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

**Author Names:** Ian Winick1, Madeleine Wallace1, Fern Bromley1, Cecilia Martinez1,2, Cameron Crowder1, Doan Goolsby1, Rachel Mitchell1

**Affiliations:** 1 School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, 85719, 2 Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ, 85719

**Corresponding Author**: Ian? Rachel?

**Abstract** (250 Word Max): Wildfires across the western United States are becoming more severe, creating the potential for alternative ecosystem successional trajectories in the absence of management intervention, many of which have already been realized. We characterized understory plant communities across a burn severity gradient in a dry ponderosa pine forest outside of Flagstaff, Arizona, and evaluated differences in taxonomic composition and the functional traits associated with vegetation types. While understory communities were similar pre-fire, unburned, low-severity, and high-severity understory communities were significantly distinct from each other five years post-fire. With increasing burn severity (unburned to low- to high-severity), understories became decreasingly graminoid dominated and increasingly occupied by forbs and woody plants. Along this gradient, non-native plant increased dramatically, from < 1% relative cover in the unburned plots to nearly 40% in the high-severity plots. Plant species with resprouting ability, an important trait in fire-adapted systems, were more abundant in unburned and low-severity than in the high-severity plots, indicating that emerging fire regimes can damage native resprouters and overwhelm their regeneration capacity. High-severity communities also had the highest specific leaf area (SLA), revealing that understories in these areas, where fire killed most of the canopy, were colonized and subsequently dominated by fast-growing plants. Species were tallest in the low-severity plots, and seed mass was not associated with a specific burn status. Altogether, the persistence of novel understory communities that differ from their references under native disturbance regimes highlights the need for fire prevention through forest management, as well as prompt restoration after severe wildfires.

**Keywords** (1-7 words): ponderosa pine, fire, Arizona, drylands, forest management

EDITING SCHEDULE

~~May 19 - May 22 Maddie~~

~~May 23 - May 26 Fern~~

~~May 27 - May 30 Ceci~~

~~May 31 – June 3 Cameron~~

June 4 - June 8 Ian

June 9 - June 13 Doan

June 14 Rachel

**1. INTRODUCTION**

Forest stand dynamics across western North America have been reshaped by many factors over the past century and a half, including early 20th century fire suppression policies, the loss of indigenous burning practices, nonnative animal grazing, increasing climate variability, and atmospheric warming and drying trends (Belsky and Blumenthal 1997; Seager et al., 2015; Swetnam et al., 2016; Zhang et al., 2021). As a result, contemporary wildfire behavior across the western United States (U.S.) has changed considerably, and is now occurring less frequently, at unprecedented severities, and over longer fire seasons (Dennison et al., 2014; Balch et al., 2017; Burke et al., 2020; Mueller et al., 2020; McClure et al. 2024). This shift in fire regime is being exacerbated by a warming and drying climate (Mueller et al., 2020; Parks and Abatzoglou, 2020; Wasserman and Mueller, 2023), resulting in a greater proportion of wildfires burning at high severity (Singleton et al., 2019). These shifts in climate, along with fire frequency and severity, can have significant consequences for forested plant communities, potentially leading to alterations in regeneration strategies, changes to historically observed successional pathways, and even loss of species not adapted to high-severity fires (Davis et al., 2019; Boucher et al., 2020; Coop et al., 2020).

In the dry conifer forests of western North America, which are historically adapted to frequent, low-severity fires, shifts in both climate and fire behavior may lead to alternate successional trajectories rather than a return to pre-fire communities (Falk et al., 2022; Guiterman et al., 2022; Coop, 2023). These forests were historically characterized by surface fires occurring every 7 to 25 years, which limited ground fuel accumulation and promoted open canopies with diverse understory plant communities. Typically, understory vegetation in these dry forested ecosystems is composed of surface-fire adapted perennial grasses, forbs, and some woody shrubs (Laughlin et al., 2008), which respond quickly to disturbance compared to the canopy community and play a key role in post-fire recovery dynamics (Seidl and Turner 2022). However, decades of altered fire management practices, coupled with increasing aridity across the West (Seneviratne et al., 2010; Overpeck & Udall, 2020), have led to denser forest structures and altered fuel profiles (Hagmann et al. 2021), making them more vulnerable to stand-replacing, high-severity fires (Parks et al. 2023). These novel disturbance regimes may push ecosystems beyond recovery thresholds, leading to state shifts that are difficult to reverse and have implications for ecosystem processes and associated socio-ecological services (Turner, 2010). Accurately predicting alternative successional trajectories will be key for effective forest management in this era of increasing anthropogenic change.

Western dry conifer forests house most of their biodiversity in their understories. Following fire, due to the rapid time to maturity compared to trees, these understory plant communities respond more swiftly than the canopy, and as such, play a key role in shaping successional trajectories (Seidl and Turner 2022). Although ecosystem responses to high-severity fire and their underlying mechanisms are not yet fully understood, abnormal high-severity fire has been shown to reduce the diversity of understory communities (Richter et al., 2019). Communities recovering from unprecedented high-severity fire demonstrate a shift toward xerophilic and thermophilic species, accompanied by a decline in mesic and sensitive species (Stevens et al., 2015, 2019; Dickson-Hoyle et al., 2024). In contrast, plant diversity is maximized when fires are aligned with their historic disturbance regime (Miller and Safford, 2020; Weeks et al., 2023). An example of which occurs in the yellow pine (*Pinus ponderosa* and *P. jeffreyi*) forests of California, which are adapted to low-severity fire. Richter et al. (2019) found that diversity follows a strong unimodal curve wherein 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.

To better understand shifts in diversity and composition following fire, ecologists have increasingly turned to functional traits as a tool to explain plant community response to disturbance. Functional traits can offer a mechanistic framework for understanding plant community responses to wildfire (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 acts as an ecological filter by favoring certain functional traits, the nature of this filter shifts with increasing fire severity, and the specific traits that confer competitive advantages can vary with fire severity. This is observed in Taber and Mitchell (2023), who found that high-severity fire differentially selected species with lower leaf dry matter content (LDMC) and height in the first year after wildfire along a burn severity gradient. Wang and Kemball (2005) found that the regeneration strategies in Canadian boreal forest understories changed as fire severity increased; they found that, across a gradient of scorched, lightly burned, and severely burned plots, the understory was dominated by resprouters, seed-banking species, and dispersal-dependent colonizers, respectively. These results suggest that high-severity fire, through effects on the abiotic environment (Savage, Mast, & Feddema, 2013; Haffey et al., 2018), can limit the ability of reference forest communities to regenerate, instead favoring species with alternative regeneration strategies. This shift may initiate an ecosystem type conversion. Once an alternate plant community is established, dense grasses and woody plants can inhibit the recruitment of conifer seedlings, further driving alternate assembly trajectories (Pearson 1942; Singleton et al., 2021).

Given the mechanistic framework of functional traits, we can use them to predict compositional outcomes of increasing fire severity. It is expected that high-severity disturbance will increase the abundance of ruderal species (Grime 1977), which are characterized by rapid growth, short life span, and high reproductive output. Ruderal species often possess resource-acquisitive traits such as high specific leaf area (SLA) and low seed mass (Westoby, 1998; Wright et al., 2004), which enable rapid exploitation of post-fire resources, e.g., high light. Resprouting ability is another highly adaptive trait common in fire-adapted ecosystems, typically providing a competitive advantage in low- and moderate-severity fire regimes (Falk et al., 2022). ~~Under historic fire conditions, frequent burning can increase the relative abundance of resprouters over obligate seeders~~. However, the intense soil heating associated with higher severity fires can damage basal buds and root crowns, limiting the survival of resprouters (Clarke et al. 2013). As a result, only the most deeply rooted species, such as shrubs (Minor et al. 2017, Coop 2022), may retain the ability to resprout following high-severity fire. Additionally, plant height, a trait linked to competitive ability in Westoby’s (1998) leaf-height-seed (LHS) framework, also varies with fire severity. Plant height is expected to increase following fire because it is anticipated or shown that disturbance will initiate competition for released resources (Grime 1977). In contrast, high-severity fire often resets competitive dynamics, favoring shorter, faster-colonizing species over taller, slower-growing competitors.

Understanding post-fire vegetation dynamics is essential not only for ecological theory, but also for informing land management decisions and restoration efforts. As wildfires across the western U.S. grow more severe, predicting how plant communities will reorganize can guide actions to conserve biodiversity, maintain ecosystem services, and reduce undesirable state shifts. Here, we use understory plant community data collected five years after a mixed-severity fire in a ponderosa pine ecosystem to examine how fire severity influences community composition and to investigate whether these 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, whereas unburned and low-severity fire areas will contain similar understory communities.
2. Differences in community composition following high-severity fire will be driven by species with these functional traits: 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). The Museum Fire burned a total of 793.6 hectares in late July of 2019 and was of mixed severity, with very low-, low-, moderate-, and high-severity patches all present within the perimeter (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. The burn scar ranges from approximately 2240 m to approximately 2760 m in elevation. 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 521.7 mm (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 North American Monsoon that affects the southwestern U.S. (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**

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 each. 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. For our species pool, we removed rare species that occurred on 3 or fewer plots (species retained *n* = 19). Due to post-fire management actions and a small landslide at the study site, three plots were lost over the five years of data collection associated with this project: two in low-severity, one in high-severity. These three plots were removed from our data, bringing the total number of plots to *n* = 57. All taxonomic nomenclature follows the USDA NRCS Plants Database (https://plants.usda.gov/) accessed in March 2025.

*2.3.2 Plant functional traits*

Over the five 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: 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 (<2 m) 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 positively 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 three and ten 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 six hours 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 hours, 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

e, Seed Information Database, NRCS Plants Database, and other primary literature sources (see Appendix: Table S2a and S2b 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 regeneration, 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 (*Cologania angustifolia*, seed mass). We used the average seed mass of all species included in the species list as a substitute. See Appendix: Table S3 for a detailed trait table.

**2.4 Statistical Analyses**

All analyses were conducted using R version 4.5.0 (R Core Team 2022).Differences in composition according to burn severity were analyzed using PERMANOVA (Anderson, 2008, 2017) 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. Relative abundance values were used in all analyses involving abundance; percent cover for vegetation was relativized 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 used the *envfit* function in the *vegan* package to explore differences in functional traits associated with plots across burn severities.

**3. RESULTS**

**3.1 Compositional differences across burn severities**

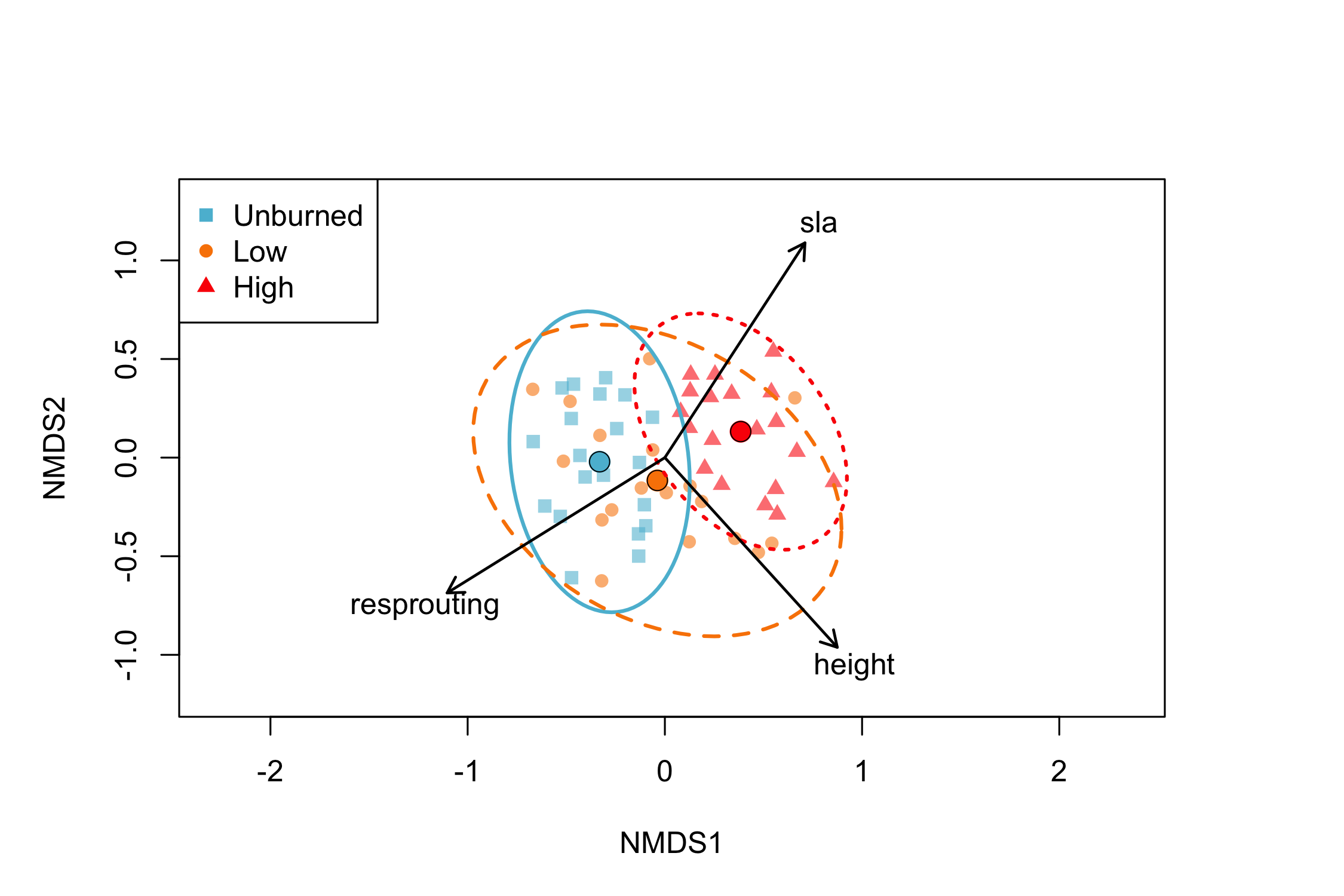
Our PERMANOVA revealed that fire severity had a significant effect on community composition (F(2, 54) = [5.050], p = 0.0001, Figure 1). Pairwise comparisons from our PERMANOVA showed significant differences between unburned and low-severity (F = 2.50, p = 0.029), unburned and high-severity (F = 8.830, p = 0.0003), and low and high severity plots (F = 4.024, p = 0.0003). Taxonomic species composition differences between the high-severity and other plots are also revealed in the NMDS results (Figure 1). Our test of beta dispersion revealed that there were significant differences in dispersion across the severity gradient (F(2, 54) = [4.4693], p = 0.016). A post-hoc Tukey’s honestly significant difference test revealed that only the unburned and low-severity plots differed in dispersion (p= 0.014). Therefore, the unburned and low-severity plots differed in both beta dispersion and group centroid, while the remaining severity classes differed only in group centroid (Figure 1).

Indicator species analysis revealed several significant indicator species associated with specific burn conditions (Table 1). *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 straminea* (*IndVal* = 0.314, p < 0.05), and *Piptochaetium pringlei* (*IndVal* = 0.275, 0.05 < p < 0.1), were significant indicators of low-severity and unburned plots respectively. Several other species demonstrated a marginal significance (0.05 < p < 0.1) as indicators of high-severity plots (Table 1).

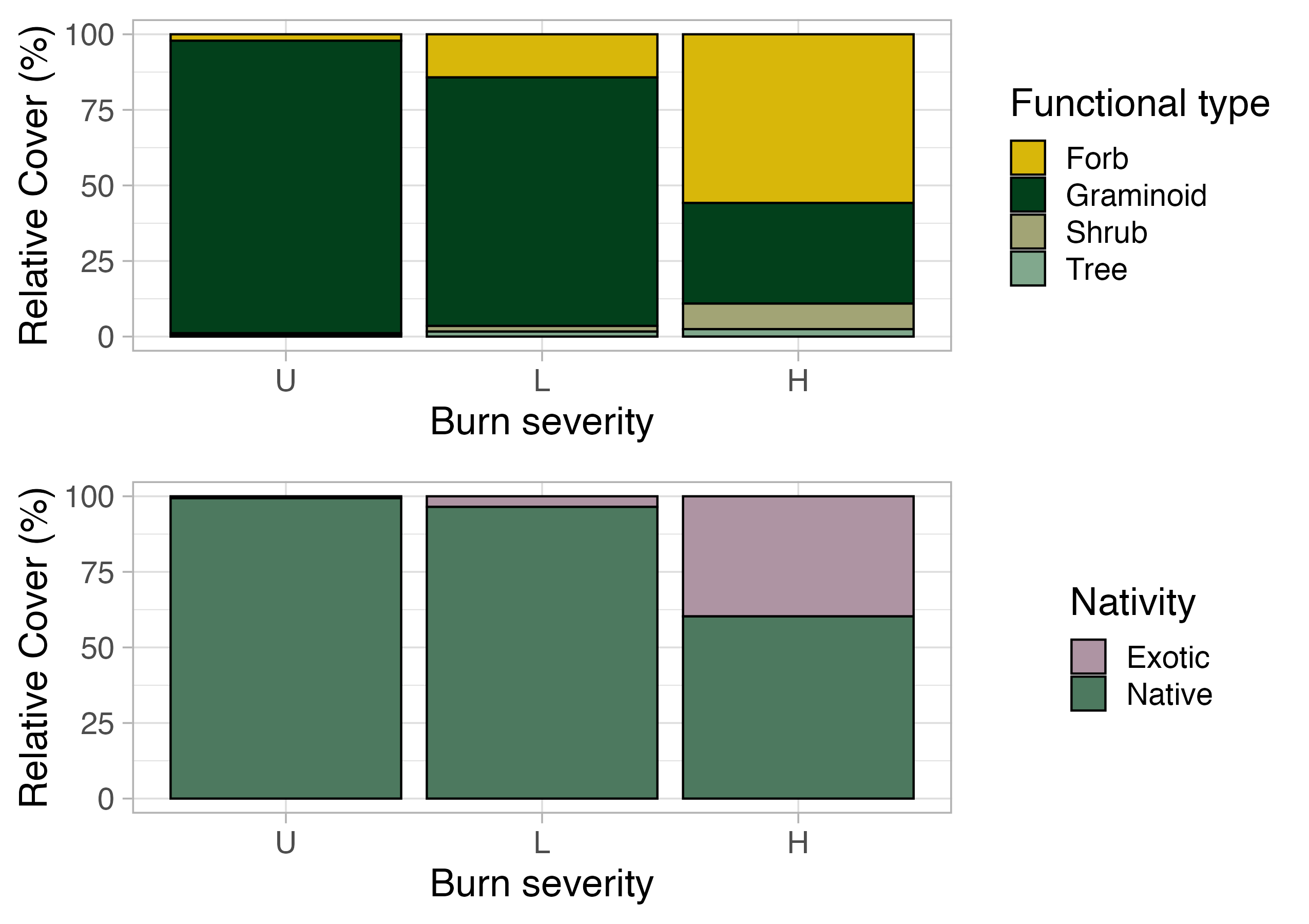
**3.2 Plant functional trait associations with burn severities**

We used the *envfit* function to explore differences in functional traits associated with burn severities based on vegetation community compositions (Figure 1, Table 3). 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 explained the most variability in understory communities between plots and treatments. SLA increased across plots with the presence of fire and fire severity, whereas increasing plant height showed strongest associations with low-severity plots. Seed mass was not significantly correlated with any plots across burn severities (Table 3).

Although we did not include functional or nativity groups in our *envfit* analysis, we found significant differences in the abundances of these groups across the severity gradient.



**Figure 1.** Results from the nonmetric multidimensional scaling (NMDS) analyses. Symbols represent individual plots in 2024 distributed according to taxonomic composition weighted by cover. Vectors indicate correlation between number of species with functional trait and NMDS axes.



**Figure 2.** Relative cover for a) functional type across burn severity and for b) nativity status across burn severity.

**a)**

**b)**

****

**Table 1.** Indicator species for unburned, low, and high severity, with mean relative cover values. p-values = 0.05 < *#* *p* < 0.1; \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001. Signiﬁcant terms are shown in bold; terms in italics are marginally signiﬁcant. 9,999 permutations.

****

**Table 2.** Indicator species analysis results with mean relative cover ± standard deviation, and number of plots in each treatment with species present. Bolded values indicate indicator status for the severity. Species with *IndVal* > 0.2 and *p* < 0.1 are shown. Cover values and number of plots are bolded for the fire severity that the species was an indicator for. Values in parentheses next to different fire severities indicate the number of plots per treatment.

****

**Table 3.** Envfit results for taxonomic NMDS ordinations. p-values = 0.05 < *# p* < 0.1; \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001.

**4. DISCUSSION**

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

In partial agreement with our first prediction, understory composition differed across all three severity classes (Figure 1). Based on both PERMANOVA and tests of beta-dispersion, all three severity classes differed in their central tendencies, while unburned and low-severity plots differed in both centroid locations and beta diversity. Interestingly, the unburned plant community subsets that of the low-severity community. This result is consistent with past findings in forested ecosystems, where species richness is maximized at disturbance severities which match the historical disturbance regime (Miller & Safford, 2020; Weeks et al., 2023). At our site, low-severity fire, a disturbance that is consistent with the historical fire-regime of the area, may have reduced dominance by shade-tolerant or fire-sensitive species, creating some niches for disturbance-adapted species while also retaining some pre-fire community structure. The unburned plots, which have not undergone recent natural fires or silvicultural treatments, , likely reflect altered successional trajectories due to fire exclusion. Fire exclusion is known to reduce understory diversity and favor late-successional dominants (Covington & Moore, 1994; Laughlin et al., 2004). In contrast, the composition of low-severity plots may reflect a community structure where periodic low-intensity fires maintained plant heterogeneity and functional diversity (Allen et al., 2002; Swetnam & Baisan, 2003). These findings support theoretical expectations that ecosystem resilience and diversity are tightly coupled to disturbance regimes, particularly in fire-adapted systems.

^^^ possible condensing of above paragraph as the opening of this paragraph ^^^ In partial agreement with our first prediction, understory composition differed across all three severity classes (Figure 1). This result is consistent with findings in other forested ecosystems, where increasing fire severity has altered the composition of ponderosa forests of the mid-western United States (Roberts et al. 2018) and *Araucaria*‐*Nothofagus* forests of Chile (Arroyo‐Vargas 2022). Consistent with our second prediction, these compositional differences across burn severities were explained by differences in functional traits in each severity class (Figure 1, Table Whatever (3?)). As fire severity increased, the understory communities became increasingly ruderal, expressing traits which favor rapid resource acquisition, short life spans, and high dispersal capacity (Grime, 1977; Diaz et al., 2016). In the high-severity plots, high SLA reflects a strategy optimized for rapid growth in high resource environments, while the absence of resprouting ability suggests a reliance on seed regeneration and opportunistic colonization following disturbances. Increased plant height may indicate competition for light in post-fire environments, where open canopy conditions and high energy availability favor fast-growing species (Westoby, 1998). In contrast, fire suppression likely selects for stress-tolerant strategies, which may be associated with low SLA and increased resprouting ability, which are advantageous in resource-limited understories (Lavorel & Garnier, 2002). Contrary to our prediction, seed mass did not vary significantly across the severity gradient, suggesting that local seed bank compositions and post-fire environmental conditions played a larger role than seed morphology alone (Leishman et al., 2000). Overall, these patterns align with trait-based theories of community assembly, where disturbance acts as an environmental filter, selecting for specific combinations of traits that confer survival and reproduction under new abiotic and biotic conditions (Keddy 1992; McGill et al. 2006).

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. *V. thapsus* and *Linaria dalmatica*, another indicator of the high-severity plots in our study, are both non-native species introduced to the United States (USDA Plants 2025). The presence of these exotics as high-severity indicators underscores the role of intense disturbance as a filter that removes established native competitors and facilitates community assembly dominated by ruderal and exotic species (D’Antonio & Vitousek 1992; McGlone et al. 2012).

The remaining indicator species in the high-severity plots represent a variety of ecological strategies and functional types, including perennial forbs, perennial grasses, a legume, and the only shrub species in our data set (Table 1). This diversity of indicator species may demonstrate that high-severity fire opened a greater breadth of niches, such that these functional groups could occur in abundance with greater consistency across plots. In other words, high-severity fire not only changed the composition of the understory, but likely the ecological strategies of the species in the understory as well. Kuenzi, Fulé, and Sieg (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 on record. 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 also 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*. Additionally, Ffolliott et al. (2010) reported that *Verbascum thapsus* was the dominant forb in high-severity areas of the same burn scar.

Changes in functional group composition further reflects this disturbance-driven shift in assembly processes. With increasing fire severity, graminoid dominance declined sharply, while the relative cover of forbs, shrubs, and trees increased (Figure 2a). Unburned plots were dominated by perennial grasses, but relative graminoid cover declined by more than 50% from low to high severity. This shift suggests a breakdown in the persistence of the historical native grass dominated understory, a pattern that may be symptomatic of reduced resilience in the face of high-severity fire (Coop et al., 2020). The observed increase in forb cover was largely driven by exotic species, further reinforcing the idea that high-severity fire creates open niches that favor fast-growing, generalist species over more conservative perennials (Funk et al., 2008). This trend aligns with models predicting increased ruderality under intensified fire regimes, particularly when coupled with propagule pressure from non-native species (Coop, 2023). 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).

The invasion dynamics observed in this study may also be shaped by the social-ecological context of the site. Located within the wildland-urban interface of Flagstaff, Arizona, and subjected to high year-round recreational use, this area is exposed to elevated levels of anthropogenic propagule pressures. Human activity has long been recognized as a vector for exotic plant introductions (Kovarik and Von Der Lippe, 2008), and high-severity fire may compound this effect by creating highly disturbed, low competition environments conducive to colonization by exotic species (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). Together, these interacting filters of disturbance severity, propagule pressure, and trait-environment mismatch are shaping novel plant communities with altered composition, structure, and potentially function, with implications for both ecosystem resilience and fire regime feedbacks (Keeley et al., 2011; Guiterman et al., 2022).

Future Directions Section – Implications for post-fire restoration and management

Our findings have important implications for land management in fire-prone ecosystems, particularly within the wildland-urban interface. Notably, the Museum Fire is unique in that no post-fire restoration interventions—such as seeding, mulching, or erosion control—were implemented following the 2019 burn. This lack of intervention is relatively uncommon, especially in areas adjacent to human infrastructure and recreational use.This offers a rare opportunity to evaluate early successional dynamics under a passive recovery scenario and raises questions about the desired future state of these ecosystems.

The observed shifts in composition and functional traits within the first five years post-fire suggests that successional trajectories are already diverging from those that are characteristic of historically low-severity fire regimes in ponderosa pine forests of western North America. As ecological theory and empirical studies suggest, community assembly following disturbance can have long lasting effects on forest structure, composition, and function (Seidl & Turner 2022). Our findings suggest that without post-fire restoration actions, high severity fires could potentially alter community trajectories and subsequently ecosystem processes and functions.

As forests, particularly the dry conifer forests of the American West, continue to experience novel anthropogenically-induced changes, ecosystem management approaches may include a much larger decision space than previously considered. Restoration efforts have historically focused on fixed reference communities; however, in this unprecedented era of global change, consideration of multiple different community/compositional pathways/strategies for restoration is crucial (Higgs et al. 2014). The RAD framework (Resist – Accept – Direct; Lynch et al., 2021) offers a useful lens for evaluating potential management responses in this context. A resist strategy might look like one where high-severity fire is prevented using active management and silvicultural treatments. However, given the threat of high-severity fire with which managers are faced, a resist strategy might include rigorous efforts to reseed and replant native species with traits characteristic of low-severity reference communities such as perennial graminoids. A direct strategy might facilitate succession towards an alternative but stable and desirable state, such that novel but native-dominated assemblages more resilient to increasing fire severity or climate change, such as an oak shrubland. Finally, an accept strategy- what has occurred here by default- allows post fire succession to proceed without intervention. This strategy resulted in communities dominated by ruderal and often exotic species, which may have initiate an alternate and undesirable successional trajectory. As such, acceptance at this site may drive vegetation type conversion from dry ponderosa pine forest to a non-forested vegetation type (Barton, 2002; Haffey et al., 2018).

Given the Museum Fire’s proximity to recreational infrastructure and ongoing anthropogenic disturbance, a passive acceptance of these changes may have consequences for ecosystem function and future fire behavior and fuel structure. We have shown that community composition is altered within the first five years following high-severity fire, and 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 desired, our results underscore the importance of post-fire restoration. Our results suggest that if reference communities or ecosystem services associated with them are a priority for management, early and proactive restoration actions will be critical following high-severity fire.

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

**5. REFERENCES**

Allen, C. D., Savage, M., Falk, D. A., Suckling, K. F., Swetnam, T. W., Schulke, T., Stacey, P. B., Morgan, P., Hoffman, M., & Klingel, J. T. (2002). Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications,* *12*(5), 1418-1433.

Anderson, M. J. (2008). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>

Anderson, M. J. (2017). Permutational Multivariate Analysis of Variance (PERMANOVA). In *Wiley StatsRef: Statistics Reference Online* (pp. 1–15). John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118445112.stat07841>

Barton, A. M. (2002). Intense wildfire in southeastern Arizona: Transformation of a Madrean oak–pine forest to oak woodland. *Forest Ecology and Management*, *165*(1), 205–212. <https://doi.org/10.1016/S0378-1127(01)00618-1>

Belsky, A. J., & Blumenthal, D. M. (1997). Effects of Livestock Grazing on Stand Dynamics and Soils in Upland Forests of the Interior West. *Conservation Biology*, *11*(2), 315–327. <https://doi.org/10.1046/j.1523-1739.1997.95405.x>

Biswell, H. H.; Kallander, H. R.; Komarek, R.; Vogl, R. J.; Weaver, H. 1973. Ponderosa pine management. Tall Timbers Research Station Miscellaneous Publication No. 2, Tallahassee, FL. Tall Timbers Research Station. 49 p.

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., Enright, N. J., & Knox, K. J. E. (2013). Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytologist*, *197*(1), 19–35. <https://doi.org/10.1111/nph.12001>

Connell, J. H. (1978). Diversity in Tropical Rain Forests and Coral Reefs: High diversity of trees and corals is maintained only in a nonequilibrium state. *Science*, *199*(4335), 1302–1310. <https://doi.org/10.1126/science.199.4335.1302>

Coop, J. D. (2023). Postfire futures in southwestern forests: Climate and landscape influences on trajectories of recovery and conversion. *Ecological Applications*, *33*(1), e2725. <https://doi.org/10.1002/eap.2725>

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Steege, H. T., Morgan, H. D., Heijden, M. G. A. V. D., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*(4), 335. <https://doi.org/10.1071/BT02124>

Covington, W. W., & and Moore, M. M. (1994). Postsettlement Changes in Natural Fire Regimes and Forest Structure: Ecological Restoration of Old-Growth Ponderosa Pine Forests. *Journal of Sustainable Forestry*, *2*(1–2), 153–181. <https://doi.org/10.1300/J091v02n01_07>

D’Antonio, C. M., & Vitousek, P. M. (1992). Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annual Review of Ecology and Systematics*, *23*, 63–87.

De Cáceres M, Legendre P (2009). “Associations between species and groups of sites: indices and statistical inference.” *Ecology*, **90**, 3566-3574. doi:10.1890/08-1823.1 <https://doi.org/10.1890/08-1823.1>.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. <https://doi.org/10.1038/nature16489>

Dickson-Hoyle, S., Nation), S. (Bonaparte F., Corporation, S. N. R., Eatherton, A., Baron, J. N., Tiribelli, F., & Daniels, L. D. (2024). Fire severity drives understory community dynamics and the recovery of culturally significant plants. *Ecosphere*, *15*(3), e4795. <https://doi.org/10.1002/ecs2.4795>

Falk, D. A., van Mantgem, P. J., Keeley, J. E., Gregg, R. M., Guiterman, C. H., Tepley, A. J., JN Young, D., & Marshall, L. A. (2022). Mechanisms of forest resilience. *Forest Ecology and Management*, *512*, 120129. <https://doi.org/10.1016/j.foreco.2022.120129>

Ffolliott, Peter F.; Stropki, Cody L.; Chen, Hui; Neary, Daniel G. 2010. Rodeo-Chediski wildfire: A summary of impacts. Hydrology and Water Resources in Arizona and The Southwest. 40: 27-30.

Fowler, J. F., Sieg, C. H., Dickson, B. G., & Saab, V. (2008). Exotic Plant Species Diversity: Influence of Roads and Prescribed Fire in Arizona Ponderosa Pine Forests. *Rangeland Ecology & Management*, *61*(3), 284–293. <https://doi.org/10.2111/07-059.1>

Fox, J. F. (1979). Intermediate-Disturbance Hypothesis. *Science*, *204*(4399), 1344–1345. <https://doi.org/10.1126/science.204.4399.1344>

Fulé, P. Z., Covington, W. W., & Moore, M. M. (1997). Determining Reference Conditions for Ecosystem Management of Southwestern Ponderosa Pine Forests. *Ecological Applications*, *7*(3), 895–908. <https://doi.org/10.2307/2269441>

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2008). Restoration through reassembly: Plant traits and invasion resistance. *Trends in Ecology & Evolution*, *23*(12), 695–703. <https://doi.org/10.1016/j.tree.2008.07.013>

Garnier, E., Shipley, B., Roumet, C., & Laurent, G. (2001). A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology*, *15*(5), 688–695. <https://doi.org/10.1046/j.0269-8463.2001.00563.x>

Grime, J. P. (1973). Competitive Exclusion in Herbaceous Vegetation. *Nature*, *242*(5396), 344–347. <https://doi.org/10.1038/242344a0>

Grime, J. P. (1977). Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist*, *111*(982), 1169–1194.

Guiterman, C. H., Gregg, R. M., Marshall, L. A. E., Beckmann, J. J., van Mantgem, P. J., Falk, D. A., Keeley, J. E., Caprio, A. C., Coop, J. D., Fornwalt, P. J., Haffey, C., Hagmann, R. K., Jackson, S. T., Lynch, A. M., Margolis, E. Q., Marks, C., Meyer, M. D., Safford, H., Syphard, A. D., … Stevens, J. T. (2022). Vegetation type conversion in the US Southwest: Frontline observations and management responses. *Fire Ecology*, *18*(1), 6. <https://doi.org/10.1186/s42408-022-00131-w>

Haffey, C., Sisk, T. D., Allen, C. D., Thode, A. E., & Margolis, E. Q. (2018). Limits to Ponderosa Pine Regeneration following Large High-Severity Forest Fires in the United States Southwest. *Fire Ecology*, *14*(1), 143–163. <https://doi.org/10.4996/fireecology.140114316>

Hereford, R., 2007, Climate variation at Flagstaff, Arizona-1950 to 2007: U.S. Geological Survey Open-File Report 2007-1410, 17 p.

Huffman, D. W., & Moore, M. M. (2004). Responses of Fendler ceanothus to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. *Forest Ecology and Management*, *198*(1), 105–115. <https://doi.org/10.1016/j.foreco.2004.03.040>

Keddy, P. A. (1992). Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*, *3*(2), 157–164. <https://doi.org/10.2307/3235676>

Keddy, P. A., & Shipley, B. (1989). Competitive Hierarchies in Herbaceous Plant Communities. *Oikos*, *54*(2), 234–241. <https://doi.org/10.2307/3565272>

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: A brief review and suggested usage. *International Journal of Wildland Fire*, *18*(1), 116–126. <https://doi.org/10.1071/WF07049>

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, *16*(8), 406–411. <https://doi.org/10.1016/j.tplants.2011.04.002>

Kowarik, I., & der Lippe, M. von. (2007). Pathways in Plant Invasions. In W. Nentwig (Ed.), *Biological Invasions* (pp. 29–47). Springer. <https://doi.org/10.1007/978-3-540-36920-2_3>

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), 299–305. <https://doi.org/10.1890/08-2244.1>

Laughlin, D. C., Bakker, J. D., Stoddard, M. T., Daniels, M. L., Springer, J. D., Gildar, C. N., Green, A. M., & Covington, W. W. (2004). Toward reference conditions: Wildfire effects on flora in an old-growth ponderosa pine forest. *Forest Ecology and Management*, *199*(1), 137–152. <https://doi.org/10.1016/j.foreco.2004.05.034>

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*(5), 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>

Leishman, M. R., Wright, I. J., Moles, A. T., & Westoby, M. (2000). The evolutionary ecology of seed size. In *Seeds: The ecology of regeneration in plant communities* (pp. 31–57). <https://doi.org/10.1079/9780851994321.0031>

Lynch, A. J., Thompson, L. M., Beever, E. A., Cole, D. N., Engman, A. C., Hawkins Hoffman, C., Jackson, S. T., Krabbenhoft, T. J., Lawrence, D. J., Limpinsel, D., Magill, R. T., Melvin, T. A., Morton, J. M., Newman, R. A., Peterson, J. O., Porath, M. T., Rahel, F. J., Schuurman, G. W., Sethi, S. A., & Wilkening, J. L. (2021). Managing for RADical ecosystem change: Applying the Resist-Accept-Direct (RAD) framework. *Frontiers in Ecology and the Environment*, *19*(8), 461–469. <https://doi.org/10.1002/fee.2377>

Martinez Arbizu P (2017). *pairwiseAdonis: Pairwise Multilevel Comparison using Adonis*. R package version 0.4.1, commit cb190f7668a0c82c0b0853927db239e7b9ec3e83, <https://github.com/pmartinezarbizu/pairwiseAdonis>.

McClure, E. J., Coop, J. D., Guiterman, C. H., Margolis, E. Q., & Parks, S. A. (2024). Contemporary fires are less frequent but more severe in dry conifer forests of the southwestern United States. *Communications Earth & Environment*, *5*(1), 1–11. <https://doi.org/10.1038/s43247-024-01686-z>

McCune, B., Grace, J. B., & Urban, D. L. (2002). *Analysis of ecological communities* (2nd printing). MjM Software Design.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>

McGlone, C. M., & Egan, D. (2009). The Role of Fire in the Establishment and Spread of Nonnative Plants in Arizona Ponderosa Pine Forests: A Review. *Journal of the Arizona-Nevada Academy of Science*, *41*(2), 75–86. <https://doi.org/10.2181/036.041.0206>

McGlone, C. M., Sieg, C. H., & Kolb, T. E. (2011). Invasion resistance and persistence: Established plants win, even with disturbance and high propagule pressure. *Biological Invasions*, *13*(2), 291–304. <https://doi.org/10.1007/s10530-010-9806-8>

McGlone, C. M., Stoddard, M. T., Springer, J. D., Daniels, M. L., Fulé, P. Z., & Wallace Covington, W. (2012). Nonnative species influence vegetative response to ecological restoration: Two forests with divergent restoration outcomes. *Forest Ecology and Management*, *285*, 195–203. <https://doi.org/10.1016/j.foreco.2012.08.022>

Meador, A. J. Sánchez., Parysow, P. F., & Moore, M. M. (2010). Historical Stem-Mapped Permanent Plots Increase Precision of Reconstructed Reference Data in Ponderosa Pine Forests of Northern Arizona. *Restoration Ecology*, *18*(2), 224–234. <https://doi.org/10.1111/j.1526-100X.2008.00442.x>

Miller, J. E. D., & Safford, H. D. (2020). Are plant community responses to wildfire contingent upon historical disturbance regimes? *Global Ecology and Biogeography*, *29*(10), 1621–1633. <https://doi.org/10.1111/geb.13115>

Mueller, S. E., Thode, A. E., Margolis, E. Q., Yocom, L. L., Young, J. D., & Iniguez, J. M. (2020). Climate relationships with increasing wildfire in the southwestern US from 1984 to 2015. *Forest Ecology and Management*, *460*, 117861. <https://doi.org/10.1016/j.foreco.2019.117861>

National Weather Service. (2025) 2024 Northern Arizona Climate Review, weather.gov. Available at: <https://www.weather.gov/media/fgz/MonthlyYearlyReview/2024Review.pdf>

Noll, J. & Malis-Clark, K. (2020) Ask a Ranger: The Museum Fire, one year later, part two. AZ Dly. Sun. Available from: https://azdailysun.com/news/local/enviro/ask-a-ranger-themuseum-fire-one-year-later-part-two/article\_01b01126-8aa9-5240-b942f39effe0fecf.html [Accessed 24th April 2025].

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J, Borman T (2025). *vegan: Community Ecology Package*. doi:10.32614/CRAN.package.vegan, R package version 2.6-10, [https://CRAN.R-project.org/package=vegan](https://cran.r-project.org/package=vegan).

Overpeck, J. T., & Udall, B. (2020). Climate change and the aridification of North America. *Proceedings of the National Academy of Sciences*, *117*(22), 11856–11858. <https://doi.org/10.1073/pnas.2006323117>

Parks, S. A., & Abatzoglou, J. T. (2020). Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017. *Geophysical Research Letters*, *47*(22), e2020GL089858. <https://doi.org/10.1029/2020GL089858>

Parson, Annette; Robichaud, Peter R.; Lewis, Sarah A.; Napper, Carolyn; Clark, Jess T. 2010. **Field guide for mapping post-fire soil burn severity**. Gen. Tech. Rep. RMRS-GTR-243. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 49 p.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., Vos, A. C. de, … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167–234. <https://doi.org/10.1071/BT12225>

Plumanns-Pouton, E., Swan, M., Penman, T., & Kelly, L. T. (2024). Using plant functional types to predict the influence of fire on species relative abundance. *Biological Conservation*, *292*, 110555. <https://doi.org/10.1016/j.biocon.2024.110555>

Poorter, H., Niklas, K. J., Reich, P. B., Oleksyn, J., Poot, P., & Mommer, L. (2012). Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytologist*, *193*(1), 30–50. <https://doi.org/10.1111/j.1469-8137.2011.03952.x>

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reich, P. B., Wright, I. J., Cavender‐Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., & Walters, M. B. (2003). The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies. *International Journal of Plant Sciences*, *164*(S3), S143–S164. <https://doi.org/10.1086/374368>

Richter, C., Rejmánek, M., Miller, J. E. D., Welch, K. R., Weeks, J., & Safford, H. (2019). The species diversity × fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. *Ecosphere*, *10*(10), e02882. <https://doi.org/10.1002/ecs2.2882>

Savage, M., Mast, J. N., & Feddema, J. J. (2013). Double whammy: High-severity fire and drought in ponderosa pine forests of the Southwest. *Canadian Journal of Forest Research*, *43*(6), 570–583. <https://doi.org/10.1139/cjfr-2012-0404>

Seager, R., Hooks, A., Williams, A. P., Cook, B., Nakamura, J., & Henderson, N. (2015). *Climatology, Variability, and Trends in the U.S. Vapor Pressure Deficit, an Important Fire-Related Meteorological Quantity*. <https://doi.org/10.1175/JAMC-D-14-0321.1>

Seidl, R., & Turner, M. G. (2022). Post-disturbance reorganization of forest ecosystems in a changing world. *Proceedings of the National Academy of Sciences*, *119*(28), e2202190119. <https://doi.org/10.1073/pnas.2202190119>

Seneviratne, S. I., Corti, T., Davin, E. L., Hirschi, M., Jaeger, E. B., Lehner, I., Orlowsky, B., & Teuling, A. J. (2010). Investigating soil moisture–climate interactions in a changing climate: A review. *Earth-Science Reviews*, *99*(3–4), 125–161. <https://doi.org/10.1016/j.earscirev.2010.02.004>

Shepherd, H. E. R., Catford, J. A., Steele, M. N., Dumont, M. G., Mills, R. T. E., Hughes, P. D. M., & Robroek, B. J. M. (2021). Propagule availability drives post-wildfire recovery of peatland plant communities. *Applied Vegetation Science*, *24*(3), e12608. <https://doi.org/10.1111/avsc.12608>

Singleton, M. P., Thode, A. E., Sánchez Meador, A. J., & Iniguez, J. M. (2019). Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. *Forest Ecology and Management*, *433*, 709–719. <https://doi.org/10.1016/j.foreco.2018.11.039>

Singleton, M. P., Thode, A. E., Sánchez Meador, A. J., & Iniguez, J. M. (2021). Moisture and vegetation cover limit ponderosa pine regeneration in high-severity burn patches in the southwestern US. *Fire Ecology*, *17*(1), 14. <https://doi.org/10.1186/s42408-021-00095-3>

Stevens, J. T., Miller, J. E. D., & Fornwalt, P. J. (2019). Fire severity and changing composition of forest understory plant communities. *Journal of Vegetation Science*, *30*(6), 1099–1109. <https://doi.org/10.1111/jvs.12796>

Stevens, J. T., Safford, H. D., Harrison, S., & Latimer, A. M. (2015). Forest disturbance accelerates thermophilization of understory plant communities. *Journal of Ecology*, *103*(5), 1253–1263. <https://doi.org/10.1111/1365-2745.12426>

Swetnam, T. W., & Baisan, C. H. (2003). Tree-Ring Reconstructions of Fire and Climate History in the Sierra Nevada and Southwestern United States. In T. T. Veblen, W. L. Baker, G. Montenegro, & T. W. Swetnam (Eds.), *Fire and Climatic Change in Temperate Ecosystems of the Western Americas* (pp. 158–195). Springer. <https://doi.org/10.1007/0-387-21710-X_6>

Swetnam, T. W., Farella, J., Roos, C. I., Liebmann, M. J., Falk, D. A., & Allen, C. D. (2016). Multiscale perspectives of fire, climate and humans in western North America and the Jemez Mountains, USA. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1696), 20150168. <https://doi.org/10.1098/rstb.2015.0168>

Taber, E. M., & Mitchell, R. M. (2023). Rapid changes in functional trait expression and decomposition following high severity fire and experimental warming. *Forest Ecology and Management*, *541*, 121019. <https://doi.org/10.1016/j.foreco.2023.121019>

Taber, E. M., & Mitchell, R. M. (2024). Experimental warming has limited impacts on post-fire succession across a burn severity gradient. *Journal of Vegetation Science*, *35*(2), e13248. <https://doi.org/10.1111/jvs.13248>

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*(10), 2833–2849. <https://doi.org/10.1890/10-0097.1>

USDA Forest Service, 2019. Museum Fire Incident Information [WWW Document]. URL https://inciweb.nwcg.gov/incident/6450/ (last accessed 11/5/19).

Wang, G. G., & Kemball, K. J. (2005). Effects of fire severity on early development of understory vegetation. *Canadian Journal of Forest Research*, *35*(2), 254–262. <https://doi.org/10.1139/x04-177>

Wasserman, T. N., & Mueller, S. E. (2023). Climate influences on future fire severity: A synthesis of climate-fire interactions and impacts on fire regimes, high-severity fire, and forests in the western United States. *Fire Ecology*, *19*(1), 43. <https://doi.org/10.1186/s42408-023-00200-8>

Weeks, J., Miller, J. E. D., Steel, Z. L., Batzer, E. E., & Safford, H. D. (2023). High-severity fire drives persistent floristic homogenization in human-altered forests. *Ecosphere*, *14*(2), e4409. <https://doi.org/10.1002/ecs2.4409>

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*(2), 213–227. <https://doi.org/10.1023/A:1004327224729>

Westoby, M., Leishman, M., & Lord, J. (1997). Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *351*(1345), 1309–1318. <https://doi.org/10.1098/rstb.1996.0114>

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827. <https://doi.org/10.1038/nature02403>

Zhang, F., Biederman, J. A., Dannenberg, M. P., Yan, D., Reed, S. C., & Smith, W. K. (2021). Five Decades of Observed Daily Precipitation Reveal Longer and More Variable Drought Events Across Much of the Western United States. *Geophysical Research Letters*, *48*(7), e2020GL092293. <https://doi.org/10.1029/2020GL092293>

Zhang, Y., Meiners, S. J., Meng, Y., Yao, Q., Guo, K., Guo, W.-Y., & Li, S. (2024). Temporal dynamics of Grime’s CSR strategies in plant communities during 60 years of succession. *Ecology Letters*, *27*(6), e14446. <https://doi.org/10.1111/ele.14446>