Article Title: Understory plant community is taxonomically and functionally distinct five years after high severity fire.

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**1. INTRODUCTION**

Dry conifer forests of the American West are adapted to a regime of frequent, low-severity fire (Fule, Covington, and Moore 1997). However, many factors including early 20th century fire suppression policies, the loss of indigenous burning practices, nonnative animal grazing, an increasingly variable climate, and atmospheric warming and drying trends (Seager et al. 2015; Zhang et al. 2021) have affected forest stand dynamics (Belsky and Blumenthal 1997; Swetnam et al. 2016). These changes have led to less frequent and higher severity fires to which these forests are not adapted (Falk et al. 2022). Recent research suggests that forested ecosystems may not recover from high-severity fire, and instead initiate alternate successional trajectories (Falk et al. 2022; Guiterman et al. 2022; Coop 2023). Following fire, the understory community responds before the canopy and can strongly influence successional trajectories, therefore changes to the understory can impact forest recovery after high-severity severity (Seidl and Turner 2022). We examine the responses of forest understory community composition and functional traits across a fire severity gradient to understand the consequences of increasing fire severity on post-fire understory recovery.

An increasing proportion of wildfires are burning at high-severity (Singleton et al. 2019). This shift is being exacerbated by a warming and drying climate (Mueller et al. 2020; Parks and Abatzoglou 2020; Wasserman and Mueller 2023). Although the responses of ecosystems to high-severity fire, and the underlying mechanisms, have yet to be fully understood, high-severity fire has been observed to reduce the diversity of understory communities (Richter et al. 2019). Communities recovering from high-severity fire exhibit a shift toward xerophilic and thermophilic species and a loss of mesic and sensitive species (Stevens et al. 2015, 2019; Dickson-Hoyle et al. 2024). In contrast, diversity is maximized when fires match historic regimes (Miller and Safford 2020; Weeks et al. 2023). In yellow pine forests of California, which are adapted to low-severity fire, Richter et al. (2019) found that diversity follows a strong unimodal curve; the extreme ends of a burn severity gradient (no fire and high-severity fire) had the lowest richness and diversity, while low and moderate severity resulted in the greatest richness and diversity.

Functional traits offer a mechanistic view of how fire acts on plant communities (Keeley et al. 2011). Plumanns-Pouton et al. (2024) were able to accurately predict the change in relative abundance of plant functional types, based on reproductive and life-history strategies, across an 81-year post-fire chronosequence in Australia. While fire can filter species based on functional traits, trait filtering changes as fire severity increases. Taber and Mitchell (2023) found that, along a burn severity gradient, high-severity fire differentially selected species with lower leaf dry matter content (LDMC) and height in the first year after wildfire. Wang and Kemball (2005) found that regeneration strategy changed with fire severity in boreal forests of Canada, with resprouters giving way to seed banking species and then dispersal-dependent colonizers as fire severity increased. These results demonstrate that, through effects on the abiotic environment (Savage, Mast, and Feddema 2013; Haffey et al. 2018), high-severity fire can limit the ability of reference forest communities to regenerate, and instead favor species with alternate regeneration strategies. This may initiate ecosystem type conversion. Once an alternate plant community is established, grasses and woody plants can have an inhibitive effect on the recruitment of conifer seedlings, reinforcing alternate assembly trajectories (Singleton et al. 2021).

The regeneration strategies that favor some species over others following high-severity fire can be explained using functional traits. Ruderality is a syndrome that is expected to increase following high-severity fire (Grime 1977), and is associated with resource-acquisitive traits such as high specific leaf area (SLA) and low seed mass (Wright et al. 2004, missing ref?). Resprouting ability is a highly adaptive trait that can be seen commonly in fire-adapted ecosystems (Falk et al. 2022). It is expected that, under historic conditions, burning can increase the relative abundance of resprouters over obligate seeders. However, species that would typically survive and resprout following low severity fire may not be able withstand the soil heating associated with high-severity fire. If resprouting does occur following high-severity fire, it will likely be only from deeply rooted species. Following Westoby’s (1998) leaf-height-seed scheme (LHS), plant height is associated with competitiveness, and the importance of competitiveness increases following low-severity disturbance (Grime 1977). Therefore, it is expected that plant height will increase following fire, but with greater height following low-severity fire rather than high-severity fire.

We use understory community data collected after a mixed-severity fire in a ponderosa pine ecosystem to investigate the effect of fire severity on community composition. We also investigate if changes in composition can be explained by community functional traits. We predict that:

1. High-severity fire will be associated with a distinct understory community, while no fire and low-severity fire will be associated with similar understory communities.
2. Differences in community composition following high-severity fire will be driven by species with increased specific leaf area and height, decreased seed mass, and a decrease in resprouting ability.

**2. METHODS**

**2.1 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).

**2.2 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.

**2.3 Data collection**

*2.3.1 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. We removed rare species by removing species that occurred on 3 plots or fewer. (species retained *n* = 19). Due to post-fire management actions at the site and a small landslide, 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. All nomenclature follows the USDA NRCS Plants Database (https://plants.usda.gov/) accessed in 2025.

*2.3.2 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 S1). 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 S2 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 1998). 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 (Poorter et al. 2011; Clarke et al. 2012)

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 S2 for a detailed trait table.

**2.4 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, and Urban 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).

**3. RESULTS**

**3.**  **Results**

Overall, the mean relative cover of exotic species in the unburned, low, and high severity plots was <1%, 3.5%, and 39.7% respectively. Some indicator species, e.g. *Elymus elymoides* of high severity fires, actually had higher average cover in the unburned and low severity sites; but because indicator species analysis weights both abundance and fidelity, *Elymus elymoides* is an indicator species because it was consistently abundant across high severity plots and not in unburned and low severity plots (De Cáceres & Legendre 2009).

**3.1 Taxonomic differences across burn severities**

PERMANOVA results suggest differences in taxonomic (F(2, 54) = [5.0497], p = 0.0001) community composition across all burn severities. Pairwise comparisons of burn severity from our PERMANOVA showed significant taxonomic differences between unburned and low severity (p = 0.0285), unburned and high severity (p = 0.0003), and low and high severity plots (p = 0.0003). Taxonomic species composition differences are also revealed in NMDS plots between high severity plots and others. Unburned and low severity centroids are closer together but still significantly different in locations (Fig. 1). We then used the *beta.disper* function*-* 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. This shows a significantly lower beta diversity in unburned versus low severity plots (p = 0.0140752), whereas other burn severity plots are only different in location of centroids and not in dispersion (F(2, 54) = [4.4693], p = 0.01599).

Indicator species analysis revealed several significant indicator species associated with specific fire severity conditions. *Verbascum thapsus*, a nonnative forb,(*IndVal* = 0.618, p < 0.001) is strongly associated with high severity locations. *Pseudognaphalium macounii,* a native forb, (*IndVal* = 0.283, p < 0.05) was also significantly associated with high severity plots. Perennial grasses, *Muhlenbergia virescens* (*IndVal* = 0.314, p < 0.05), and *Piptochaetium pringlei* (*IndVal* = 0.275, 0.05 < p < 0.1), were significant indicators of low and unburned plots respectively . Several other species demonstrated a marginal significance (0.05 < p < 0.1) as indicators of high severity plots (Table 1).

**3.2 Plant functional trait associations with burn severities**

We used the *envfit* function to explore differences in functional traits associated with burn severities based on vegetation community compositions. Species composition differences across burn severities are correlated to differences in height, resprouting ability, and SLA. Resprouting influenced species composition across burn gradients the most, such that this trait was most strongly associated with unburned and low severity plots. High SLA is most strongly associated with high severity plots with increasing plant height showing stronger associations with low severity plots. Seed mass was not significantly correlated with any plots across burn severities. (Fig. 1).

**4. DISCUSSION**

* Recap

Before the early 1900s, frequent, low-severity fires kept dry conifer forests of the American west relatively open and park-like, with abundant grass and forb cover dominating the understory (Biswell et al. 1973). However, fire regimes have changed from historic norms, with consequences for forest composition and structure. Here, we examined the responses of a ponderosa pine forest understory community to a fire severity gradient. We used functional trait data to better understand changes in composition.

* Prediction 1 – communities are different
  + PERMANOVA
  + Centroids, dispersions

Understory composition differed across all three severity classes (Table X), which is in partial agreement with our first prediction. Given our combination of PERMANOVA and tests of beta dispersion, all three severity classes differed in centroid, but the unburned and low-severity plots differed in both centroid and beta dispersion (Table X; Fig. X?). Visualizing these plots in ordination space using NMDS, it appears that the unburned community is a subset of the low-severity community. This is potentially consistent with the IDH, where low-intensity disturbance allows for a greater diversity of ecological strategies to occupy a community.

This supports the intermediate disturbance hypothesis, which states that diversity is maximized under low levels of disturbance relative to the ecosystem’s ability to recover (Fox 1979).

* Prediction 2 – differences are explainable by traits
  + Envfit

Consistent with our second prediction, the compositional differences across the burn severity gradient were explainable with functional traits. As fire severity increased, the plots were dominated by species with high SLA, no resprouting ability, and with increased height. Contrary to our prediction, however, the fire severity classes did not differ in seed mass. The traits that did have explanatory power demonstrate that high-severity fire increases community ruderality, as seen with high SLA and lack of resprouting. Fire also increased plant height, suggesting increased plant competition, or inversely, suppression of fire increased the importance of stress-tolerance.

* Trait expression across severity gradient matches expectations of ecological strategies
  + Indicator species

The use of indicator species analysis allowed us to relate the expression of community traits–and the ecological strategies associated with these traits–to the species that are representative of each severity class. The only indicator species for the unburned and low-severity plots were *Piptochaetium pringlei* and *Muhlenbergia straminea*, respectively, which are both perennial bunchgrasses. The high-severity plots had several indicator species, but the strongest indicator was *Verbascum thapsus*, which is a ruderal biennial forb. This is consistent with our trait vectors, which showed that traits associated with ruderality became more important in the high-severity plots. The remaining indicator species in the high-severity plots represent a variety of ecological strategies and include functional perennial forbs, perennial grasses, a legume, and the only shrub species in our data set (Table X). This variety of indicator species may demonstrate that high-severity fire opened a greater breadth of niches, such that these functional groups could occur with greater consistency across plots. In other words, high-severity fire not only changed the composition of the understory, but also the ecological strategies of the species in the understory. Kuenzi et al. (2008) found similar results following the Rodeo-Chediski fire, which at the time of its ignition in 2002 was the largest and most severe fire in the southwestern United States. They found that low-severity fire was indicated by perennial bunchgrasses, while indicators of high-severity fire included ruderal species. Interestingly, as with our results, they found that high-severity fire increased the number of indicator species. These species included some of our high-severity indicators, such as *Lotus wrightii* and *Ceanothus fendleri*.

Several plant species were determined to be indicators of different burn severities. The perennial grass *Piptochaetium pringlei* was an indicator within the unburned area, and the perennial grass *Muhlenbergia virescens* was indicative of low-severity burns. High severity indicator species were more abundant, and included one shrub, two grasses, and four forbs; two of these indicator forbs- *Verbascum thapsus* and *Linaria dalmatica*- are introduced in the United States (USDA Plants). Removal of established native vegetation by the high-severity fire reduced competition, allowing for the re-assembly of exotic-rich communities (McGlone et al. 2010).

* Functional groups

Increasing fire severity was associated with decreased relative graminoid cover and increased relative forb, shrub, and tree cover. In unburned plots, graminoids were by far the most abundant functional group; there was a large decrease of more than 50% in relative graminoid cover from low to high severity (Figure number). Trends in forb cover were largely driven by changes in exotic species abundance. This trend is consistent with observations that abnormally severe fires can favor woody species and trigger conversion to shrublands, ultimately contributing to an altered fire regime (Wang and Kemball 2005; Guiterman et al. 2022). Sentence about evidence/models predicting increased ruderality (Coop 2022).

* Native vs exotic
  + Traits expressed in high-severity plots are expressed by non-native species
  + Native community is not adapted to high-severity fire

Our study site is positioned within the wildland-urban interface of Flagstaff, Arizona, and is in an area with high recreational use year-round. Human activity serves as a vector of exotic species (Kovarik and Von Der Lippe 2008), and they appear to readily colonize severely burned areas in this ecosystem (McGlone and Egan 2009). The proximity of our study site to urban infrastructure–including roads, trails, and residential developments–has likely influenced the local species pool available for post-fire assembly of understory communities (Fowler et al. 2008). These anthropogenic factors interact with ecological processes, influencing both the composition and trajectory of vegetation post-fire. Despite the physical proximity of the low and high severity plots in our study site, the distinct increase in exotic cover between low severity and high severity (Fig. #) suggests that the wildland-urban interface..

* + wildland vs urban interface!!! domination of exotics, due to a lot of things, like post fire maintenance, proximity to a road, foot traffic
  + a unique situation in that this area has a lot of human interaction!
  + not super remote but also
  + unusual species pool for the area because of the closeness to humans
  + low and high severity are IMMEDIATELY adjacent but the dominant species are sooo different
* Implications for management <3 <3
  + this fire unique because they did not do ANy post fire restoration/seeding, which in my head is uncommon (not even a little bit of wheat)
  + RAD framework? given that this area is proximal to a lot of recreation and other human activities, does it make sense to recommend a resist strategy here, or an accept/direct → we could lay out what these scenarios might look like for each approach
    - resist - reseed with natives with reference community as low severity
    - accept - what they did was accept with no management/intervention
    - direct

We have shown that community composition is altered within the first five years following high-severity fire. Long-term successional trajectories can be determined by the plant community that establishes immediately post-disturbance (Seidl and Turner 2022). Therefore, the altered understory community that we observed may have profound implications for the long-term ability of the reference community and canopy to recover. If reference communities are a desired management goal, our results underscore the importance of post-fire restoration.

Our findings suggest that without post-fire restoration actions, high severity fires could potentially alter community trajectories and subsequently ecosystem processes and functions. Differences in taxonomic composition suggest that restoration such as seeding and revegetation will be critical if understory communities reflective of the historic fire regime are desired.

Traits aligned with ruderality, increasing SLA and decreasing resprouting ability, are associated with the taxonomic community in high severity plots.

Management intervention is necessary post-fire in areas where high severity fire passes through to restore an understory ecosystem back to its native communities and ecosystem functioning. Exotics will dominate in a high severity post-fire condition without intervention.

RAD

Resist -> Ideally, preventing high severity fires is best; managing fire severity before burns occur would be the best way to resist these vegetation changes or reseeding with native community/species pool opst-fire

Accept: what they did; accepting that a new community will persist on the landscape that is mostly composed of exotic species

Direct: facilitate towards something that will already probably happen (towards a vegetation type change - VTC) (PJ woodland or oak scrubland),

Knowledge gap: is management capable of resist in this ecosystem? is it feasible at this point?

**5. REFERENCES**