THE POST-FIRE ENVIRONMENT: UNDERSTORY PLANT RECOVERY FOLLOWING HIGH-SEVERITY FIRE AND PLANT TRAIT RESPONSES TO INCREASED SOIL TEMPERATURE IN A PONDEROSA PINE ECOSYSTEM

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ABSTRACT

THE POST-FIRE ENVIRONMENT: UNDERSTORY PLANT RECOVERY FOLLOWING HIGH-SEVERITY FIRE AND PLANT TRAIT RESPONSES TO INCREASED SOIL TEMPERATURE IN A PONDEROSA PINE ECOSYSTEM

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The ponderosa pine forests of the Southwest have experienced dramatic changes since Euroamerican settlement which has led to stands with a closed overstory canopy with few fragmented grass openings intermixed. Long periods of drought combined with overly dense forests have increased the frequency of high-severity, stand replacing fires in forests that are historically adapted to high frequency, low-severity wildfires. Under climate change and the Southwest's changing precipitation pattern, it is anticipated that high-severity wildfires and dry fuel loads will continue to occur at increasing rates. In order to prepare these ecosystems for future change and predict changes in biodiversity, it is imperative to understand how the understory plant community of ponderosa pine ecosystems is altered following a severe wildfire, and how plants respond to an increasingly stressful post-fire environment. We monitored vegetation in understory communities impacted by high-severity fire in 2019 to ask: 1) How does high-severity fire change the proportion of plant functional groups and native/nonnative species in the understory of ponderosa pine ecosystems? 2) Following high-severity fire, do *Festuca arizonica, Muhlenbergia virescens*, and *Ceanothus fendleri* occur in different microhabitats? 3) How do the plant communities immediately surrounding *F. arizonica, M. virescens*, and *C. fendleri* in the high-severity burn area differ? and 4) How does soil temperature affect trait expressions of *F. arizonica, M. virescens*, and *C. fendleri*? Monitoring of plant cover and composition for three years following the Museum Fire determined that high-severity fire

promoted an increase in nonnative forb cover, and a decrease in perennial graminoid cover compared to low-severity and unburned patches of forest. Species cover in neighborhoods immediately surrounding three species in the high-severity burn area revealed higher biodiversity near the dominant C4 grass, *M. virescens*, and a decrease in biodiversity near the C3 grass, *F. arizonica*. Evenness and Shannon index values were highest near *F. arizonica*. Increasing soil temperature decreases neighborhood richness for all species, indicating that increased environmental stresses can decrease understory biodiversity. *C. fendleri* and *F. arizonica* responded to increasing soil temperatures with opposite leaf dry matter content (LDMC) strategies. This suggests that under increasing temperature stress, some species increase LDMC to be resource conservative, and others can decrease LDMC suggesting they have not hit a temperature stress threshold that is limiting growth rate. Under projected climate change scenarios and following high-severity fire, we may see a decrease in understory biodiversity that needs active management for recovery.

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PREFACE

The following chapters discuss similar topics and concepts. Chapter 1 is an introduction and literature review. Chapter 2 is a manuscript to be submitted to the journal Forest Ecology and Management in the summer of 2023. Chapter 3 includes conclusions and implications for management. There are redundancies and repetition between the three chapters, as Chapter 2 is organized as a standalone manuscript.

CHAPTER 1: INTRODUCTION

Literature Review

Prior to Euroamerican settlement, Southwestern ponderosa pine forests were characterized by a productive, grass-dominated understory with a temporary accumulation of litter and woody debris that supported low-intensity surface fires every 2-20 years (Cooper, 1960; Pyne et al. 1995; Swetnam & Baisan, 1996). Euroamerican settlement altered these ecosystems through grazing, logging, and fire suppression, allowing for the growth of higher density, lower tree diameter forests across the landscape (Moore et al., 1999). Contemporary ponderosa pine forests in the Southwest are characterized by a closed overstory canopy with a few fragmented grass openings intermixed (Covington et al., 1997; Covington and Moore, 1994). These dense ponderosa pine stands result in more shade, deep litter horizons, low soil moisture and temperatures, and low nutrient availability due to long decomposition intervals of pine litter (Kaye and Hart, 1998). As a result, there has been a decline in understory plant foliar cover, species richness, and functional diversity in these ecosystems (Laughlin et al., 2011).

There is evidence of occasional high-severity fires in southwestern ponderosa pine ecosystems (Baker et al., 2007; Hessburg et al., 2007; Williams and Baker, 2012), however, these were infrequent with a fire rotation interval of 522 years (Williams and Baker, 2012) and thought to have a minor affect in shaping ecosystem structure (Fornwalt et al., 2016; Fulé et al., 2014; Iniguez et al., 2009; Margolis and Balmat, 2009). However, the combination of increased forest density, decreased precipitation, elevated temperatures, and expanded wildland-urban interface have led to more frequent ignitions and larger higher severity fires within southwestern ponderosa pine ecosystems (Abatzoglou and Williams, 2016; Coop et al., 2020; Dennison et al., 2014; Westerling et al., 2006). Severely burned stands are exhibiting trajectories to non-forested

types with high abundances of resprouting species in the understory and midstory (Woolman et al., 2022). With the absence of nearby forest that has been minimally affected by fire, it has been documented that high-severity fires decrease understory biodiversity (Coop, 2022), and increase recovery time by decades post-fire (Strand et al., 2019). Despite the generally negative effects of high severity fire in this ecosystem, impacts within the understory can be surprisingly variable. High-severity burning can remove the forest canopy, but not achieve high enough temperatures to overcome the resilience mechanisms of fire-adapted understory assemblages (e.g., resprouting, serotiny; Downing et al., 2020). Alternatively, the understory can be eliminated through burn intensities beyond the recovery thresholds of understory species (Strand et al., 2019; Coop, 2022).

Climate change in the southwest

Dense forests are at higher risk of crown fires and high-severity fire disturbance due to the presence of low-diameter and short-statured ladder fuels and a tightly packed canopy layer. Fuel management and restoration of *Pinus ponderosa* forests is reliant upon the removal of low-diameter trees alongside the reestablishment of historical fire regimes via prescribed fire (Abatzoglou and Williams, 2016; Dennison et al., 2014; Westerling et al., 2006). However, the efficacy and safety of these restoration practices and management goals are being questioned as the southwestern USA faces long-term drought and global climate change (Fulé, 2008). Pine regeneration is heavily influences by cooler and wetter conditions for seedling establishment (Korb et al., 2018). Therefore, the application of frequent, low-severity prescribed fire under changing climate to dryer and warmer conditions could result in regeneration failures, declines in

biomass, and earlier conversion of ponderosa forests to dominance by lower elevation species under projected climate scenarios (Flatley and Fulé, 2016).

The changing precipitation regime in the southwest is one of decreasing precipitation amounts with longer time intervals in-between precipitation events (Zhang et al., 2021) generating longer periods of hotter, more intense drought in-between rain events, which increases forest susceptibility to fire due to the presence of increased dry standing fuel (Hurteau et al., 2014). Rising temperatures and decreased precipitation have resulted in an ongoing southwestern "mega-drought" that is predicted to continue and intensify under projected warming and precipitation regimes (Williams et al., 2022). Hotter droughts are the number one threat to forest health across the globe (Millar and Stephenson, 2015). Climate is an important driver of wildfire activity in the southwest, with increased warming driving an earlier snowmelt that increases the length of wildfire season and reduces fuel moistures (Mueller et al., 2020). High-severity fires and longer fire seasons are increasing in the western U.S. as a result of decreased precipitation, climate warming, and human ignited fires (Balch et al., 2017; Brown et al., 2021; Coop et al., 2020). Understanding how these high-severity wildfires affect the understory community can aid in restoration efforts and in preparing these ecosystems for climate change (Savage and Mast, 2005).

Fire effects on understory structure

Understory plant species in Southwestern ponderosa pine forests are adapted to frequent, low-severity fires and exhibit life-histories and regeneration strategies that allow for rapid regeneration of cover and biodiversity following typical fires. This diverse understory protects soil from erosion, provides fuels for surface fires and forage for wildlife, and contains the vast

majority of the plant biodiversity in these ecosystems (Moore et al., 2006). The effect of fire on the understory plant community is dependent on the frequency, intensity, and season of burning, as well as species composition and abiotic factors during time of burning (Kerns et al., 2006; Kerns and Day, 2018; Moore et al., 2006; Zald et al., 2020). For example, low-severity prescribed burning in the fall season has shown to reduce cover of C4 graminoids and increase cover of C3 graminoids (Moore et al. 2006). Additionally, plant groups with fire resistant and resilient traits such as resprouting perennials, annual forbs, and nonnative species have shown a short-term increase of cover to initial low-severity burning, but reduce in cover after repeated burning (Kerns & Day 2018). Fire alters understory species composition by removing fuels, temporarily increasing nutrient availability, exposing bare mineral soil, and reducing competition for moisture and light (Wright and Bailey 1982; Pyne et al. 1996). The understory of ponderosa pine forests was historically dominated by a matrix of perennial graminoids, forbs, and shrubs (Covington et al., 1997). Following low-severity fire, these understory plants rapidly regenerate through basal resprouting, seed banking, and fire germination cues (Falk et al., 2022; Huffman, 2006; Kerns and Day, 2018; Rodman et al., 2021). High-severity fires are outside of the severity to which these dominant species are adapted. As such, the resistance and recovery mechanisms of these ecosystems can be inhibited following high-severity fire, resulting in species reorganization and understories that are dramatically different from historical targets (Coop et al., 2020).

Vegetation type conversion

High-severity crown fires can push ecosystems into states that differ significantly from historical conditions (Coop et al., 2020; Falk et al., 2022; Savage and Mast, 2005). The

resistance and recovery mechanisms of forest ecosystems can be inhibited when fires with size, frequency, or intensity outside of that which species are adapted to occur in an ecosystem (Coop et al., 2020; Johnstone et al., 2016). Fire-driven forest conversion in the southwest is initiated by high-severity fire that removes large areas of mature forest from the landscape and is continued when recovery mechanisms are then impeded by the absence of seed sources, short-interval reburning, or post-fire environmental conditions unfavorable to seedling conditions (Coop et al., 2020; Falk et al., 2022). This can result in a reorganization of the ecosystem where changes in relative dominance of species is altered, or completely shifted to dominance by plants of a different functional type (Falk et al., 2022).

A shift in ponderosa pine forests to shrub dominated landscapes following fire has been documented across the southwest (Cocking et al., 2014; Coop et al., 2020; Davis et al., 2019; Downing et al., 2020; Falk et al., 2022; Haire et al., 2008). Following stand-replacing fire, *Pinus ponderosa* must regenerate from seed. However, resprouting woody species such as *Quercus gambelii*, *Populus tremuloides*, *Ceanothus sp.*, and *Robinia neomexicana* quickly recover and regenerate in high-severity areas (Cocking et al., 2014; Coop et al., 2020; Falk et al., 2022; Haire et al., 2008). This change in vegetation type from ponderosa pines with an understory dominated by perennial graminoids to shrublands can increase the flammability of a landscape, resulting in faster return intervals and reinforcing feedbacks that allow for the persistence of species change (Keyser et al., 2020). Under 50-year fire scenario projections, as fire occurrence increased, a greater proportion of landscape vegetation was classified with resprouting species (Keyser et al., 2020).

Forest-to-shrubland conversion is of concern globally because of the loss of ecosystem services, carbon sequestration, and biodiversity (Coop, 2022) that result from losses of forest

ecosystems. For example, shifts from conifer dominance towards other vegetation types may result in fuel characteristics that are very different from historical norms, resulting in a change in future fire regimes, hydrology, and carbon fluxes (Coop, 2022). With continued drought conditions and rising temperatures, high-severity fires are projected to occur with greater frequency and to burn larger areas. A shift in the proportions of vegetation cover following high-severity fire has the potential to change the trajectory of ponderosa pine ecosystems, and their resilience into the future. This requires active management for persistence of ponderosa pine ecosystems, recovery after high-severity fire, and reorganizational periods following high-severity fires (Falk et al., 2022).

Plant functional traits

The use of plant functional traits (PFTs) to explain variations in plant response to abiotic and biotic factors has been defined as the "Holy Grail" of ecology (Lavorel & Garnier, 2002). The effect of abiotic and biotic factors on species presence, abundance, and plant function, can be described and predicted by PFTs (Lavorel and Grigulis, 2012). Different plant traits are associated with different ecological processes, which relate to different niche axes (Violle et al., 2007). For example, specific leaf area (SLA) is associated with relative growth rate, which corresponds to a plant's investment in leaf structure. As such, species in resource rich environments tend to have larger SLA than those in environments with resource stress (Cornelissen et al., 2003). Multivariate functional diversity may mask community assembly processes when traits are associated with these opposing niche axes (Spasojevic and Suding, 2012). For example, a trait with an opposing niche axis to SLA is leaf dry matter content (LDMC). LDMC aligns with investment in leaf structure by defining how dense the cell

structure of a leaf is. The denser the cell structure of the leaf, the higher the LDMC value, which correlates to longer lasting leaves. SLA and LDMC highlight the tradeoff between rapid production of biomass (high SLA, low LDMC), and efficient conservation of nutrients (low SLA, high LDMC) (Garnier et al. 2001). Therefore, determining an overall pattern in functional diversity depends on the compilation of patterns of many individual traits and interpreting their mechanisms (Weiher et al., 2011). The worldwide leaf economic spectrum describes the return on investments of nutrients and dry mass in leaves and provides additional insight to variation in plant traits combined with functional groups (Wright et al., 2004). Understanding leaf economics is crucial for understanding vegetation boundaries and how they respond to shifts in land-use and climate change.

Plant "response" traits reflect a plant's response to changes in its habitat (Lavorel et al., 2007). Specific leaf area is often used in models because it is generally positively correlated with relative growth rate and is a response to above ground resource competition (Cornelissen et al., 2003). SLA is derived by dividing a leaf's area by its dry matter content. Leaf dry matter content, while a component of SLA, can provide insights into tissue allocation in response to habitat conditions. Specifically, leaves with high LDMC tend to be relatively tough with slow decomposition rates, and are assumed to be more resistant to physical hazards such as wind (Peréz-Harguindeguy et al., 2016). Plant height is another commonly measured plant functional trait, as it is associated with competitive ability, fecundity, and ability to persist in light of disturbance events (Peréz-Harguindeguy et al., 2016). PFTs can be used to explain plant response to stressful environments, including variability in fire severity (Fernández-García et al., 2020; Huerta et al., 2021).

Plant functional traits and fire

Much of the literature linking plant traits and fire are based on the life history traits of resprouting, seed banking, and seed germination. Obligate seeding species rely on dispersal from nearby patches or soil seed banks to persist after disturbance, whereas resprouting species can regrow from below-ground tissue when the disturbance is of typical frequency and severity for the ecosystem (Pausas et al., 2004). Facultative seeders can persist both through resprouting and seed germination, whereas serotinous obligate seeders are reliant on fire cues for seed germination (Pausas and Keeley, 2014). Post-fire germination conditions may not always be viable for serotinous and obligate seeding species, especially after events that are a far ecological distance from the historical norms, such as a high-severity fire occurring in an ecosystem adapted to low-severity fire, which may result in population decline (Coop et al., 2020; Enright et al., 2014; Falk et al., 2022).

Resprouting species play an important role in shaping their immediate plant communities following disturbance events through competitive exclusion, nitrogen fixation, water availability, and increasing herbaceous fine fuel biomass, depending on their lifeform (Owen et al., 2020; Simpson et al., 2021). The ability of resprouting species to vigorously regenerate following disturbance and persist post-fire allows for greater competitive ability after a high-severity burn. Resprouting species also benefit from priority effects, being on the landscape pre-fire and having immediate access to the open forest floor following fire (Fukami et al., 2016). Rapid regeneration of woody resprouting species can drive the early post-fire dynamics in the understory, until regeneration from seeds establishes and reaches competitive size (Matula et al., 2020). In our system, *Ceanothus fendleri* is a nitrogen fixing, resprouting shrub. As such, communities immediately surrounding *C. fendleri* in the high-severity burn area may be sparse

through competitive exclusion. This study system is also nitrogen limited, so the communities surrounding *C. fendleri* could be more diverse if plants are seeking available nitrogen. Our system also consists of resprouting perennial graminoids. These graminoids, such as *Festuca arizonica* and *Muhlenbergia virescens*, may shape their immediate communities through increased shading or water availability.

It is known that the frequency and severity of disturbance affects the variability of plant functional traits present within a disturbed area (Fernández-García et al., 2020; Huerta et al., 2021; Jung et al., 2010). Species with high SLA are associated with faster relative growth rates and shorter leaf- lifespans, which is a beneficial resource-use strategy in ecosystems affected by frequent high-severity fires (Huerta et al., 2021). It has been shown that high SLA values are associated with increasing wildfire recurrence and burn severity (Fernández-García et al., 2020). Species in our study that exhibit high SLA values could be better adapted to high-severity fires, allowing for species persistence under changing climatic conditions.

The removal of vegetation by high-severity fire results in post-fire environments that reduce leaf transpiration and water infiltration, and increase solar radiation and run-off (El Maayar & Chen, 2006; Aguilar et al., 2010; Dore et al., 2010; Nolan et al., 2014; Wine & Cadol, 2016; Poon & Kinoshita, 2018). Plants occurring in this environment face multiple stressors, including increases in soil temperature due to increased solar radiation. Soil temperature can influence physiology and plant processes such as nutrient and water uptake, photosynthesis, and root growth (Aidoo et al., 2016; Landhäusser et al., 2001; Nóia Júnior et al., 2018). Up to a certain threshold, warmer soil temperatures can increase water and nutrient uptake (Toselli et al., 1999; Grossnickel, 2000; Onwuka, 2016) and thresholds are likely to be different for each species given their functional group, phylogeny, and tolerances. Though little research has been

conducted on the effects of soil temperature on plant traits, we would expect that under increasing stress from soil temperature, plants would exhibit lower SLA values and higher LDMC values, showing a slow relative growth rate and conservative resource use strategy. For plants that may not have hit their threshold, we might see a faster relative growth rate with high SLA values and low LDMC values. Understanding how soil temperature is affecting plant community assembly, growth, and survival is important for predicting plant function and persistence after high-severity wildfire.

Summary: Linking Fire Severity, Understory Cover, and Climate

Ponderosa pine forest structure and function has been altered since the arrival of Euroamerican settlement via changes in land use and fire management, such as grazing, logging, and fire suppression (Moore et al., 1999). These changes have resulted in dense canopies, changes in perennial grass functional type composition, and overgrown understories that fuel high-severity fires in an ecosystem not adapted to them. The impacts of high-severity fire on the understory community can result in changes in species composition, land conversion to non-forest systems, and alter ecosystem function (Donato et al., 2016; Guiterman et al., 2018; Walker et al., 2018). There is a lack of knowledge regarding how the post-fire environment of high-severity fire, in particular increased soil temperature, affects plant functional traits in southwestern ponderosa pine understories. Understanding understory cover change over time across a fire severity gradient, and plant responses to increasing soil temperature, will inform management efforts before and after wildfires in these ecosystems.

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CHAPTER 2: THE POST-FIRE ENVIRONMENT: UNDERSTORY PLANT RECOVERY FOLLOWING HIGH-SEVERITY FIRE AND PLANT TRAIT RESPONSES TO INCREASED SOIL TEMPERATURE IN A PONDEROSA PINE ECOSYSTEM

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Highlights

- The high-severity burn area of our study site saw an increased abundance of forbs and nonnative species, and a decrease in perennial graminoid cover. This is proportionately different from the understory communities in the unburned and low-severity burn areas.
- Dominant perennial graminoid *Festuca arizonica* is found in cooler soil temperatures than the resprouting shrub *Ceanothus fendleri*.
- Communities surrounding *F. arizonica* had higher Shannon index biodiversity scores compared to *Muhlenbergia virescens* and *C. fendleri* following high-severity fire. Richness in 1-m2 quadrats around the above species decreases as soil temperatures increase in the high-severity burn area.
- *F. arizonica* created less dense leaves with increasing soil temperature, while *C. fendleri* increased in leaf density.
- *F. arizonica* may serve as an indicator for understory refugia by resprouting in sites with lower soil temperatures and higher biodiversity.

Abstract

Unusually high-severity fire in ecosystems not adapted to such disturbance is of concern globally due to its effects on ecosystems adapted to less severe fire regimes. For example, southwestern *Pinus ponderosa* forests are adapted to frequent, low-severity fire regimes, but a century of fire suppression has led to an increase in fire extent and severity within this ecosystem. These high-severity fires create a more stressful environment for plant recovery, with increased soil hydrophobicity, solar radiation, erosion, runoff, and soil evaporation. To understand the impact of high-severity fire on understory regeneration, we sampled vegetation on the Museum Fire, a mixed-severity fire in northern Arizona to understand the extent to which high-severity fire is changing understory exotic species presence and abundance, and functional group composition. Further sampling in the high-severity burn area was conducted to understand the effects of soil temperature stress on three dominant resprouting species (*Ceanothus fendleri, Festuca arizonica,* and *Muhlenbergia virescens*) and the neighboring plant communities that surround them. Our analysis revealed that high-severity fire increased the proportion of forbs and nonnative species on the landscape when compared to low-severity and unburned sites. Importantly, perennial graminoid cover was reduced following high-severity fire compared to the other burn areas. Across the soil temperature gradient in the high-severity burn area, *Ceanothus fendleri* occurred in sites with warmer soil temperatures with no significant difference in neighborhood biodiversity compared to the perennial graminoids. Neighborhood biodiversity differed between our two dominant perennial graminoids, with *F. arizonica* occurring in areas with the highest Shannon index scores and the lowest temperatures. Species richness in 1-m^2 quadrats declined with increasing soil temperature for all three target species. Increasing soil temperature also affected dominant resprouting individuals' plant functional traits (PFTs). Our results indicate opposite responses from *C. fendleri* and *F. arizonica*, with the former increasing

leaf dry matter content (LDMC) and the latter decreasing LDMC with increasing soil temperature. The results of this study indicate a shift in dominant understory functional groups after high-severity fire, from perennial graminoids to forbs, and nonnative species. In addition, dominant resprouting species exhibited different resource use strategies across a temperature gradient following high-severity fire. *Festuca arizonica* was associated with the lowest soil temperatures, and displayed higher biodiversity in the plant neighborhoods immediately surrounding each individual. These results suggest that cooler post-fire soil temperatures promote the resprouting of a dominant C3 grass and support higher plant biodiversity generally, than hotter soil conditions dominated by *C. fendleri*.

1. Introduction

Southwestern ponderosa pine forests have experienced dramatic alterations to stand density and understory productivity due to fire suppression, grazing pressure, and logging (Moore et al., 1999). Prior to Euroamerican settlement, *Pinus ponderosa* forests were characterized by frequent, low-severity fire regimes that allowed for open, park-like forest structures with a productive understory (Cooper, 1960; Pyne et al. 1996; Swetnam and Baisan, 1996). A century of fire suppression and forest management has allowed for the growth of higher density, lower diameter trees across the forest creating a closed overstory canopy with few fragmented grass openings intermixed (Covington et al., 1997; Covington and Moore, 1994). This has resulted in a decline in understory plant foliar cover, species richness, and functional diversity in these ecosystems (Laughlin et al., 2011). Dense forested stands increase the landscape risk of high-severity fires. High-severity fires are expected to increase in the southwest in response to decreasing precipitation amounts, longer time intervals in-between precipitation

events (Zhang et al., 2021), increased temperatures (Brown et al. 2021), and increasing forest susceptibility to due increasingly dry fuel loads (Hurteau et al., 2014). Rising temperatures and decreased precipitation has resulted in an ongoing southwestern "mega-drought" that is predicted to continue under future warming and precipitation regimes (Williams et al., 2022). The combination of increased forest density, decreased precipitation, elevated temperatures, and expanded wildland-urban interface have led to more frequent ignitions and larger higher severity fires within southwestern ponderosa pine ecosystems (Abatzoglou and Williams, 2016; Coop et al., 2020; Dennison et al., 2014; Westerling et al., 2006).

Fire-driven forest conversion in the southwest is initiated by high-severity fire that removes large areas of mature forest from the landscape, and is continued when recovery mechanisms are impeded or altered by the absence of seed sources, short-interval reburning, or post-fire environmental conditions that are unfavorable to forest seedling establishment (Coop et al., 2020; Falk et al., 2022). This can result in a reorganization of the ecosystem where relative species dominance is altered or completely shifted to other vegetation types (Falk et al., 2022). Forest conversion to other vegetation types is of concern globally due to the loss of ecosystem services, carbon sequestration, and biodiversity (Coop, 2022) associated with forest ecosystems. For conifer dominated forests, shifts towards other vegetation types may result in fuel characteristics that are very different from historical norms, resulting in a change in future fire regimes, hydrology, and carbon fluxes (Coop, 2022).

A recent shift from ponderosa pine forests to shrub dominated landscapes has been documented across the southwest (Cocking et al., 2014; Coop et al., 2020; Davis et al., 2019; Downing et al., 2020; Falk et al., 2022; Haire et al., 2008). While *Pinus ponderosa* must regenerate from seed, resprouting species such as *Quercus gambelii*, *Populus tremuloides*,

Ceanothus sp., and *Robinia neomexicana* can quickly recover and regenerate in high-severity areas (Cocking et al., 2014; Coop et al., 2020; Falk et al., 2022; Haire et al., 2008). This change in vegetation type from ponderosa pine dominated overstory and perennial graminoid dominated understory to shrubland can further increase the flammability of a landscape, resulting in faster return intervals and reinforcing feedbacks that allow for the persistence of species change (Keyser et al., 2020). Under 50-year fire scenario projections, as fire occurrence increased, a greater proportion of landscape vegetation was classified as dominated by resprouting species (Keyser et al., 2020). High-severity fire can also rearrange and eliminate understory vegetation through burning intensities beyond recovery thresholds (Coop, 2022; Strand et al., 2019). With the absence of fire refugia such as nearby forest that remained unburned or minimally impacted by fire, high-severity fires can decrease understory biodiversity (Coop, 2022), and increase how long it takes for the vegetation to recover (Strand et al., 2019).

Atypical severity fires can create post-fire environments that are more stressful for plant establishment. The removal of vegetation by high-severity fires results in post-fire environments that reduce leaf transpiration and water infiltration and increase solar radiation and run-off (El Maayar & Chen 2006; Aguilar et al. 2010; Dore et al. 2010; Nolan et al. 2014; Wine & Cadol 2016; Poon & Kinoshita 2018). Importantly, increased solar radiation can affect soil temperatures in these high-severity areas but minimal research has been conducted on the effects of increasing soil temperatures on plant fitness following fire or outside of agricultural settings. Soil temperature can influence physiology and plant processes such as nutrient and water uptake, photosynthesis, and root growth (Aidoo et al., 2016; Landhäusser et al., 2001; Nóia Júnior et al., 2018). And, up to a certain threshold, warmer soil temperatures can increase water and nutrient uptake (Toselli et al. 1999; Grossnickel 2000; Onwuka, 2016). However, thresholds are likely to

be different for each species given their functional group, phylogeny, and tolerances. Understanding how soil temperature is affecting plant community assembly, growth, and survival is important for predicting plant function and persistence after high-severity wildfire.

The effects of fire severity can be examined through the lens of plant functional traits (PFTs) and the leaf economic spectrum. The worldwide leaf economic spectrum describes the return on investments of nutrients and dry mass in leaves and provides additional insight into plant variation when combined with plant functional groups (Wright et al., 2004). Understanding leaf economics is crucial for understanding vegetation boundaries under climate change including plant recovery after high-severity fire. Specific leaf area (SLA) is often used in trait-based ecology because it is generally positively correlated with relative growth rate, and is a response to above ground resource competition (Cornelissen et al., 2003). Leaf dry matter content (LDMC) provides insight into tissue allocation in response to habitat conditions. Specifically, leaves with high LDMC tend to be relatively tough, and assumed to be more resistant to physical hazards such as wind and show a conservative nutrient use strategy (Peréz-Harguindeguy et al., 2016). Plant height is another commonly measured plant functional trait, as it is associated with competitive ability, fecundity, and ability to persist in light of disturbance events (Peréz-Harguindeguy et al., 2016). PFTs can be used to explain plant response to stressful environments, including variability in fire severity (Fernández-García et al., 2020; Huerta et al., 2021).

Much of the literature linking plant traits and fire are based on the life history traits of resprouting, seed banking, and seed germination. Obligate seeding species rely on dispersal from nearby patches or soil seed banks to persist after disturbance, whereas resprouting species can regrow from below-ground tissue when the disturbance is of typical frequency and severity for

the ecosystem (Pausas et al., 2004). Resprouting species play an important role in shaping their immediate plant communities following disturbance events through competitive exclusion, nitrogen fixation, water availability, and increasing herbaceous fine fuel biomass, depending on their lifeform (Owen et al., 2020; Simpson et al., 2021). The ability of resprouting species to vigorously regenerate following disturbance and persist post-fire allows for greater competitive ability after a high-severity burn. Resprouting species also benefit from priority effects, having immediate access to the open forest floor following fire. Rapid regeneration of woody resprouting species can drive early post-fire dynamics in the understory until regeneration from seeding species occurs and individuals reach a competitive size (Matula et al., 2020).

The frequency and severity of disturbance affects the variability of plant functional traits present within a disturbed area (Fernández-García et al., 2020; Huerta et al., 2021; Jung et al., 2010). Species with high SLA are associated with faster relative growth rates and shorter leaf-lifespans, which could be a beneficial resource-use strategy in ecosystems affected by frequent high-severity fires (Huerta et al., 2021). High SLA values are associated with vegetation in post-fire sites that burn with increasing wildfire recurrence and burn severity (Fernández-García et al., 2020). Species in our study with high SLA values could be better adapted to recovery from high-severity fires, allowing for species persistence under changing climatic conditions. The effects of soil temperature on leaf traits is understudied, especially in post-fire environments. For plants that may not have hit their soil temperature threshold, we might see a faster relative growth rate with large SLA values and low LDMC values. We would expect that others that are under stress from increasing soil temperature would exhibit lower SLA values and higher LDMC values, showing a slower relative growth rate and conservative resource use with increasing soil temperature.

This study takes place on the Museum Fire burn scar, located just north of Flagstaff, Arizona, USA, that burned over 1,961 acres in July of 2019. This was a heterogeneous burn, with patches of very low, low, moderate, and high-severity areas throughout the site (Inciweb 2019). This burn site provides a unique opportunity to investigate plant response within and across species to varying severity and climate stresses. We look across a fire severity gradient that includes unburned, low-severity, and high-severity areas to ask: 1) How does fire severity change the proportion of native and nonnative species, and plant functional groups in the understory of ponderosa pine ecosystems? 2) Following high-severity fire, do *Festuca arizonica, Muhlenbergia virescens*, and *Ceanothus fendleri* resprout in different microhabitats? 3) How do the plant communities immediately surrounding *F. arizonica, M. virescens*, and *C. fendleri* in the high-severity burn area differ? and 4) How does soil temperature affect trait expressions of *F. arizonica, M. virescens*, and *C. fendleri*?

2. Materials and Methods

2.1 Study Area

This study was conducted within the burn scar of the 2019 Museum Fire, located North of Flagstaff, Arizona (35.263 latitude, -111.639 longitude). This fire burned a total of 793.6 hectares in late July of 2019. The Museum Fire is characterized by a heterogeneous patchwork of varying severities. Within its perimeter are patches of very low, low, moderate, and high severity burn (Inciweb 2019). The burn occurred on a site characterized by a dominant overstory of *Pinus ponderosa*, with patches of *Quercus gambelii* and *Juniperus deppeana*, and interspersed individuals of *Pinus edulis*. For this study, all research was completed at elevations ranging 2277 m to 3000 m on southeasterly aspects. Annual precipitation of the area averages between 500-

710 mm with 40-50% of precipitation falling in the summer (Miller et al. 1995; Hereford 2007; NOAA 2023). Precipitation for the summer 2022 monsoon was 304.8-381 mm (NOAA 2023) with a mean annual temperature of 9.7°C (climate-data.org 2023).

2.2 Experimental Design

A combination of long-term monitoring plots and "neighborhood plots" established around target individuals of dominant resprouting species were used to answer our three research questions. To understand how cover of plant functional groups was changing over time across the burn severity gradient, we used data collected from the long-term monitoring plots. Monitoring plots were established in May 2020, with twenty plots in each burn severity comprising a total of sixty research plots (Taber, 2021). Burn severity categories include unburned, low-severity, and high-severity. The low-severity burn area is representative of the historic fire regime in this ecosystem of frequent, low-severity fires. The vegetation present in the unburned areas is representative of the understory under fire suppression forest management techniques. Burn severity classifications were derived from Burned Area Reflectance Classification (BARC) remote sensing data mapped by the USDA and ground truthed by field crews (Parsons et al., 2010; Noll & Malis-Clarke, 2020). Plots are censused annually in September, with absolute plant cover measured to the nearest 0.25% for each species following a modified Daubenmire method.

Using plant cover data collected for question 1, we used indicator species analysis (Bakker, 2008) to identify which species were most closely associated with high-severity fire. The resprouting shrub *C. fendleri* was identified as a species with both high abundance in and high fidelity to the high-severity burn area in 2020 (Taber, 2021). *Muhlenbergia virescens* and *F.*

arizonica were the most abundant perennial graminoids in the high-severity burn area (Taber, 2021). Twenty target individuals of similar basal diameter and height for each of *M. virescens*, *F. arizonica*, and *C. fendleri* were identified by walking across the high-severity burn area marking resprouting individuals (Figure 1). Perennial graminoids had a minimum diameter of 10 cm to ensure that plants were resprouted and not individuals establishing from seed post-fire. *C. fendleri* individuals were chosen with a minimum height of 20 cm with similar branching structures. We established a "neighborhood" sampling plot around each target individual of each species to understand how community composition and assembly differs around resprouting plant species following fire (n=20 plots per species, 60 plots total). Within each neighborhood sampling plot, we measured absolute cover identified to species, substrate cover, canopy openness and soil temperature immediately adjacent to the target individual as well as in the southern corner of the plot (located 50 cm away).

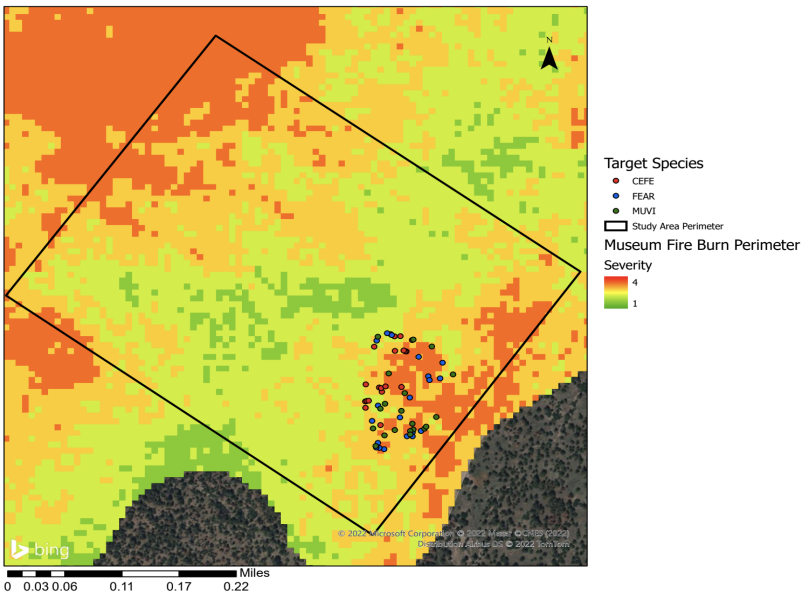

Figure 1: Map of the study area outlined in black, with selected target individuals in the high-severity burn area. Individuals were selected based on resprouting structure and size. Individual locations were collected with a Garmin, and GPS points are up to 10 m away from actual location due to range of accuracy.

2.3 Data Collection

Data collection of monitoring plots occurred in September of 2020, 2021, and 2022. Percent cover for vegetation and substrates were measured within 1-m^2 monitoring plots across the burn severity, and in 1-m^2 neighborhood plots around target individuals. Percent cover was visually assessed using a modified Daubenmire method. Data collection of neighborhood plots occurred in September 2022. In each neighborhood plot, the target individual was centered within a 1-m^2 sampling frame oriented on a north-south axis (Figure 2). Soil temperature and moisture measurements were collected using the Fieldscout TDR 150 Soil Moisture Meter by Spectrum Technologies Inc. Soil measurements were taken directly north of the target individual basal area, as well as in the south corner of each quadrat (50 cm away). All vegetation was identified to species using the same modified Daubenmire method as Question 1, and vegetation and substrate cover estimated to the nearest 0.25%. All nomenclature follows the USDA plants database accessed in 2022.

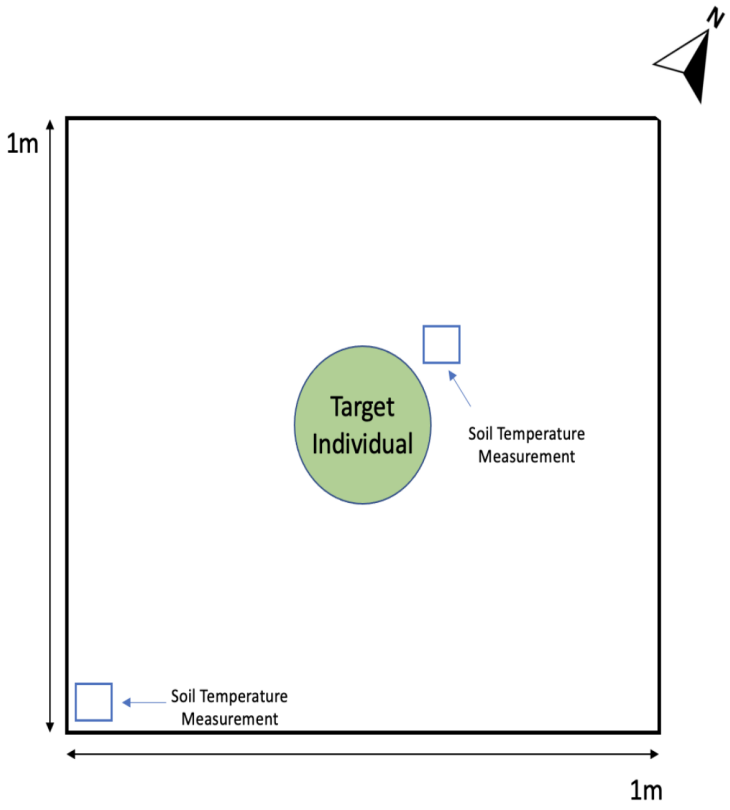

Figure 2: Diagram showing each target individual plot layout. Each target individual was centered in a 1-m^2 quadrat, with a corner oriented on a north-south axis. Soil temperature measurements were taken directly north of the basal area of the target individual and in the south corner of the quadrat.

Trait data was collected for each target individual, including height, basal diameter, specific leaf area (SLA), and leaf dry matter content (LDMC). All traits were measured according to standard trait protocols (Cornelissen et al., 2003; Peréz-Harguindeguy et al., 2016). All fresh leaf samples were rehydrated by placing petioles in distilled water for 6 hours prior to scanning and weighing (Garnier et al., 2001). Leaf area for all samples was determined using CID-203 leaf area meter manufactured by CID Bio-Science. After leaf area and fresh mass were measured, samples were dried at 70° for 72 hours. Once dry, leaf samples were re-weighed. SLA and LDMC were calculated from the area and mass of each sample.

2.4 Statistical Analysis

All statistical analyses were performed using R version 4.1.1 (R Core Team 2023). Vegetation cover data for all monitoring plots across the severity gradient and neighborhood plots around target individuals were standardized using Wisconsin transformation (McCune and Grace, 2002). Standardized cover values were then used for all analyses involving plant cover. Monitoring plot cover data across the severity gradient was grouped by native status and the following functional groups according to the USDA plants database: annual forb, biennial forb, perennial forb, perennial graminoid, and woody. For all native vs. invasive, and functional group cover we used a Kruskal-Wallis test using the function *kruskal.test* to determine differences in median cover across the severity gradient for the previous three years. Kruskal-Wallis tests were followed by a pairwise Dunn test with Bonferroni correction to determine between which severity classes differences occurred. We used soil temperature data near and away from target individuals to determine whether there was a significant impact of the target species on soil temperature using a paired t-test. Species evenness, species richness, and Shannon diversity index were calculated for neighborhood plots surrounding target species using the R package *vegan*. Because we found no significant difference in soil temperature near the plant from that collected away from any plants in the corner of the plot, we used Kruskal-Wallis and Dunn tests with Bonferroni correction to quantify differences in soil temperature and diversity metrics between species neighborhoods.

Outlier tests were performed for all soil temperatures and species traits using the *grubbs.test* function in the R package *outliers.* All trait data met normality assumptions as is or through transformations and passed heteroscedastic assumptions using the function *ncvTest* for the Breusch Pagan test in the R package *car*. Linear models were then used to assess the effects

of soil temperature and species on trait expression and biodiversity measurements in the high-severity burn area. The interaction of species and soil temperature was included as a fixed effect in our first order linear regression to measure if traits responded to environmental stress by species, and if biodiversity was correlated with soil temperature stress. Linear regressions were followed by ANOVA using the function *Anova* within the *car* package in R to quantify the main effects of species and soil temperature independently, and effects of the interaction of species and soil temperature on our response variables.

3. Results

3.1 Understory composition change over three years along a burn severity-gradient

Nonnative vegetation cover was higher in the high-severity burn area when compared to the low-severity and unburned area within all three years of post-fire cover data (Figure 3). In 2022, native vegetation was 52.46% higher in the low-severity ($p<0.0001$) and 49.28% higher in the unburned ($p<0.0001$) sites compared to the high-severity area (Figure 3, Table 1). Nonnative cover was 68.92% higher in the high-severity burn area compared to the low-severity ($p<0.0001$) and 66.23% higher compared to the unburned ($p<0.0001$) sites. 2021 and 2020 data yielded similar results between the low-severity and unburned sites compared with the high-severity for both native and nonnative vegetation cover (Table 1).

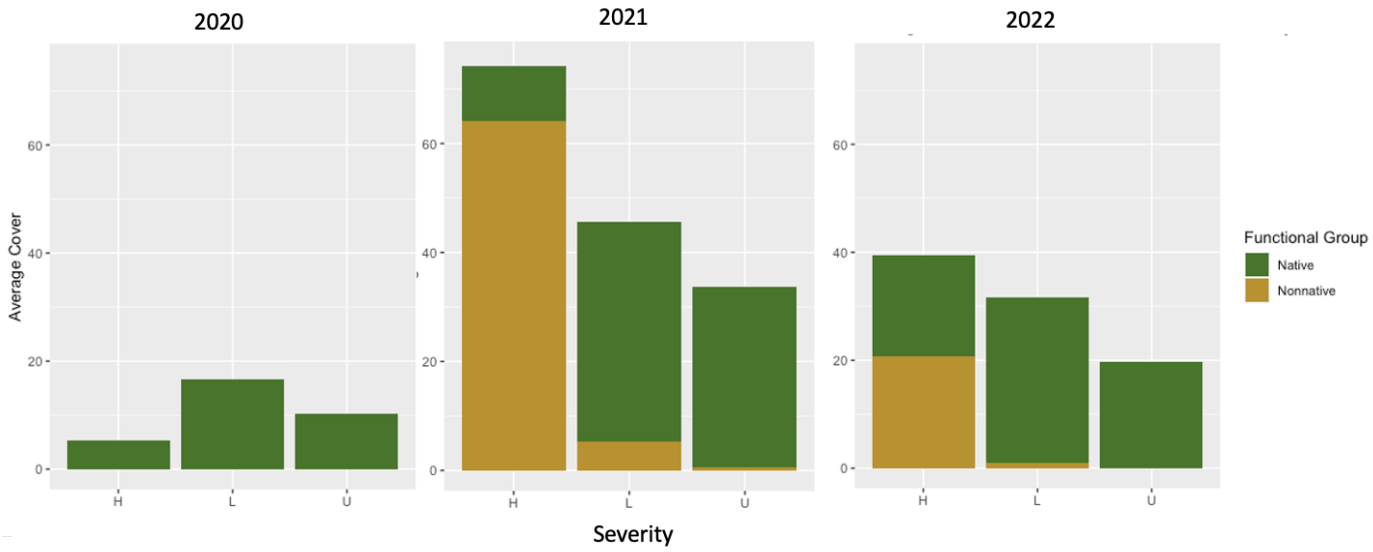

Figure 3: Average native and nonnative cover for each burn severity for 2020, 2021, and 2022.

Native vs Nonnative By Severity Kruskal-Wallace Test Results			
2022	**H Stat**	**df**	**P-Value**
Native	38.242	2	4.97E-09***
Nonnative	38.242	2	4.97E-09***
2021			
Native	41.447	2	1.00E-09***
Nonnative	36.229	2	1.36E-08***
2020			
Native	10.522	2	0.00519**
Nonnative	1.0178	2	0.6012

Table 1: Kruskal-Wallis test results for native and nonnative cover change across severity for 2022, 2021, and 2020. *, **, and *** represent p values < 0.05, 0.01, and 0.001 respectively. See supplementary materials for Dunn Test results with Bonferroni correction for p-values of differences between severities.

Functional group cover varied significantly over the severity gradient in each year (Table 2). In 2020, there was significantly higher grass cover in unburned, compared to low- and high-severity plots. The abundance of perennial graminoid cover in 2020 was 5.65% lower between the high-severity burn area compared to the low-severity ($p=0.00388$) and 26.28% lower

compared to unburned sites (*p<0.0001*) (Figure 4). In 2021, the high-severity burn area had 77.4% more cover of annual forbs (*p=5.8e-05*) and 2.29% more biennial forbs (*p= 0.0147*) compared to the low severity, and 88.96% more cover of annual forbs (*p=8.8e-08)* and 2.64% more biennial forbs (*p<0.0001)* in unburned areas (Figure 4). The low-severity burn area had 5.28% more perennial forbs than the high-severity burn area (*p=0.0332*). Perennial graminoid cover continues to be significantly higher in the low-severity (*p=0.00012*) and unburned (*p<0.0001*) areas compared to the high-severity burn area (Figure 4), with 74.25% more cover in the low-severity and 89.62% more cover in the unburned. In 2022, the high-severity burn area promoted 50.6% more cover of annual forbs (*p=0.0021*) than the low-severity and 61.24% more cover than unburned areas (*p<0.0001*) (Figure 4). The abundance of biennial forbs was 14.17% higher in the high-severity (*p<0.0001)* and 3.64% higher in the low-severity (*p=0.0092)* compared to the unburned site. The low-severity (*p=0.0016*) and unburned (*p<0.0001*) areas have 54% and 75.67% more perennial graminoid cover than the high-severity burn area respectively (Figure 4).

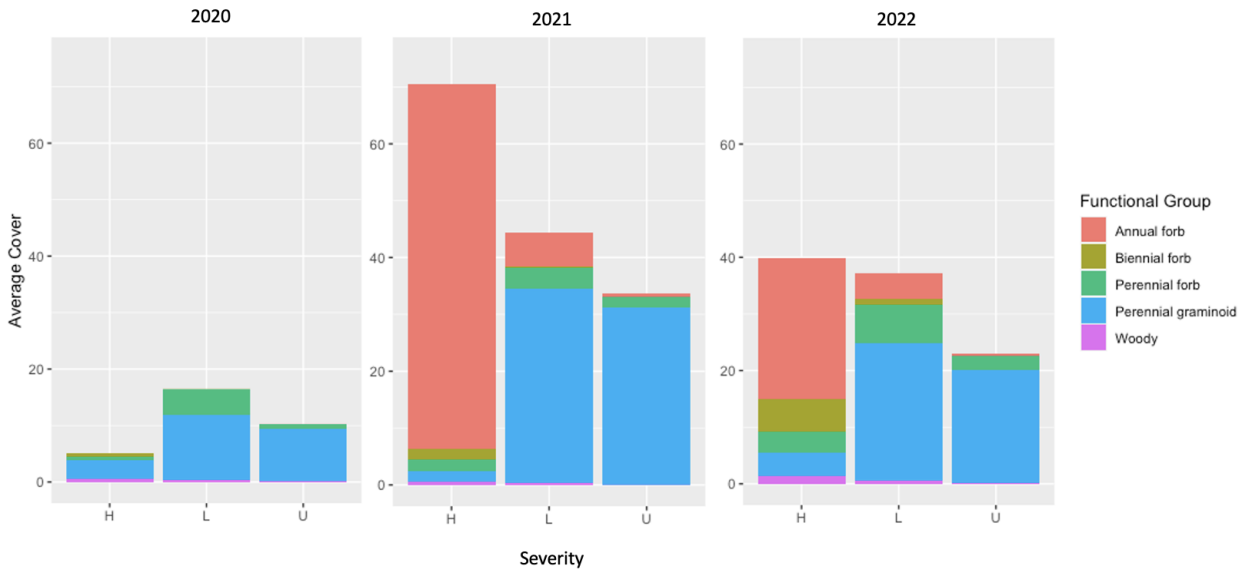

Figure 4: Average functional group cover by severity for 2020, 2021, and 2022. The high-severity burn area had significantly less perennial graminoid cover for all three years of data, and significantly more annual forb cover for 2021 and 2022.

Functional Group Kruskal-Wallace Test Results			
2022	**H Stat**	**df**	**P-Value**
Annual Forb	29.006	2	5.03E-07***
Biennial Forb	24.102	2	5.84E-06***
Perennial Forb	1.6762	2	4.33E-01***
Perennial Graminoid	29.292	2	4.36E-07***
Woody	1.1647	2	5.59E-01***
2021			
Annual Forb	33.963	2	4.22E-08***
Biennial Forb	21.056	2	2.68E-05***
Perennial Forb	6.5349	2	0.0381*
Perennial Graminoid	41.82	2	8.30E-10***
Woody	5.6358	2	5.97E-02***
2020			
Annual Forb	4.0678	2	0.1308
Biennial Forb	1.0178	2	0.6012
Perennial Forb	5.3859	2	0.06768
Perennial Graminoid	18.703	2	8.69E-05***
Woody	4.3114	2	0.1158

Table 2: Kruskal-Wallis test results of each functional group across the burn severity gradient for 2022, 2021, and 2020. *, **, and *** represent p values < 0.05, 0.01, and 0.001 respectively. See supplementary materials for Dunn Test results with Bonferroni correction for p-values of differences between severities.

3.2 Neighborhood-level Differences

Soil temperature measurements near and away from target individuals revealed no significant difference between soil temperature within 1-m^2 quadrats (FEAR $p=0.1536$; MUVI $p=0.3979$; CEFE $p=0.1625$). Soil temperature measurements between species neighborhoods revealed higher soil temperatures near *C. fendleri* than *F. arizonica* neighborhoods (Figure 5).

Kruskal-Wallis tests of canopy openness measurements of each species neighborhood did not yield a significant difference (*p=0.129*).

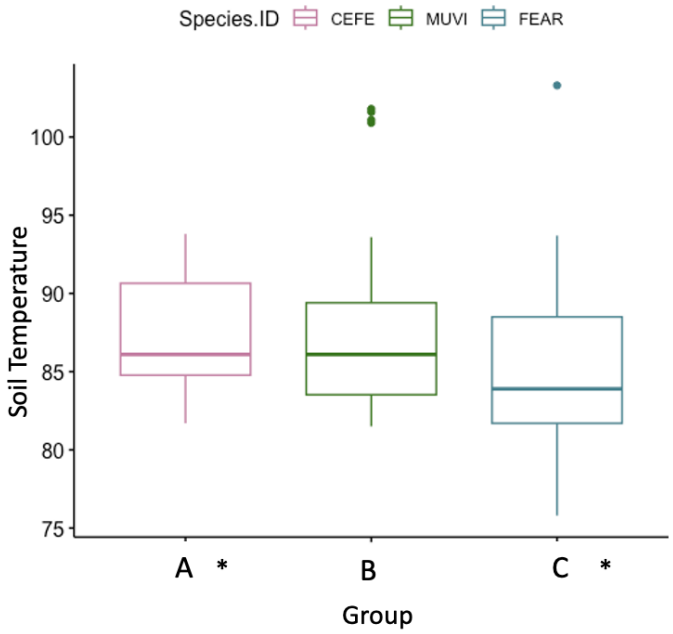

Figure 5: Box plots of soil temperature measurements for *F. arizonica*, *M. virescens,* and *C. fendleri* neighborhoods. Group A is *C. fendleri*, B is *M. virescens*, and C is *F. arizonica*. AB analysis yielded a p value of 1, AC analysis yielded a p value of 0.0405, and BC analysis yielded a p value of 0.2782. * Indicates a significant difference between the two groups. Boxplots represent the minimum and maximum values, the first and third quartiles, and the median value. Outliers are represented by filled circles.

There were significant differences in richness, evenness, and Shannon diversity index measurements in neighborhood plots around each of our three focal resprouting species. Overall, *F. arizonica* had the highest evenness and Shannon index measurements, and the lowest richness score (Figure 6). *Muhlenbergia virescens* had the highest richness scores, and *C. fendleri* neighborhood scores were consistently in between the perennial graminoids (Figure 6). Richness scores for *M. virescens* neighborhoods were significantly higher than neighborhood richness scores for *F. arizonica* (*p=0.0487*). Evenness scores for *F. arizonica* neighborhoods were significantly higher than *M. virescens* neighborhoods (*p=0.0150*). Shannon Index scores for *F. arizonica* neighborhoods were significantly higher than *M. virescens* neighborhoods (*p=0.0127*).

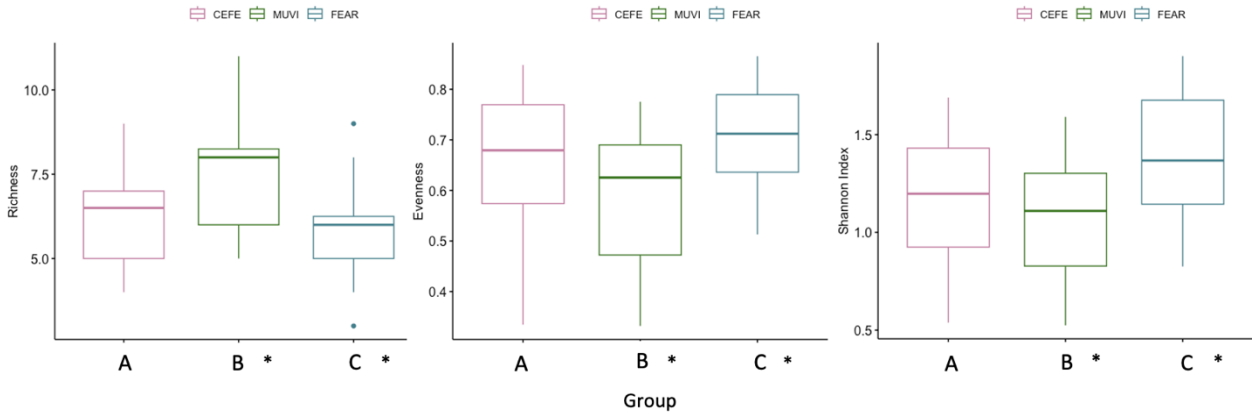

Figure 6: Boxplots of Species Richness, Evenness, and Shannon Index measurements for *F. arizonica*, *M. virescens,* and *C. fendleri* neighborhoods. Group A is *C. fendleri*, B is *M. virescens*, and C is *F. arizonica*. Boxplots represent the minimum and maximum values, the first and third quartiles, and the median value. Outliers are represented by filled circles. Kruskal-Wallis test results for each diversity measurement between groups displayed in supplementary materials. * Indicates a significant difference between the two groups.

Neighborhood Diversity Kruskal-Wallis Test Results			
Measurement	**H Stat**	**df**	**P-Value**
Richness	6.5926	2	0.03702*
Shannon Diversity	8.4062	2	0.01495**
Evenness	8.1613	2	0.0169**

Table 3: Kruskal-Wallis test result for Richness, Evenness, and Shannon Index measurements between species neighborhoods. *, **, and *** represent p values < 0.05, 0.01, and 0.001 respectively.

As soil temperatures increased, richness in all three neighborhoods decreased (Figure 7). The interaction of species and temperature was not significant, however, the main effects of species and temperature independently affected species richness (Table 4). For both evenness and Shannon diversity, soil temperature had no effect (Table 4).

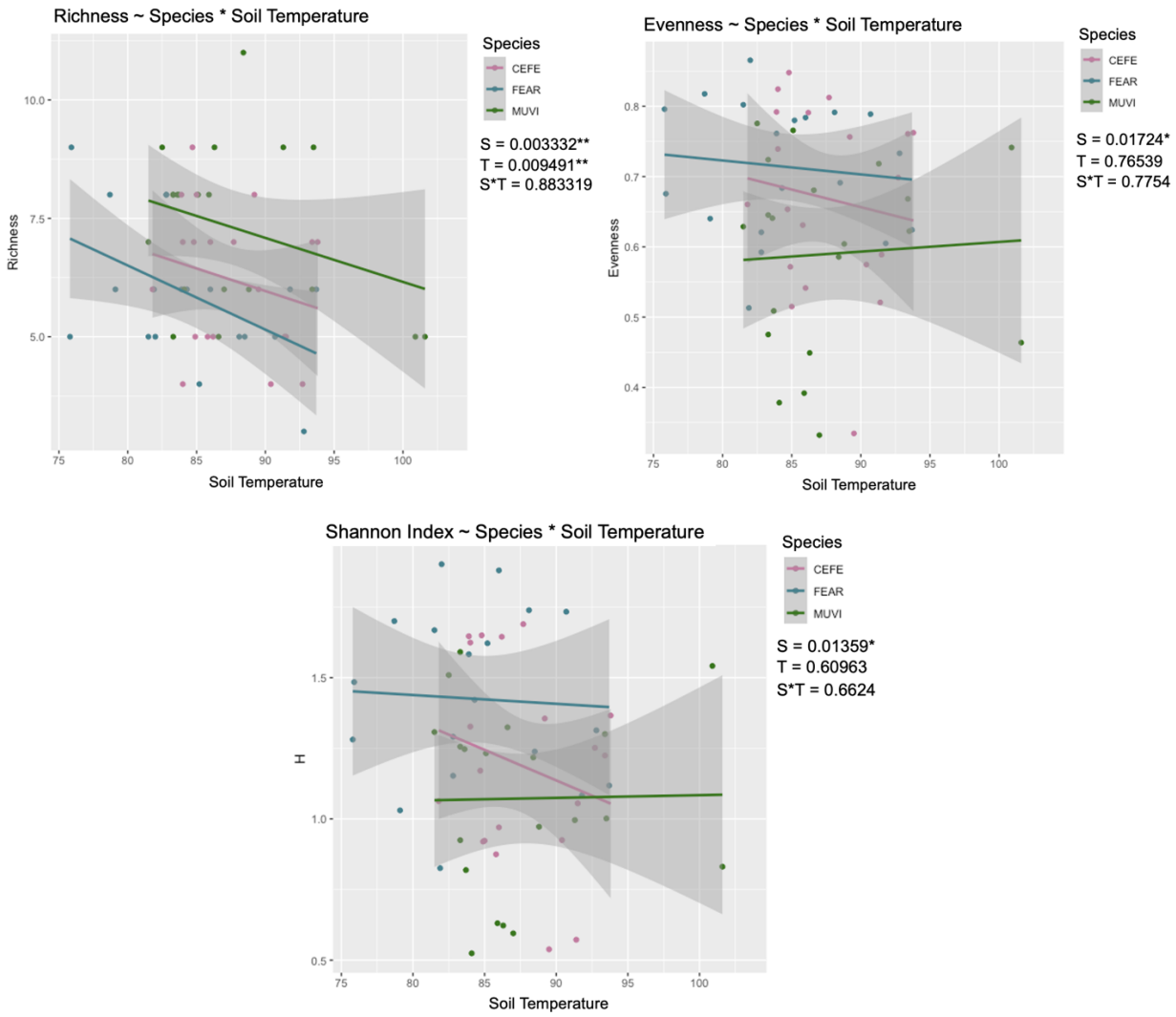

Figure 7: Linear regression models of neighborhood richness, evenness, and Shannon index values by species and soil temperature to determine the effects of soil temperature and species on neighborhood species diversity.

Analysis of Variance Table (Type II)			
Response: Richness			
	DF	**F Stat**	**P (>F)**
Species ID	2	6.3646	0.003332**
Soil Temperature	1	7.2454	0.009491**
Species ID:Soil Temperature	2	0.1244	0.883319
Residuals	53		
Analysis of Variance Table (Type II)			
Response: Evenness			
	DF	**F Stat**	**P (>F)**
Species ID	2	4.3881	0.01724*

Soil Temperature	1	0.09	0.76539
Species ID:Soil Temperature	2	0.2556	0.7754
Residuals	53		
Analysis of Variance Table (Type II)			
Response: Shannon Diversity Index			
	DF	**F Stat**	**P (>F)**
Species ID	2	4.667	0.01359*
Soil Temperature	1	0.238	0.60963
Species ID:Soil Temperature	2	0.4152	0.6624
Residuals	53		

Table 4: Anova analysis output for richness, evenness, and Shannon index by soil temperature and species. *, **, and *** represent p values < 0.05, 0.01, and 0.001 respectively.

3.4. Plant trait response to increasing soil temperature

Specific leaf area (SLA) and height did not differ across species or with soil temperature (figure 8, Table 5). In contrast, leaf dry matter content (LDMC) in *C. fendleri* and *M. virescens* increased with increasing soil temperature (Figure 8). Conversely, LDMC in *F. arizonica* individuals decreased with increasing soil temperature (Figure 8). *C. fendleri* and *M. virescens* are making more dense leaves with increasing soil temperature, and *F. arizonica* is creating less dense leaves. The significant interaction between species and soil temperature in the LDMC model supports this finding that the effect of soil temperature on LDMC is dependent on species, and the variables do not act independently on LDMC (Table 5).

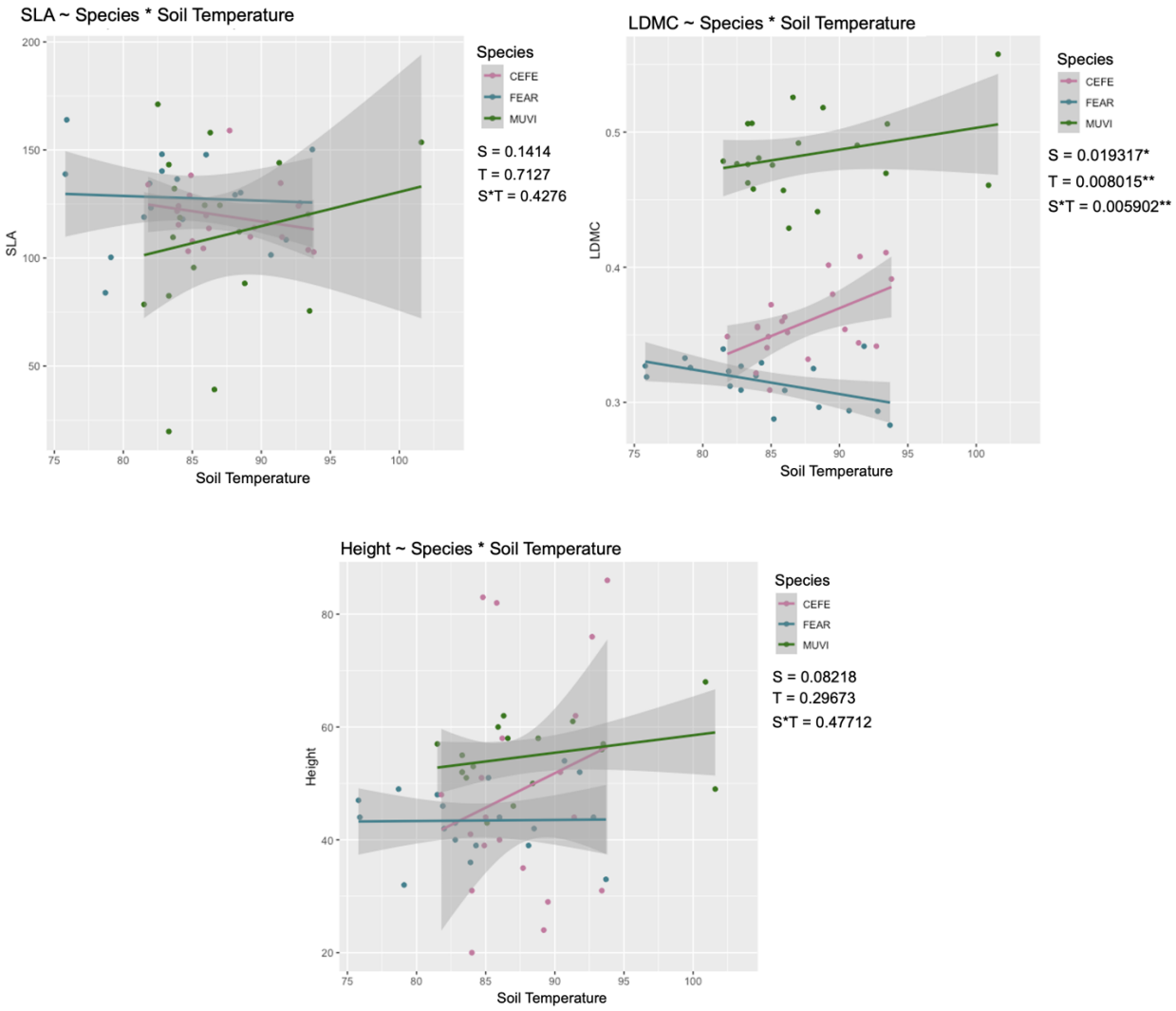

Figure 8: Linear regression models of specific leaf area (SLA), leaf dry matter content (LDMC), and height by the interaction of species and soil temperature. Models used to determine the effects of species and soil temperature on trait expression.

Analysis of Variance Table (Type II)			
Response: SLA			
	DF	**F Stat**	**P (>F)**
Species ID	2	2.0328	0.1414
Soil Temperature	1	0.1371	0.7127
Species ID:Soil Temperature	2	0.8639	0.4276
Residuals	51		
Analysis of Variance Table (Type III)			
Response: LDMC			
	DF	**F Stat**	**P (>F)**

Species ID	2	4.2558	0.019317*
Soil Temperature	1	7.5929	0.008015**
Species ID:Soil Temperature	2	5.6632	0.005902**
Residuals	53		
Analysis of Variance Table (Type II)			
Response: Height			
	DF	**F Stat**	**P (>F)**
Species ID	2	2.6254	0.08218
Soil Temperature	1	1.1115	0.29673
Species ID:Soil Temperature	2	0.7508	0.47712
Residuals	51		

Table 5: Anova analysis output for richness, evenness, and Shannon index by soil temperature and species. *, **, and *** represent p values < 0.05, 0.01, and 0.001 respectively.

4. Discussion

We found that native and nonnative species cover differed between high- and low-severity. Additionally, functional group cover was altered following high-severity fire in each year of our study. Taken together, the increase of invasive species and forbs, and decrease in perennial graminoids in the high-severity area, highlights a change in understory proportions from typically dominant native perennial graminoids to invasive and annual species. When comparing the habitats and biodiversity around two native perennial graminoids and one resprouting shrub following high-severity fire, we found that *F. arizonica* was found in sites with the coolest soil temperatures, and the highest biodiversity. The resprouting shrub *C. fendleri* was found in sites with the hottest soil temperatures. Biodiversity in the neighborhoods around all three species decreased with increasing soil temperature. The effects of increasing soil temperature on neighborhood biodiversity and individual leaf traits provide us insight into species persistence after high-severity fire.

4.1 High-severity fire alters understory functional composition

Our results show that high-severity fire leads to different plant functional composition compared to low-severity and unburned areas. Across the three years, we saw the same trend of significantly more annual forbs and significantly less perennial graminoids in the high-severity burn area. These changes in the proportion of dominant understory matrix-forming perennial graminoids may influence the trajectory of recovery in the understory. Dominant functional group change from perennial graminoids to forbs has the potential to influence watershed resources by increasing erosion and runoff through differences in rooting structures (Wilsey & Polley, 2006) Additionally, these forbs compete for resources with perennial and woody species trying to establish in the high-severity burn area (Coop, 2022). Shifts toward weedy and nonnative understory vegetation may be indicative of a growing threat to biodiversity (Peeler and Smithwick, 2018). Much of the biodiversity in ponderosa pine ecosystems is held in the understory (Moore et al., 2006). With a change in plant composition following high-severity fire compared to the low-severity and unburned areas of the site, it is anticipated that understory biodiversity may decline. Our results are consistent with other research in the system, where areas burned at high to moderate severity had greater forb cover than low-severity areas (Barton, 2005; Shive et al., 2013; Abella & Fornwalt, 2015; Owen et al., 2020).

We observed an increase in invasive species cover in the high-severity burn in years two and three after fire. This increased abundance of invasive species can inhibit native plant establishment through changes in phenology and competition (Alexander and Levine, 2019), and increase fuel loading and the potential for a reburn (Brooks et al., 2004; Fusco et al., 2022). For example, the annual grass *Bromus tectorum* has an early season phenology that makes it a good competitor compared to other species, and leaves fine dry fuels on the landscape as an ecosystem

enters fire season (Bradley et al., 2018). An abundance of *B. tectorum* on a landscape increases the amount of dry fuels available to burn. It is also able to rapidly recover following fire events, which can result in a positive feedback where high-severity fire begets high-severity fire (Coop et al., 2020). Other invasive species can also drive a change in fire regime by increasing burn severity and creating faster return intervals (Brooks et al., 2004; Fusco et al., 2022). *Salsola tragus*, the dominant invasive species in the high-severity burn area of our site, is known to be highly flammable when dry (Crist et al., 2019; Lambert et al., 2010), which increases the risk of rapid reburning and could reinforce a positive fire feedback. Land managers are still determining if a *S. tragus* infestation is potentially harmful to a landscape and if it should be actively managed (Thomas & Redsteer, 2023). Further research on the influences of *S. tragus* on landscape scale reburning and fire-severity would help inform management decisions regarding this species.

4.2 Target species differ in their immediate neighborhood community

Resprouting species can influence the trajectory of succession by altering community composition via priority effects (Fukami et al., 2016). These priority effects refer to the order or timing of species arrival on a site (Weidlich et al., 2021). Priority effects can both negatively and positively affect later-arriving species through the reduction of available resources, or habitat modification (Weidlich et al., 2021) and high-severity fire. Areas burned to a severity outside of the historical norm in ponderosa pine systems are documented to be transitioning toward non-forested vegetation with a high dominance by resprouting species (Woolman et al., 2022). We determined that resprouting target individuals in our high-severity burn area are not modifying their immediate environment in regards to soil temperature, however, three dominant resprouters

did occur on different soil temperatures microhabitats (Figure 5). *C. fendleri* was found in the highest soil temperatures and are occurring in warmer microhabitats than *F. arizonica*. This indicates the persistence of *C. fendleri* in increasingly stressful environments while *F. arizonica* and *M. virescens* may become uncommon on the landscape with increasing soil temperature pressure. With increasing ambient temperatures and risk of high-severity wildfires, shrubs like *C. fendleri* may outcompete matrix-forming perennial graminoids.

Biodiversity metrics in our neighborhood plots around *C. fendleri*, *F. arizonica*, and *M. virescens* differed between our two perennial graminoids (Figure 6). The highest evenness and Shannon Index scores were near *F. arizonica*. Importantly, the highest Shannon index values being in *F. arizonica* neighborhoods show a higher overall biodiversity when taking into consideration number of species and distribution of species cover compared to *M. virescens* neighborhood plots. Taken together with soil temperature data, *F. arizonica* is occurring in habitats with the highest biodiversity and the coolest soil temperatures. The presence of *F. arizonica* may indicate "refuge" neighborhoods due to lower soil temperatures and increased biodiversity found near these individuals. When considering understory restoration after high-severity fires, it is important to determine where on the landscape management efforts should be focused. It has been shown that for ponderosa pine seedlings, natural regeneration after high-severity fire may occur in areas that are close to a nearby seed source or in cooler and moister environments (Korb et al., 2019). Our results suggest that understory plants, specifically *F. arizonica*, may follow this same pattern of regenerating in cooler microsites. Therefore, planting and seeding species near *F. arizonica* may yield higher restoration success to increase understory biodiversity following high-severity fire.

As soil temperature increased, species richness in the plant communities around all three species declined. This indicates that with increasingly stressful environments such as increased soil temperatures, perennial grasses may become uncommon, and understory community biodiversity more generally may decline. Continued climate warming, drought, and high-severity fires may accelerate a loss in biodiversity.

4.3 Plant trait response to soil temperature under increasingly stressful environment

Leaf economics can help us understand vegetation boundaries under shifts in land-use and climate change. The responses of some leaf traits to changing environments such as drought, and climate warming, are dependent on the strength of the stressor (Cui et al., 2020). Further, species from different functional groups may have different eco-physiological constraints when experiencing environmental change (Díaz et al., 2016). When considering our three species and their different functional characteristics, it is likely not all species are experiencing the same level of stress under identical environmental conditions. Species that are adapted to warmer and drier conditions may tolerate and maintain faster growth rates with increasing soil temperatures, with a higher threshold than other species. For example, a C3 grass which is considered to be adapted to cooler and wetter microclimates, would show a slower relative growth rate of decreasing SLA, and increasing LDMC with increasing soil temperature stress. Whereas a C4 grass, that is considered to be adapted to warmer and drier conditions, would be expected to have a higher soil temperature threshold, and continue resource allocation for a faster relative growth rate until that threshold was met. This suite of trends is not expressed in our experiment. Rather, our C3 grass did not exhibit a conservative stress response in LDMC to increasing soil temperature. *F. arizonica* decreased LDMC with increasing soil temperature, suggesting a more

rapid production of biomass, and little concern for nutrient conservation (Peréz-Harguindeguy et al., 2016). The summer of 2022, during which this data was collected, was uncharacteristically cool and wet. Average summertime temperatures were 73°F, which is almost 6°F less than the 10-year average of 78.7°F (NOAA 2023). Average monthly precipitation was 4.5 inches, 3.3 inches higher than the summer average of 1.2 inches (NOAA 2023). With this cooler and wetter summer, it is possible that *F. arizonica*, and all target species, were not experiencing the level of stress that we would expect in a typical summer. Therefore, *F. arizonica* had plentiful water and temperature conditions to contribute to the rapid production of biomass. Sampling in a more typical year could yield more significant results to highlight this relationship for all species.

Limitations

All biodiversity, trait, and soil temperature regressions in this study would benefit from a larger sample size to increase accuracy and repetition. Further, sampling neighborhood plots in a more typical year may yield more accurate results for predicting vegetation responses to climate change. 2022 was considered a cooler and wetter summer than normal, thus these plants did not experience the level of environmental stress that they might in a more typical year, or under future climate change. In addition, other trait measurements such as root length, photosynthetic rate, and leaf nutrients would give a fuller picture for how soil temperature impacts plant trait expression and resource-use strategy. Finally, more physiologically relevant explanatory variables such as soil moisture and slope would allow us to better understand the mechanisms behind this trait expression, and soil temperature thresholds for individual species.

5. Conclusions

Our results indicate that ponderosa pine forest understories subjected to high-severity fire exhibit an increased forb and nonnative species cover in the years following fire, and a decrease in perennial graminoid and native species cover compared to low-severity and unburned sites. In addition, drought tolerant shrub and grass species occurred in areas with higher soil temperatures in the high-severity area, and biodiversity of the understory plant community also declined. The return of a productive understory that mirrors those found under a more typical, low-severity fire regime is necessary to reduce threats of biodiversity loss, erosion, reburning, and persistent type conversion to a non forested landscape. As wildfire severity has been increasing in this region, it is likely that the changes in the proportion of different functional groups we have observed in our study will become more prevalent in the southwestern U.S. On-going management efforts to return these forests to historical stand densities are the best insurance against high-severity fires and the persistence of understory communities into the future. Stand density reduction may also assist areas adapting to the drier and warmer climate projected in the region for coming decades by reducing resource competition for water (Tepley et al., 2020; Young et al., 2020a). This reduction affects the understory by providing more light, and allowing for the return of low-severity fires that enables the persistence of understory species (Huffman et al., 2020).

The post-fire recovery process is being challenged by increasingly stressful environmental conditions as a consequence of climate change (Guiterman et al., 2022). High-severity burn areas create more stressful environments for species recovery due to an absence of canopy and alterations of soil infiltration rates. Plants with traits such as resprouting and serotinous seeds, along with species that persist in warmer ambient and soil temperatures, and drought conditions, will have a higher fitness in post-fire high-severity sites. These factors are driving management to consider alternative states as potential management objectives (Falk et

al., 2022). The Resist-Accept-Direct framework allows managers to consider broader objectives to vegetation management beyond the focus of resisting ecosystem change (Lynch et al., 2021). Managers can then consider whether accepting inevitable vegetation change or directing it along a desirable pathway is more practical and appropriate under different post-fire recovery scenarios. When approaching at the landscape scale, it may be beneficial for land managers to direct vegetation to create a heterogeneous, patchwork of vegetation types, and consider alternative vegetation states as a potential management objective (Lynch et al. 2021). It remains unclear whether conversion to non forested types on patches of the landscape will enhance landscape diversity and resilience, or erode it in large swaths (Falk et al., 2022). However, promoting a diverse landscape-scale mosaic of forest, shrubland, and grassland ahead of disturbances can moderate the severity of vegetation type conversion (Lynch et al., 2021; Stevens et al., 2021).

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CHAPTER 3: CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Ponderosa pine forests of the southwestern United States are adapted to a high frequency, low-severity fire regime. Land use and management decisions over the past century have resulted in increased stand densities and fuel loads, increasing the probability of stand replacing, high-severity fire. High-severity fires in these southwestern forests have been increasing in frequency and size since the 1990s, and are expected to continue to increase in size and severity under global climate change.

The focus of management efforts to reduce the likelihood of stand replacing fires in this region has been placed on "thin and burn" restoration treatments that reduce fuel loads and restore historical stand structures. These treatments reduce the density of small diameter trees on the landscape. This density is then maintained by prescribed fire and the return of low-severity, frequent fire on the landscape. Thinning small diameter trees reduces the likelihood of undesirable fire severities in the future, and returns ecosystem dynamics to states more similar to forests prior to Euroamerican settlement. Our results suggest that following high-severity fire, the functional composition of the understory is significantly altered, containing more forbs and nonnative species, and a decrease in perennial graminoids. Following low-severity fire, we would expect a higher proportion of resprouting, perennial graminoids on the landscape like we observed in our low-severity and unburned study sites. Post-fire restoration of high-severity sites would benefit from the focus on seed mixes that promote native perennial grass establishment.

Post-fire seeding treatments were not completed by the U.S. Forest Service in this study area. Post-fire seeding is often performed to prevent erosion and increase water infiltration on a burned area (Robichaud, 2000). However, seeding efforts have been largely ineffective at these goals in northern Arizona (U.S. Forest Service, 2010). Typically applied seeding mixes often

contain fast-growing, non-native annuals such as cereal grains (e.g., sterile oats) as well as native forbs, and graminoids (Robichaud, 2000). In the absence of seeding, the high-severity burn area in our study exhibited a shift away from perennial grass dominance and toward exotic annual forb dominance. Thus, we recommend that future understory seeding and planting efforts seek to match local native understory assemblages with an emphasis on native perennial species. Current seed sourcing protocols state that seeds of local origin, from sites that have similar environmental and climate similarity, have the greatest adaptive potential to succeed on a site (Erickson & Halford, 2020). However, seed sourcing protocols may be modified to selecting seed based on similarity to future climate at a site (Erickson & Halford, 2020). Seeds for focal species can be obtained from non-local ecotypes that are believed to be better adapted to the new conditions at the planting site (Aitken and Bemmels, 2016; Young et al., 2020a), however, further research is needed specifically on understory species seed sources that may be better adapted to planting site conditions.

When revegetation efforts do not follow fire, or there is very little natural regeneration of the plant community, high-severity fire comes with its own suite of post-fire consequences. Of concern to many managers in the region is fire driven forest conversion to a non forested landscape. Fire driven forest conversion is considered a two step process. First, vegetation shifts are initiated by high-severity fire that removes large portions of forest stands from the landscape. This is then followed by a post-fire environment that inhibits the recovery mechanisms of these forests, limiting establishment of species of the prefire forest (Coop et al., 2020). The Resist-Accept-Direct (RAD) framework can aid land managers in making restoration and management decisions following high-severity fire (Lynch et al., 2021). Resisting ecosystem change would include management actions that focus on maintaining historical ecosystem structure and

services. In ponderosa pine forests, this includes efforts to thin dense stands, and re-introduce low-severity fires through prescribed fire. Accepting ecosystem change in ponderosa pine forests would include allowing natural regeneration after high-severity fire, not intervening, and accepting the changes that emerge from that. Directing ecosystem change in ponderosa pine forests would include accepting that change will occur and directing the change toward a state with a particular structure and function. The RAD framework allows managers to consider broader objectives beyond the focus of resisting ecosystem change (Lynch et al., 2021). Managers can consider whether accepting inevitable change or directing it along a desirable pathway is more practical and appropriate under some post-fire recovery scenarios. This allows management strategies to consider the challenges placed on post-fire recovery processes, and determine site specific strategies for landscape resiliency to climate change. Our study is an example of "accept" within this framework, because there was no post-fire restoration to aid the return of vegetation to the landscape. The understory in the high-severity burn area of the Museum Fire is showing variation from the historical understory, with declines in perennial grass cover and increases in forb and nonnative vegetation cover. Continued monitoring of fire events outside the range of natural variability in a landscape is vital for assessing landscape risk to conversion to non forested vegetation. When looking across a landscape scale, it may be beneficial for land managers to direct landscapes towards heterogeneity following high-severity fire, and consider alternative vegetation states as a potential management objective (Falk et al., 2022). More research is needed on whether conversion to non forested types on patches of the landscape will enhance landscape diversity and resilience, or erode it in large swaths (Falk et al., 2022). However, promoting a diverse landscape-scale mosaic of forest, shrubland, and grassland

ahead of disturbance events can moderate the severity of vegetation type conversion (Lynch et al., 2021; Stevens et al., 2021).

Ongoing management efforts in Arizona that continue to reduce the likelihood of high-severity fires should be supported and increased. Efforts in the northern Arizona region include the Flagstaff Watershed Protection Project and the Four Forest Restoration Initiative, both aimed at reducing fuels and creating fire resilient forests and communities. The Museum Fire was accidentally ignited by heavy machinery used in one such treatment effort in July of 2019. Monsoonal rains in the region strongly dictate fire risk, and the 2019 monsoon rain totals were far below average. With the continued and increasingly variable precipitation regime of the southwest, the timing of restoration activities continues to be a challenge.

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APPENDIX 1: COMPLETE SPECIES LIST

Table 6: Complete list of species observed on Museum Fire burn scar over three years. All nomenclature follows the USDA NRCS Plants Database accessed in 2022.

Species	Functional Group	Native Status
Acmispon rigidus	perennial forb	Native
Arabis drummondii	perennial forb	Native
Artemisia ludoviciana	perennial forb	Native
Astragalus humistratus	legume	Native
Bouteloua curtipendula	perennial graminoid	Native
Bromus ciliatus	perennial graminoid	Native
Calliandra humilis	legume	Native
Castilleja integra	perennial forb	Native
Carex rosii	perennial graminoid	Native
Ceanothus fendleri	perennial shrub	Native
Chenopodium album	annual forb	Non-native
Cirsium wheeleri	perennial forb	Native
Cologania angustifolia	perennial forb	Native
Conyza candensis	annual forb	Native
Cryptantha gracilis	annual forb	Native
Elymus elymoides	perennial graminoid	Native
Epilobium brachycarpum	annual forb	Native
Eriogonum alatum	perennial forb	Native
Erigeron divergens	biennial forb	Native
Erigeron neomexicanus	perennial forb	Native
Eriogonum racemosum	perennial forb	Native
Festuca arizonica	perennial graminoid	Native
Geranium caespitosum	perennial forb	Native
Heliomeris multiflora	perennial forb	Native
Hedeoma oblongifolia	perennial forb	Native
Houstonia wrightii	perennial forb	Native

Hymenoxys bigelovii	perennial forb	Native
Lactuca serriola	annual forb	Non-native
Linaria dalmatica	perennial forb	Non-native
Lithospermum multiflorum	perennial forb	Native
Lotus wrightii	perennial forb	Native
Lupinus argenteus	perennial forb	Native
Machaeranthera canescens	annual forb	Native
Muhlenbergia montana	perennial graminoid	Native
Muhlenbergia virescens	perennial graminoid	Native
Muhlenbergia wrightii	perennial graminoid	Native
Oenothera elata	biennial forb	Native
Oxalis latifolia	perennial forb	Native
Packera multilobata	annual forb	Native
Penstemon linarioides	perennial forb	Native
Penstemon virgatus	perennial forb	Native
Phaseolus angustissimus	perennial forb	Native
Piptochaetium pringlei	perennial graminoid	Native
Portulaca oleracea	annual forb	Non-native
Pseudognaphalium arizonicum	annual forb	Native
Pseudognaphalium macounii	annual forb	Native
Psoralidium tenuiflorum	perennial forb	Native
Quercus gambelii	perennial tree	Native
Salsola tragus	annual forb	Non-native
Senecio spartioides	perennial forb	Native
Scabrethia scabra	perennial forb	Native
Stephanomeria pauciflora	perennial forb	Native
Taraxacum officinale	perennial forb	Non-native
Tragia ramosa	perennial forb	Native
Verbascum thapsus	biennial forb	Non-native
Vicia puchella	perennial forb	Native

APPENDIX 3: TRAIT VALUES AND NEIGHBORHOOD METRICS

Table 7: Average trait values for each species and environmental variables used in analysis for target individual neighborhoods. Full list of trait data can be found in the TRY database.

Species ID	Soil Temperature	Canopy Openness	Basal Diameter	Height	Leaf Area	Fresh leaf Weight	Dry Leaf Weight	LDMC	SLA
FEAR	85.47	92.05	14.3	44.15	6.4855	0.17066	0.054025	0.3161465	123.434572
MUVI	87.6925	97.1	15.9	52.15	7.826	0.14742	0.09369	0.4833634105	109.5666802
CEFE	87.525	93.45	N/A	48.8	0.7255	0.01682	0.006	0.3595068395	119.2604076

APPENDIX 4: ADDITIONAL STATISTICAL ANALYSIS OUTPUTS

Table 8: Dunn test with Bonferroni correction results for native and nonnative species, functional groups, and neighborhood diversity measurements.

Native vs. Nonnative Dunn Test		
2022	**Mean Rank. Diff.**	**P-Value**
Native		
L-H	23.817251	4.6e-06 ***
U-H	27.839474	2.4e-08 ***
U-L	4.022222	1
Nonnative		
L-H	-23.817251	4.6e-06 ***
U-H	-27.839474	2.4e-08 ***
U-L	-4.022222	1
2021		
Native		
L-H	24.625	1.4e-05 ***
U-H	33.425	1.6e-09 ***
U-L	8.8	0.3062
Nonnative		
L-H	-22.35	9.3e-05 ***
U-H	-31.35	1.5e-08 ***
U-L	-9	0.28
2020		
Native		
L-H	9.6	0.0292 *
U-H	11.1	0.0084 **
U-L	1.5	1
Nonnative		
L-H	N/A	N/A
U-H	N/A	N/A
U-L	N/A	N/A

Functional Group Dunn Test Results		
2022	**Mean Rank. Diff.**	**P-Value**

Annual Forb		
L-H	-17.93529	0.0021**
U-H	-28.33529	2.60E-07**
U-L	-10.4	0.1212
Biennial Forb		
L-H	-9.982353	0.1269
U-H	-23.882353	3.6e-06 ***
U-L	-13.9	0.0095 **
Perennial Forb		
L-H	N/A	N/A
U-H	N/A	N/A
U-L	N/A	N/A
Perennial Graminoid		
L-H	19.01618	0.0015 **
U-H	29.26618	2.4e-07 ***
U-L	10.25	0.1497
Woody		
L-H	N/A	N/A
U-H	N/A	N/A
U-L	N/A	N/A
2021		
Annual Forb		
L-H	-22.675	5.5e-05 ***
U-H	-29.45	7.9e-08 ***
U-L	-6.775	0.6017
Biennial Forb		
L-H	-13.4	0.0167 *
U-H	-22	1.6e-05 ***
U-L	-8.6	0.2254
Perennial Forb		
L-H	13.575	0.0332 *
U-H	5.475	0.9166
U-L	-8.1	0.3886
Perennial Graminoid		
L-H	22.55	0.00011 ***
U-H	34.9	5.4e-10 ***
U-L	12.35	0.07212

2022		
Annual Forb		
L-H	N/A	N/A
U-H	N/A	N/A
U-L	N/A	N/A
Biennial Forb		
L-H	N/A	N/A
U-H	N/A	N/A
U-L	N/A	N/A
Perennial Forb		
L-H	N/A	N/A
U-H	N/A	N/A
U-L	N/A	N/A
Perennial Graminoid		
L-H	17.45	0.00388 **
U-H	22.3	0.00012 ***
U-L	4.85	1
Woody		
L-H	N/A	N/A
U-H	N/A	N/A
U-L	N/A	N/A

Neighborhood Diversity Dunn Test		
Richness	**Mean Rank. Diff.**	**P-Value**
FEAR-CEFE	13.025	0.0487 *
MUVI-CEFE	2.275	1
MUVI-FEAR	-10.75	0.1418
Shannon Diversity		
FEAR-CEFE	10.15	0.1982
MUVI-CEFE	-5.65	0.9188
MUVI-FEAR	-15.8	0.0127 *
Evenness		
FEAR-CEFE	5.2	1
MUVI-CEFE	-10.3	0.1865
MUVI-FEAR	-15.5	0.0150 *