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

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**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. We characterized understory plant communities across a burn severity gradient in a dry ponderosa pine forest outside of Flagstaff, Arizona, five years after a mixed-severity fire. We evaluated differences in taxonomic composition and the functional traits associated with vegetation types. Taxonomic and functional composition of unburned, low-severity, and high-severity understory communities were significantly distinct from each other five years post-fire. As burn severity increased, understories became decreasingly graminoid dominated and increasingly occupied by forbs and woody plants. Along this gradient, exotic plants 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 high-severity fire 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 were colonized and dominated by fast-growing plants. The persistence of novel understory communities following high severity fire highlights the need for fuel management and maintenance of prescribed fire, as well as prompt restoration action after severe wildfires.

**Keywords** (1-7 words): ponderosa pine, fire, forest management, functional traits, understory

**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 fires are now occurring 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 changes in fire frequency and severity, can have significant consequences for forest 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 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, abnormally 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). For example, in yellow pine forests of California, 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. High-severity wildfire outside the historical range of variability has been found to have lingering effects on understory species composition and biomass production for at least 30 years post-fire in a northern Arizona *Pinus ponderosa* understory (Bataineh et al., 2006).

To better understand the mechanisms driving shifts in diversity and composition following fire, ecologists have increasingly turned to plant 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). For example, 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 can limit the ability of reference forest communities to regenerate, instead favoring species with alternative regeneration strategies, which Savage, Mast, & Fedemma and Haffey attribute to high-severity fire effects on the abiotic environment (2013, 2018). These shifts 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). However, the intense soil heating associated with high-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 that disturbance will initiate competition for released resources (Grime 1977). In contrast, high-severity fire often resets competitive dynamics, favoring rapidly colonizing ruderals over taller 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 dry forests in 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 taxonomically and functionally 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 an acquisitive trait syndrome including higher specific leaf area and height, lower seed mass, and lower resprouting ability.

**2. METHODS**

**2.1 Study Site**

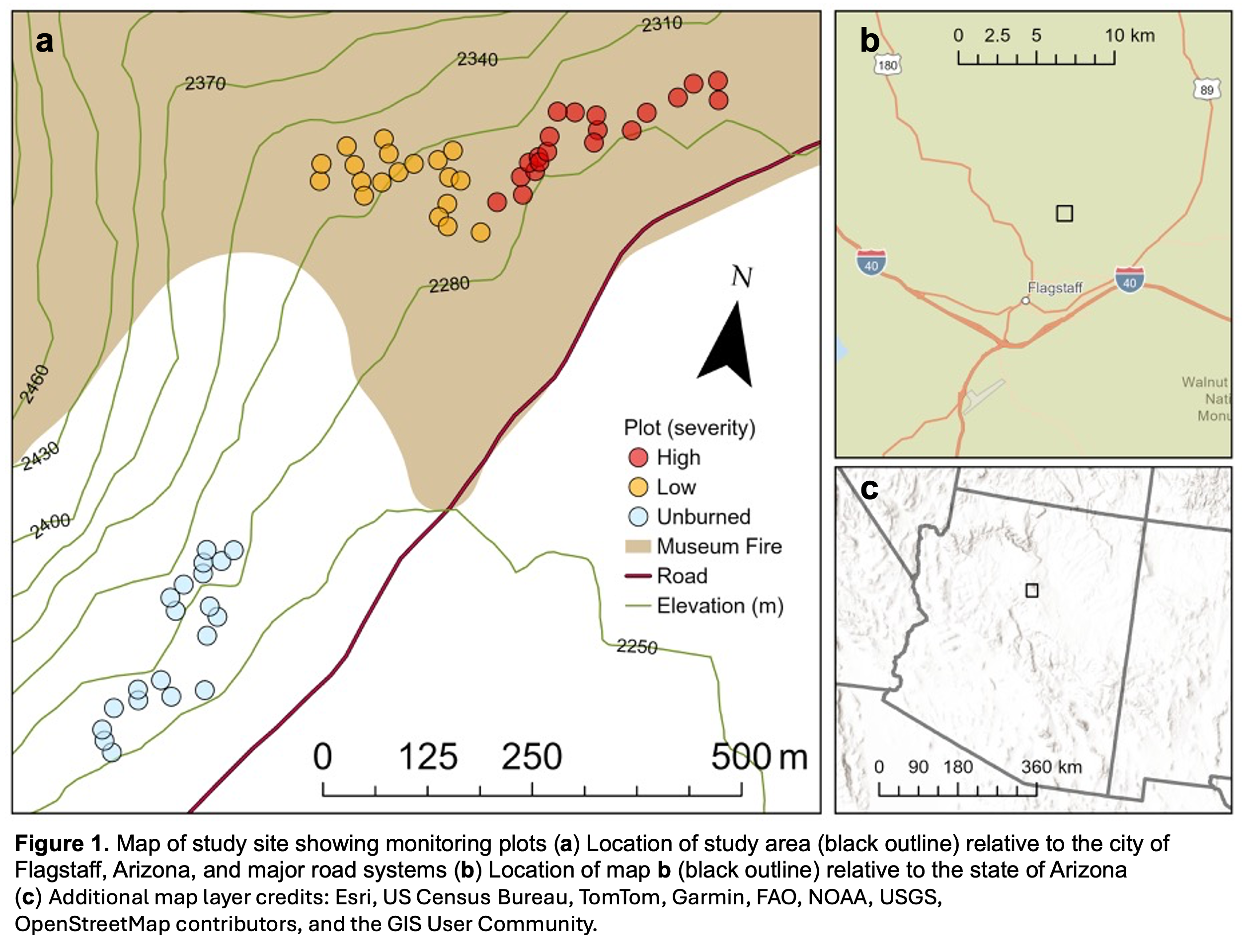
This study was conducted within and immediately adjacent to the perimeter of the 2019 Museum Fire, located approximately 1.6 km north of Flagstaff, Arizona, USA (35.252169, -111.634913 WGS84). The Museum Fire burned a total of 793.6 hectares in late July of 2019 and was of mixed severity, with very low-, 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 in elevation. 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 (Figure 1). 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.

While we did not have data on understory vegetation prior to the fire, we attempted to minimize variation in pre-fire communities by controlling for slope, aspect, and elevation when installing plots. This is necessary because ponderosa pine forests demonstrate spatiotemporal heterogeneity in understory composition (Laughlin et al., 2004). 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 final species pool, we only retained species that occurred on more than ~5% (3 out of 57) of 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). Traits were measured for the retained 19 species across the site (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. 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 (Gunton et al. 2011). See Appendix: Table S3 for a detailed trait table.

For the purposes of this analysis, we included two field collected traits (SLA, height) and four assigned traits (seed mass, resprouting ability, nativity, functional group), which were collected from the 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). Nativity status (native or exotic) and functional group classification (graminoid, forb, shrub, or tree) were retrieved from the USDA Plants database (USDA Plants 2025).

**2.4 Statistical Analyses**

All analyses were conducted using R version 4.5.0 (R Core Team 2025).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 taxonomic composition between 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). Using the same methods, we also tested for differences in functional groups (graminoids, forbs, shrubs, trees) and plant nativity (native or exotic). Additionally, we conducted an 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 2). Pairwise comparisons between severities 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). 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 2).

**3.2 Indicator species for burn severities**

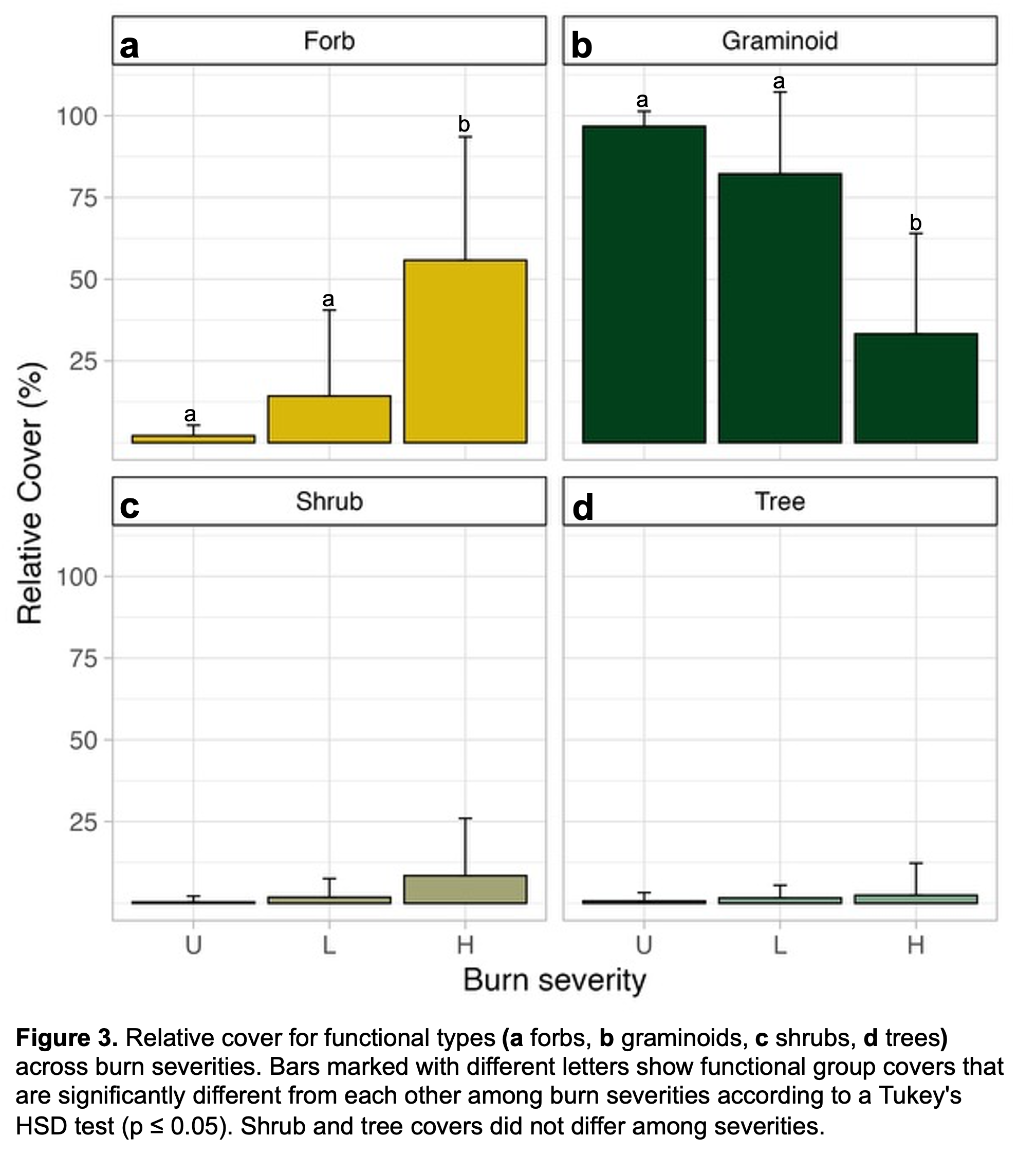
Indicator species analysis revealed several significant indicator species associated with specific burn conditions (Table 1). *Verbascum thapsus*, a nonnative forb, (*IndVal* = 0.618, p < 0.001) is strongly associated with high-severity locations. *Pseudognaphalium macounii,* a native forb, (*IndVal* = 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).

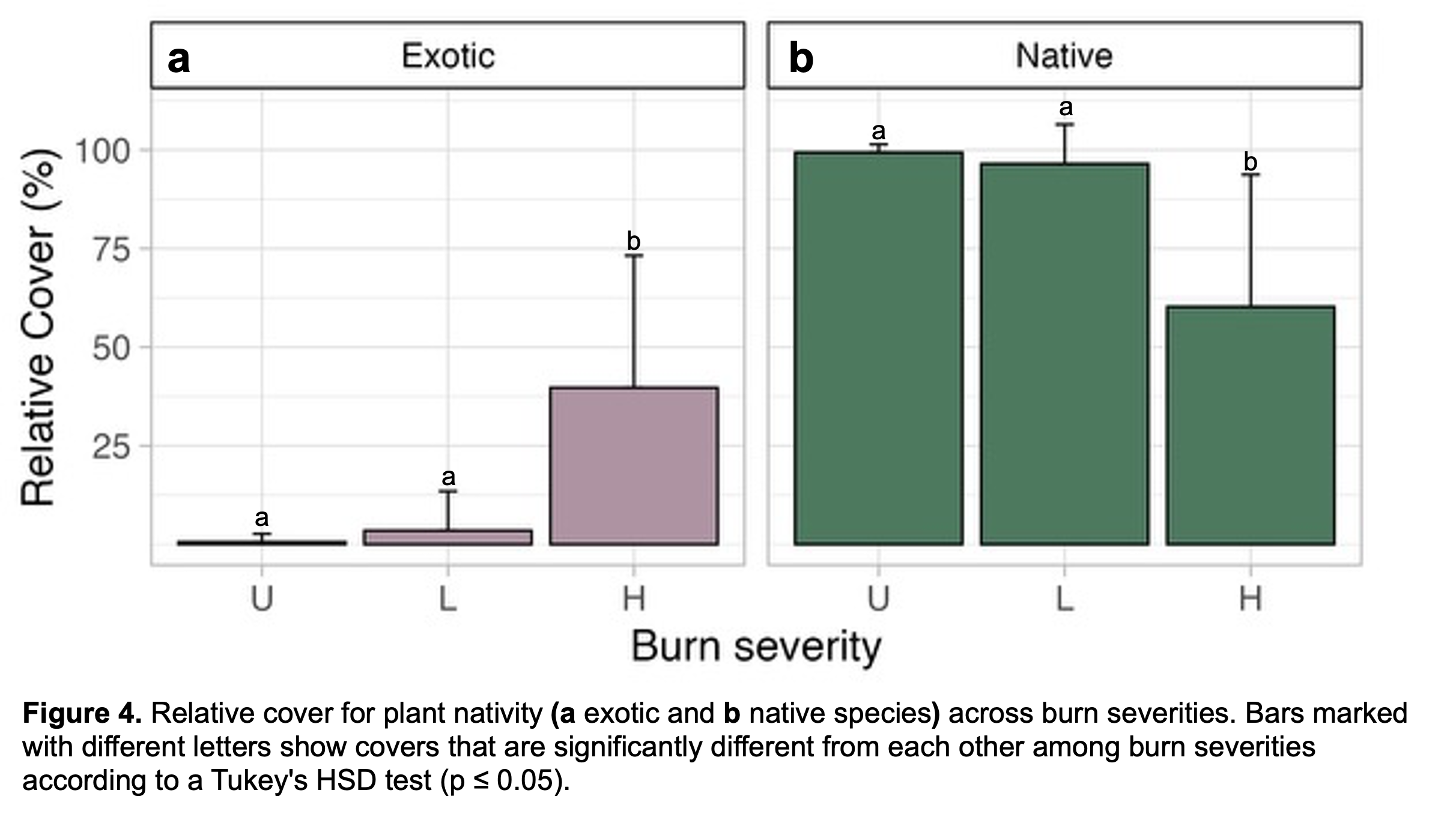
**3.3 Plant functional trait associations with burn severities**

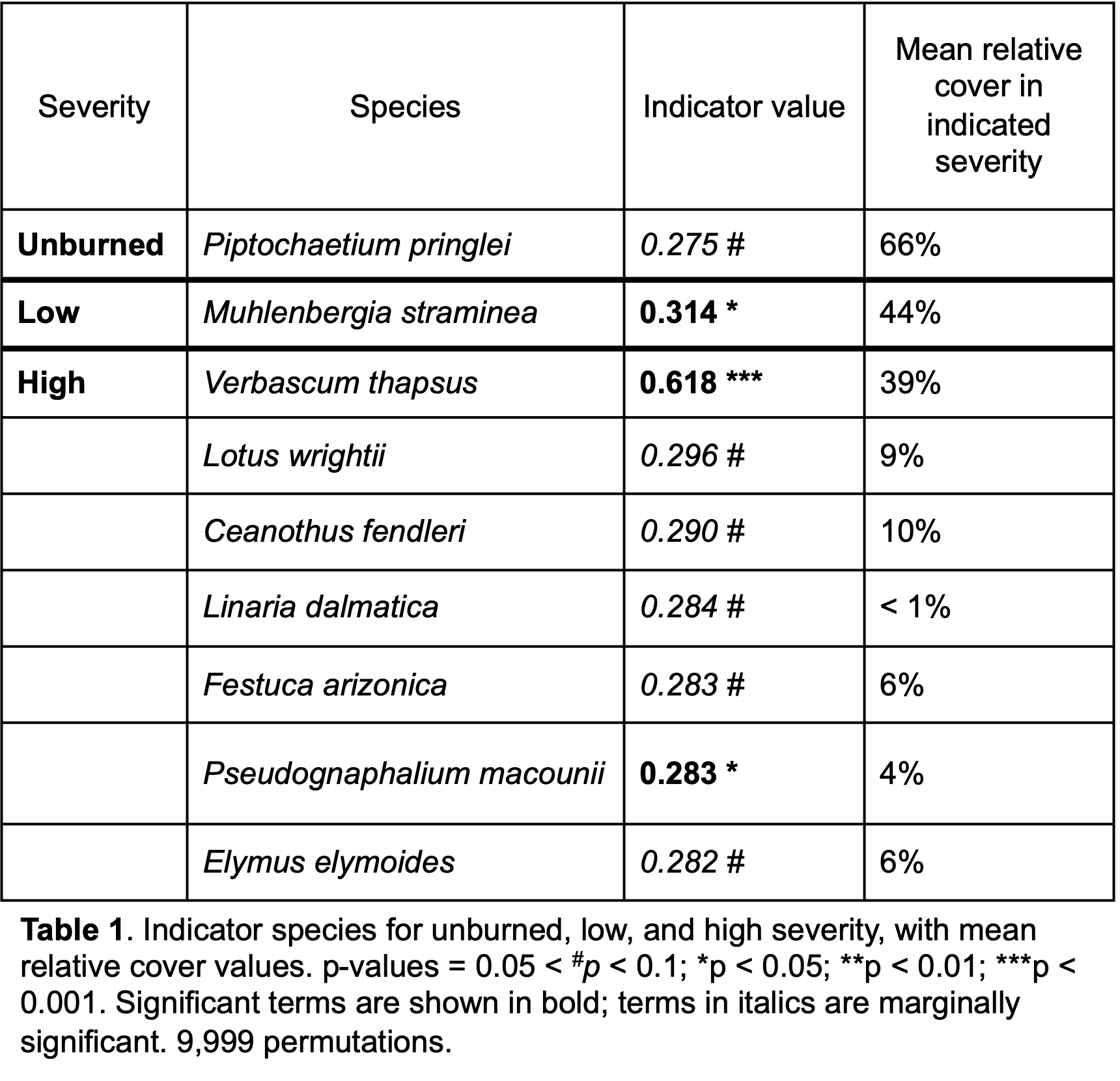
We used the *envfit* function to explore differences in functional traits associated with burn severities based on vegetation community compositions (Figure 2, Table 3). Species composition differences across burn severities are correlated to differences in height, resprouting ability, and SLA. Abundance of resprouting species decreased with increasing burn severity, and this trait explained the most variability in understory communities between plots. SLA increased across plots with the presence of fire and fire severity, whereas greater plant height showed strongest associations with low-severity plots. Seed mass was not significantly correlated with any burn severities (Table 3).

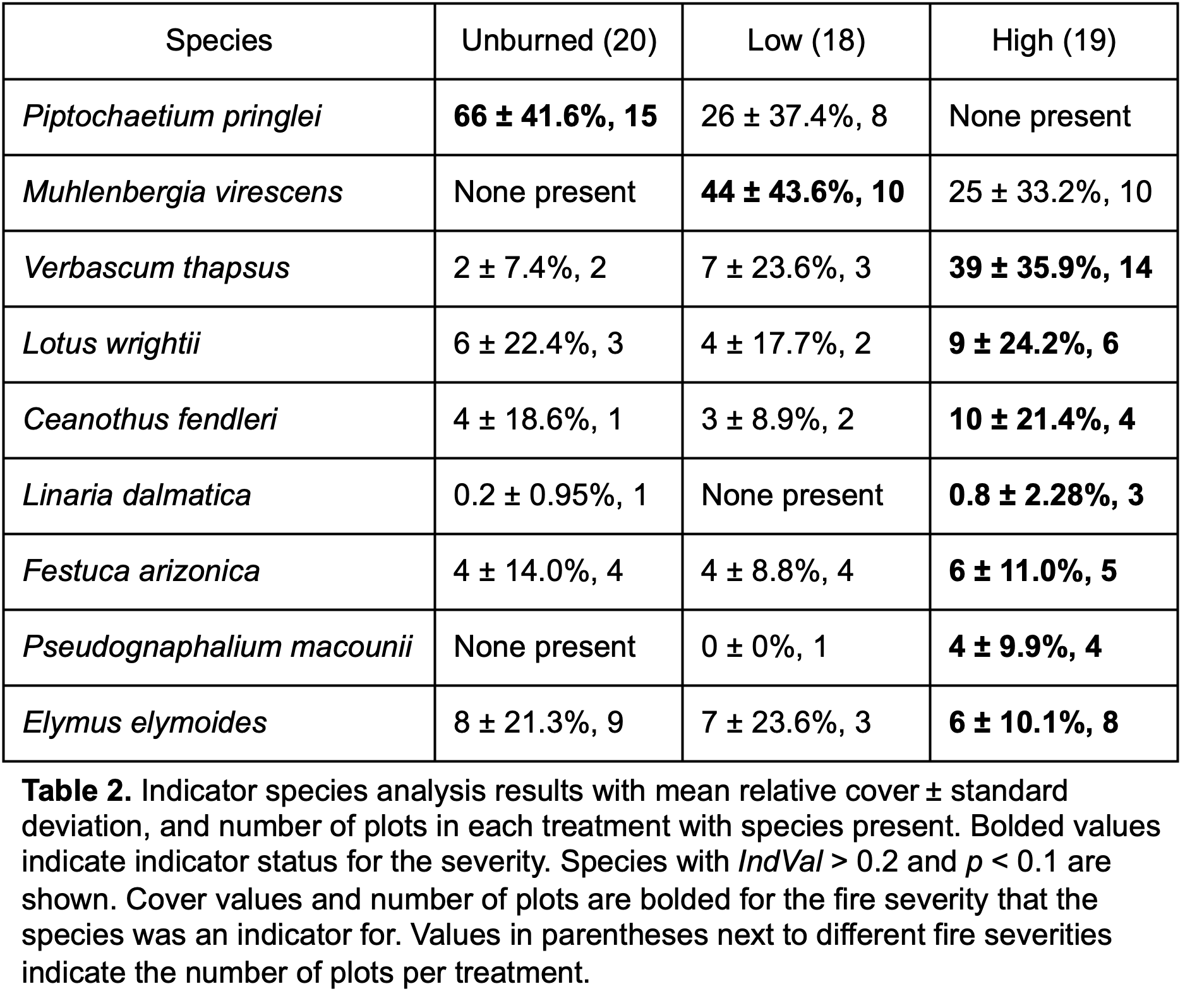
PERMANOVAs indicated that plant nativity (native or exotic) and functional group (graminoid, forb, shrub, tree) composition varied significantly across fire severities (nativity F(2, 54) = [30.221], p < 0.0001; functional group F(2, 54) = [7.9289], p = 0.0009568). Post-hoc analyses found significant differences in the abundances of these groups across different severities using Tukey’s honestly significant difference test. Functional group vegetative cover in the high-severity plots differed significantly from unburned and low-severity plots (Figure 3). Unburned and low-severity plots were dominated by grass species, whereas forb species accounted for more than 50% of the average relative cover in high-severity plots (p < 0.05). There were no significant differences in the relative cover of woody species across a burn severity gradient. Further, exotic species cover was significantly higher in high-severity plots (p < 0.05); the mean relative cover of exotic species in the unburned, low-, and high-severity plots was <1%, 3.5%, and 39.7% respectively (Figure 4). Some indicator species, such as Elymus elymoides—associated with high-severity fires—had higher average cover in unburned and low-severity sites. However, because indicator species analysis measures both abundance and site fidelity, Elymus elymoides was identified as an indicator of high-severity fire due to its consistent abundance and relative scarcity across plots in unburned and low-severity conditions (De Cáceres & Legendre, 2009).









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**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, Covington and Moore 1994)). However, as fire regimes have shifted away from historic norms, consequences for forest composition and structure have been drastic across in these systems (Laughlin et al. 2004; Laughlin et al. 2007; Laughlin, Moore, & Fule, 2011). Here, we quantified differences in plant community composition across a burn severity gradient five years after fire and used plant functional traits to understand the trait syndromes that differing severities select for.

We found that understory composition differed across all three severity classes (Figure 2). 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, Holz, and Veblen, 2022). These compositional differences across burn severities were explained by differences in functional traits in each severity class (Figure 2, Table 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). 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).

Changes in functional group composition and indicator species across the burn severity reflect a disturbance-driven shift in assembly processes. With increasing fire severity, graminoid dominance declined sharply, while the relative cover of forbs increased (Figure 3a, 3b). *Piptochaetium pringlei* and *Muhlenbergia straminea,* two native perennial bunchgrasses, were indicator species of unburned and low-severity plots, respectively. The high-severity plots had several indicator species, but the strongest indicator was *Verbascum thapsus*, which is an exotic ruderal biennial forb (USDA Plants 2025). The combined shifts in cover and indicator species suggest 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. While exotic species were nearly absent in the unburned plots, they comprised nearly 40% of cover in the high severity plots. These findings strongly suggest 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 exotic species (Coop, 2023).

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). High-severity fire changed the environmental filters acting on plant functional traits, selecting for a diverse set of ecological strategies of the species in the understory. Kuenzi, Fulé, and Sieg (2008) found similar results following the Rodeo-Chediski fire, the largest and most severe fire in the southwestern United States on record at its time. They found that low-severity fire was indicated by native perennial bunchgrasses, while indicators of high-severity fire included ruderal species. Notably, they found that high-severity fire increased the number of indicator species, which demonstrates that a larger number of species were more likely to occur in high abundance in after high severity fire, a result mirrored in our findings. These species included some of our high-severity indicators, such as *Lotus wrightii* and *Ceanothus fendleri*. Additionally, Ffolliott et al. (2010) reported that *V. thapsus* was the dominant forb in high-severity areas of the Rodeo-Chediski fire.

Our site had a large abundance of introduced species, which is unusual in these systems (Laughlin et al. 2007; Bakker, Rudebusch, & Moore 2010; Taber & Mitchell 2024). The high proportion of invasive species observed within the high severity plots may also be shaped by the social-ecological context of the site. Located within the wildland-urban interface of Flagstaff, Arizona, and subjected to 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 feedback (Keeley et al., 2011; Guiterman et al., 2022).

**4.1 Future Directions: Implications for Restoration and Management**

As dry conifer forests of the American West undergo rapid and novel changes, ecosystem management must expand beyond traditional restoration based on fixed historical reference conditions. In this era of unprecedented global change, considering multiple potential compositional pathways is essential to building future resilience in restored ecosystems (Higgs et al., 2014). The RAD framework (Resist – Accept – Direct) offers a useful lens for evaluating management responses (Lynch et al., 2021). A resist strategy may involve proactive forest management and silviculture treatments (thinning, prescribed burning) to reduce fire severity and maintain historical vegetation types. Following a high-severity fire, this strategy may include rigorous efforts to reseed and replant native species with traits characteristic of low-severity reference communities, such as perennial graminoids. A direct strategy would guide succession towards an alternative, but stable and desirable, state such as a native-dominated oak shrubland more resilient to fire or climate stress. In contrast, an accept strategy—evident at this site by default—allows post-fire succession to proceed without intervention. This has led to dominance by ruderal and often exotic species, initiating an alternate and potentially undesirable trajectory characterized by high SLA and poor resprouting ability. Over time, this may result in a vegetation type conversion from dry ponderosa pine forest to a non-forested vegetation type (Barton, 2002; Haffey et al., 2018).

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