contains 19 species (Appendix S1: Table S2). SLA, LDMC, and height were measured from individuals on-site for all species. All measurements followed standardized collection protocols (Garnier et al. 2001; Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013). Measurements on individuals were collected regardless of sun exposure, slope, or aspect, but only mature, healthy leaves were measured.

Height was measured for 20–25 individuals per species. For species with <20 individuals, height was recorded for all individuals present. The height of *Quercus gambelii* was measured as the median height of 20 understory (<2m) individuals. The median was used instead of the mean because *Q. gambelii* is a canopy species at maturity and therefore the height of individuals in the understory is skewed rather than normally distributed.

To measure SLA and LDMC, one leaf sample was taken from individuals of each species. For species with <20 individuals, we collected between 3 and 10 leaves from an individual, aiming for a total of 20 leaves per species. Leaf area for all samples was determined using a CID-203 leaf area meter (CID Bio-Science; Camas, Washington USA). All fresh samples were rehydrated by placing petioles in distilled water for at least 6 h before being scanned and weighed following Garnier et al. (2001). After leaf area and fresh mass were measured, leaf samples were dried at 70 °C for 72 h, then reweighed. SLA and LDMC were then calculated from the area and mass data for each sample.

For the purposes of this analysis, we included two field collected traits (SLA, height) and two assigned traits (seed mass, resprouting ability), which were collected from the TRY Database, Seed Information Database, NRCS Plants Database, and other primary literature sources (see Appendix S1: Table S3 for detailed sources on plant traits). In total, three of these traits represent the leaf-height-seed (LHS) plant ecology strategy scheme. The LHS scheme provides a framework for understanding how plants allocate resources to growth, competition, and reproduction through variations in these three traits (Westoby 1991). SLA represents a variation along the leaf economics spectrum and indicates a plant’s ability to respond to opportunities of rapid growth (Reich et al. 1999). Plant height at maturity is related to competitive ability and fecundity (Keddy & Shipley 1989). Seed mass reflections variation in dispersal abilities and seedling survivorship (Westoby, Leishman, & Lord 1996). Resprouting ability was included to capture an important axis of fire response that relates to species persistence and biomass allocation (Clarke et al. 2012; Poorter et al. 2011)

Only one trait value could not be found for a species or a close congener (*Coligania angustifolia*, seed mass). We used the average seed mass of all species included in the species list as a substitute. See Appendix S1: Table S3 for a detailed trait table.

**Statistical Analyses**

Differences in composition according to burn severity were analyzed using PERMANOVA (Anderson 2017; Anderson 2008) and Non-metric Dimensional Scaling (NMDS) within the *vegan* package (Oksanen et al. 2022). To understand how the three different burn severities differed, we used the function *pairwise.adonis* in the *pairwiseAdonis* package (Martinez 2017). We then used the *beta.disper* function in the *vegan* package, a multivariate analogue of Levene’s test, to test for further differences in beta diversity, i.e. variation in community composition among plots within a burn severity. Standardized abundance values were used in all analyses involving abundance; percent cover for vegetation was standardized using Wisconsin double standardization (McCune & Grace 2002). Additionally, we used Indicator Species Analysis using the function *multipatt* in the package *indicspecies* to find species associated with specific burn severities(De Cáceres & Legendre 2009).

Community weighted mean (CWM) trait values were calculated for SLA, height, seed mass, and resprouting ability using the *dbFD* function in the *FD* package (Laliberté & Legendre 2014). We then used the *envfit* function in the *vegan* package to explore differences in functional traits associated with burn severities.

All analyses were conducted using R version 4.5.0 (R Core Team 2022).

**Appendix**

**Table S1.** Annual weather data.

**Table S2**. Scientific name, common name, functional type, and nativity status of all plant species used in analysis after rare species were removed.

|  |  |  |  |
| --- | --- | --- | --- |
| **Scientific name** | **Common name** | **Functional type** | **Nativity** |
| Artemisia ludoviciana | White sagebrush | Forb | Native |
| Carex rossii | Ross’ Sedge | Grass | Native |
| Ceanothus fendleri | Fendler’s Buckbrush | Shrub | Native |
| Chenopodium album | Lamb’s-Quarter | Forb | Native |
| Cologania angustifolia | Long-Leaf Cologania | Forb | Native |
| Elymus elymoides | Western Bottle-Brush Grass | Grass | Native |
| Festuca arizonica | Arizona Fescue | Grass | Native |
| Heliomeris multiflora | Nevada Showy False Goldeneye | Forb | Native |
| Houstonia wrightii | Pygmy Bluet | Forb | Native |
| Linaria dalmatica | Dalmatian Toadflax | Forb | Exotic |
| Lotus wrightii | Wright's deervetch | Forb | Native |
| Muhlenbergia montana | Mountain Muhly | Grass | Native |
| Muhlenbergia virescens | Screwleaf muhly | Grass | Native |
| Piptochaetium pringlei | Pringle's Spear Grass | Grass | Native |
| Pseudognaphalium macounii | Macoun's cudweed | Forb | Native |
| Quercus gambelii | Gambel's Oak | Tree | Native |
| Salsola tragus | Prickly Russian-Thistle | Forb | Exotic |
| Schizachyrium scoparium | Little False Bluestem | Grass | Native |
| Verbascum thapsus | Great Mullein | Forb | Exotic |

**Table S3.** Database or primary literature sources for plant functional traits.

1. Seed mass sources for all plant species included in the study. (SER SID: Society for Ecological Restoration Seed Information Database, <https://ser-sid.org>)

|  |  |
| --- | --- |
| **Scientific name** | **Source** |
| Artemisia ludoviciana | SER SID: RBG Kew, Wakehurst Place. |
| Carex rossii | SER SID: RBG Kew, Wakehurst Place.  *subbed Carex pellita* |
| Ceanothus fendleri | SER SID: Forest Service. 1974. Seeds of Woody Plants in the United States. Agriculture Handbook Number 450. Forest Service, U.S. Department of Agriculture, Washington, D.C. Keeley, J.E. 1991. |
| Chenopodium album | SER SID: Funes, G., Basconcelo, S., Díaz, S. and Cabido, M.1999. Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. Seed Science Research, 9:341-345.  Earle, F.R. and Jones, Q. 1962. Analyses of seed samples from 113 plant families. Economic Botany, 16:221-250.  Stevens, O.A. 1932. The number and weight of seeds produced by weeds. American Journal of Botany, 19:784-794.  Thompson, K., Band, S.R. and Hodgson, J.G. 1993. Seed size and shape predict persistence in soil. Functional Ecology, 7:236-241.  Baker Seed Herbarium, California. RBG Kew, Wakehurst Place. |
| Cologania angustifolia | NA |
| Elymus elymoides | SER SID: Baker Seed Herbarium, California. |
| Festuca arizonica | SER SID: RBG Kew, Wakehurst Place. |
| Heliomeris multiflora | SER SID: RBG Kew, Wakehurst Place.  *subbed Heliomeris longifolia* |
| Houstonia wrightii | SER SID: RBG Kew, Wakehurst Place.  *subbed Houstonia micrantha* |
| Linaria dalmatica | SER SID: Rutledge, C.R. and T. McLendon. sine anno. An Assessment of Exotic Plant Species of Rocky Mountain National Park. Department of Rangeland Ecosystem Science, Colorado State University. Online. Available: http://www.npwrc.usgs.gov/resource/plants/explant/index.htm) |
| Lotus wrightii | USDA NRCS Plant Database |
| Muhlenbergia montana | SER SID: RBG Kew, Wakehurst Place. |
| Muhlenbergia virescens | SER SID: RBG Kew, Wakehurst Place. |
| Piptochaetium pringlei | SER SID: RBG Kew, Wakehurst Place.  *subbed Piptochaetium fimbriatum* |
| Pseudognaphalium macounii | SER SID: RBG Kew, Wakehurst Place.  *subbed Pseudognaphalium viscosum* |
| Quercus gambelii | SER SID: Earle, F.R. and Jones, Q. 1962. Analyses of seed samples from 113 plant families. Economic Botany, 16:221-250. |
| Salsola tragus | SER SID: Young, F. L. and R. E. Whitesides. 1987. Efficacy of postharvest herbicides on Russian thistle (Salsola iberica) control and seed germination. Weed Sci. 35:554–559. |
| Schizachyrium scoparium | SER SID: Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology, 78:81-92. |
| Verbascum thapsus | SER SID: Grime, J.P., Mason, G., Curtis, A.A., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M. and Shaw, S. 1981. A comparative study of germination characteristics in a local flora. Journal of Ecology, 69:1017-1059. |

1. Resprouting sources for all plant species included in the study. (SER SID: Society for Ecological Restoration Seed Information Database, <https://ser-sid.org>)

|  |  |
| --- | --- |
| **Scientific name** | **Source** |
| Artemisia ludoviciana | 98. Paschke, Mark W.; DeLeo, Claire; Redente, Edward F. 2000. Revegetation of roadcut slopes in Mesa Verde National Park, U.S.A. Restoration Ecology. 8(3): 276-282. [39033] |
| Carex rossii | Smith, Jane Kapler; Fischer, William C. 1997. Fire ecology of the forest habitat types of northern Idaho. Gen. Tech. Rep. INT-GTR-363. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 142 p. [27992] |
| Ceanothus fendleri | Ffolliott, P.F., Clary, W.P., Larson, F.R., 1977. Effects of a prescribed fire in an Arizona ponderosa pine forest. USDA For. Serv. Res. Note RM-336.  Vose, James M., and Alan S. White. “Biomass Response Mechanisms of Understory Species the First Year after Prescribed Burning in an Arizona Ponderosa-Pine Community.” Forest Ecology and Management 40, no. 3 (May 31, 1991): 175–87. https://doi.org/10.1016/0378-1127(91)90037-V. |
| Chenopodium album | NA |
| Cologania angustifolia | NA |
| Elymus elymoides | Bradley, Anne F.; Noste, Nonan V.; Fischer, William C. 1992. Fire ecology of forests and woodlands of Utah. Gen. Tech. Rep. INT-287. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 128 p. [18212] |
| Festuca arizonica | Need help |
| Heliomeris multiflora | NA |
| Houstonia wrightii | NA |
| Linaria dalmatica | Dodge, Rita S., Peter Z. Fulé, and Carolyn Hullsieg. “Dalmatian Toadflax *(Linaria Dalmatica)* Response to Wildfire in a Southwestern USA Forest.” Écoscience 15, no. 2 (June 1, 2008): 213–22. https://doi.org/10.2980/15-2-3043. |
| Lotus wrightii | NA |
| Muhlenbergia montana | Vose, James M.; White, Alan S. 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa-pine community. Forest Ecology and Management. 40: 175-187. [15570] |
| Muhlenbergia virescens | Need help |
| Piptochaetium pringlei | Need help |
| Pseudognaphalium macounii | NA |
| Quercus gambelii | Engle, D. M.; Bonham, C. D.; Bartel, L. E. 1983. Ecological characteristics and control of Gambel oak. Journal of Range Management. 36(3): 363-365. [3361] |
| Salsola tragus | NA |
| Schizachyrium scoparium | Limb, Ryan F., Samuel D. Fuhlendorf, David M. Engle, and Jay D. Kerby. “Growing-Season Disturbance in Tallgrass Prairie: Evaluating Fire and Grazing on Schizachyrium Scoparium.” Rangeland Ecology & Management 64, no. 1 (January 1, 2011): 28–36. https://doi.org/10.2111/REM-D-10-00022.1. |
| Verbascum thapsus | NA |