

DISSERTATION

QUANTIFYING THE BOTTLENECKS FOR WOODLAND RECOVERY

Submitted by

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ABSTRACT

QUANTIFYING THE BOTTLENECKS FOR WOODLAND RECOVERY

Fire regimes across the western US are changing and climate is becoming hotter and drier, challenging the ability of seed-obligate trees to regenerate. The recruitment of plant species is reliant upon certain conditions, like moisture, temperature, sunlight, factors that can collectively be referred to as the recruitment niche. In many ways, biotic interactions, like plant-plant or plant-microbe facilitation and competition, can increase or decrease the amount of stress a young tree is exposed to, and these biotic interactions are vastly changed in burned environments. Piñon pine and juniper (PJ) woodlands are an ideal ecosystem to study these kinds of interactions. In Chapter 1, I investigated the natural recovery of 25–27-year-old burned woodlands, to explore the role of proximity to seed source and the developing vegetation on inhibiting or assisting piñon and juniper tree recruitment. In Chapter 2, I conducted a planting study, where piñon seedlings were inoculated with soil from an unburned woodland to introduce ectomycorrhizal fungi to seedlings to Inoculated seedlings, along with non-inoculated seedlings, were grown in a greenhouse and then outplanted in a recent and an old fire. Seedlings were grown in natural conditions for 2 years; seedling height growth, survival, and soil fungal communities were assessed in the fall and spring of each year. Lastly, in Chapter 3, I expanded my study region to the broader southwest to understand implications of fire-driven vegetation conversion from forest to grassland or shrubland. Here, I selected six large wildfires that burned in 2002 and compared spatially-derived pre-fire, 1-year post-fire, and 20-years post-fire monthly and annual evapotranspiration. In all, this dissertation investigates bottlenecks to woodland

recovery, identifying factors that may cause prolonged piñon and juniper regeneration, and outlining how long-term changes to vegetation in the southwest influence ecosystem services like evapotranspiration.

Broadly, the three chapters aimed to assess how woodlands are currently recovering, what we can do to assist recovery, and what happens if forest recovery does not occur or our interventions do not work. I found that PJ woodland recovery is happening, but minimally and restricted to burned edges. Piñon and juniper recruitment mostly occurred under Gambel oak and downed logs. When conducting planting, we can facilitate recovery by planting under Gambel oak and logs to increase piñon survival, but longer timescales should be assessed before this is incorporated into management actions. While microbial inoculation may be a potential action, our findings showed that the source soil seedlings are planted into is more important than inoculation, and that inoculation did not have lasting effects on seedling survival. Lastly, using remote sensing products, we saw widespread vegetation conversion from forest to grassland or shrubland, and this was related to reduced evapotranspiration 20-years post-fire. This work demonstrates that decisions about post-fire restoration will influence not only vegetation recovery, but also long-term ecosystem processes such as evapotranspiration. As fire regimes continue to shift, understanding the mechanisms that constrain or facilitate recovery are critical for maintaining the structure and function of piñon-juniper woodlands, as well as other forest communities. This dissertation provides evidence that while recovery is increasingly uncertain, it is not uniformly constrained and that strategic management that works with, rather than against, existing biotic relationships can meaningfully influence post-fire vegetation trajectories.

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DEDICATION

To my grandparents, Jack (1929-2013) and Shirley (1930 - 2018) Norris, for instilling in me a love for things that grow.

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CHAPTER 1

Introduction

Since terrestrial plants entered the geological record, landscapes and vegetation dynamics have been shaped by, and have coevolved with, climate and disturbance (Bowman et al. 2009, Keeley et al. 2011). Disturbance, as defined by Picket and White (1985), are “relatively discrete events in time that disrupt an ecosystem, community, or population structure, and changes resources, substrate availability, or the physical environment.” Because disturbance and vegetation have influenced one another for millions of years, disturbances tend to occur in relatively predictable patterns and are characterized by specific regimes. Disturbance regimes are described by the distribution, frequency, return interval or cycle, rotation period, predictability, area/size, magnitude (including severity and intensity) and synergism (Picket and White 1985). Although these descriptors can fluctuate over time, they generally remain within a historic range of variability (Morgan et al. 1994) that allows for species across taxonomic kingdoms to adapt to them. In the western US, several disturbances are prevalent, however a disturbance which has had great shifts in its regime over the last several decades is wildfire.

Across the western US, fire regimes vary across different ecosystems, driven by topography, elevation gradients, climate, and vegetation types. Due to this diversity, different regions are experiencing different shifts in their fire regimes. For example, at higher elevations, some mixed conifer forests are experiencing fire at increased frequency (Stevens-Rumann and Morgan 2016, Turner et al. 2019). At lower elevations, ponderosa pine forests are burning at higher severity (McClure et al. 2024), with more homogenously burned patches (MacFarland et al. 2023), and piñon-juniper woodlands are burning larger areas (Board et al. 2018). Shifts in

regimes across different forest types can be attributed to factors that influence fuel build-up (such as fire suppression (Roos et al. 2020), grazing (Swetnam et al. 2016), removal of Indigenous peoples and cultural burning practices (Lake et al. 2017, Roos et al. 2021), and increasing aridity (including hotter and drier climate (Parks and Abatzoglou 2020, Crimmins et al. 2025, Parks et al. 2025), reduced snowpack, and earlier snowmelt (Balik et al. 2026)).

Because fire regimes and vegetation patterns are so tightly paired, any deviation in one can cause a shift in the other. If a fire event has characteristics within the historic range of variability (HRV), the landscape is thought to be more resilient to the event as opposed to landscapes that experience events outside of the HRV. Resilience, introduced by Holling in 1973, is the ability of an ecosystem to return to a similar functional state following a disturbance (Holling 1973). When we characterize resilience, often it is by considering whether ecological legacies remain to allow regeneration to occur (Johnstone et al. 2016). Examples of this are the presence and persistence of an aerial seed bank, suckering of resprouting trees, or patches small enough to be reseeded by nearby living trees.

When resilience is eroded – the aerial seed bank burns up and fire occurs too soon for seed production, fire burns too large of an area for seeds to disperse – the ecosystem runs the risk of converting to a different vegetation type. Vegetation type conversion, such as a forest or woodland transitioning to a shrubland or grassland (Falk et al. 2022, Guiterman et al. 2022), in some contexts, is a natural successional process and has occurred at different historical contexts. However, in contemporary situations, conversion is occurring at higher rates than what had historically occurred, and land management actions are largely unable to accommodate these persistent shifts (Coop et al. 2020). While shifting fire regimes is one cause for conversion, increasing aridity further limits post-fire regeneration of conifers (Stevens-Rumann et al. 2022,

Davis et al. 2023). Young seedlings are especially sensitive to hot and dry conditions than their older and mature counterparts, so even if tree recruitment initially occurs, it may fail due to seedlings dying from heat and moisture stress (Shiver et al. 2022, Stevens-Rumann et al. 2022).

Under changing fire regimes and intensifying climate, what are factors that increase the ability for ecosystems to recover? Often, when we consider regeneration and recruitment of trees, we look at the factors we can control through silvicultural practices: sunlight, substrate, moisture, and seed source (Nyland 2016). Expanding on this, we can call upon the recruitment niche, a framework introduced by Grubb (1977), which attempts to explain how certain species persist in different environments and how plant community assemblages are controlled. Broadly, it describes the abiotic and biotic conditions that are required for a species to germinate, emerge, survive, and establish (Grubb 1977). Variables associated with the regeneration niches of species include seed production, dispersal (temporal and spatial), germination (e.g. shade vs light, small vs large gaps, burial depth, soil chemistry, precipitation), and establishment (e.g. favorable surface type, light and water availability, predation and grazing, and presence of mutualisms) (Grubb 1977). When disturbance regimes and climate conditions that species are adapted to are altered, the niche available for seedlings to recruit in is also changed. This new environment may be outside of the conditions they have evolved to endure. When considering tree seeds and seedlings, this may be the distances seeds can disperse, the substrate that seeds are dispersed to (mineral vs organic, soil depth), the necessary abiotic conditions (water, temperature, soil moisture, solar radiation) the seedlings are exposed to, or even the biotic interactions the seedling experiences (herbivory, plant-plant facilitation and competition, plant-microbe facilitation or parasitism).

Biotic interactions are an interesting facet of the recruitment niche, because in some ways, it acts as a sliding scale of how much stress a tree seedling is exposed to. Plant-plant facilitation, such as nurse plants, can shade seedlings and decrease stress by increasing available moisture, decreasing exposure to solar radiation, and buffering from surface air temperature (Chambers et al. 1999, Pirtel et al. 2021, Shemesh 2025). On the opposite side of this spectrum, plant-plant competition, especially by non-native vegetation, increases the amount of stress that a seedling experiences, making nutrient- and water-limited habitats even more limited of these necessary resources (Kerns et al. 2020, Lazaro-Lobo et al. 2021). Plant-microbe facilitation is often looked at in the form of mycorrhizal fungi that form associations with tree (as well as other plants) roots. Mycorrhizal fungi are considered key filters for tree seedling establishment in many ecosystems (Tourville et al. 2024), as mycorrhizal-plant associations have evolved together over the course of a millennia (Brundrett 2002, Hoeksema et al. 2018). Generally, mycorrhizal fungi are poor decomposers, so in order to obtain carbon, they provide limiting nutrients (potassium and nitrogen) and water to plants in exchange for carbon in the form of photosynthesis derived byproducts (e.g. photosynthate) (Smith and Read 2010). Colonization by mycorrhizal symbionts can increase the water and nutrients tree seedlings and their limited root structures have access to.

A hot, dry, and nutrient-limited system (i.e., abiotically stressful), where tree regeneration relies on biotic interactions is piñon pine-juniper (PJ) woodlands. PJ is a prevalent ecosystem in the western US that spans over 40 million hectares. It is the third most common forest type in the US (Romme et al. 2009) and holds the highest amount of old growth and mature forests in the US (U.S. Forest Service 2024). PJ stand composition and structure varies across the landscape, where in Colorado, New Mexico, Utah, and Arizona, tree communities are generally comprised

of two-needle piñon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) or one-seed juniper (*Juniperus monosperma*). The understory of mature and intact persistent woodlands is relatively disconnected and consists of sparse shrub and perennial grass cover (Romme et al. 2009). This ecosystem lies on the ecotone boundary between forests and grasslands and occupies diverse and extreme climate conditions across its vast range (Redmond et al. 2023). While piñon and juniper are typically recognized as drought- and heat-tolerant, recent decades have shown their sensitivity to insect attacks and persistent extreme drought (Gaylord et al. 2013, McDowell et al. 2016, Shriver et al. 2022). This has led to widespread tree mortality, especially of piñon, in parts of its range.

Range-wide mortality of piñon pine and juniper, combined with increasingly hotter and drier environmental conditions, are expected to further exacerbate climate-driven ecosystem change (Williams et al. 2010, Shriver et al. 2022). Piñon-juniper systems are highly linked with climate conditions, with range contractions linked to hot and dry climate, and range expansion linked to cool and wet periods (Tauch 1999, Gray et al. 2006). With current intensifying climate conditions, research suggests that drought in these already water-limited systems may lead to over 50% mortality of piñon pine range-wide by 2100 (McDowell et al. 2016), with *Pinus edulis* and *Juniperus monosperma* being even more sensitive to intensifying conditions than other piñon-juniper woodland species (like *Pinus monophylla* and *Juniperus osteosperma*) (Noel et al. 2023). However, much of the research and projections in PJ contraction do not account for increases in wildfire activity and subsequent delayed regeneration or ecosystem conversion (Shriver et al. 2022, Redmond et al. 2023). Post-fire tree regeneration is critical to understand so we may recognize the potential, or lack thereof, for this ecosystem to persist on the landscape in the upcoming years. While great steps have been made to inform how woodlands recover and

respond following drought-induced mortality events (e.g., Mueller et al. 2005, Redmond and Barger 2013, Floyd et al. 2015, Redmond et al. 2015, Redmond et al. 2018), research looking into post-fire tree recovery and factors that can enhance recruitment in this system are still in its infancy.

While fire is a naturally occurring phenomenon that has long shaped vegetation dynamics, the ecological role of fire in PJ is less defined. Unlike many pines that exhibit a close evolutionary history with fire, piñon lack structural and life-history traits that would be considered fire-adaptive, and as such, are considered “fire-avoiders” (Keeley 2012). Within PJ woodlands, historic fire rotations are regionally variable, but are typically centuries long, ranging from 400 – 1400 years (e.g., Floyd et al. 2004; Floyd et al. 2017; Kennard and Moore 2013), with some woodlands exhibiting no evidence of fire (e.g., Kennard and Moore 2013). While large, high-severity fires were historically uncommon, fire itself was not. Lightning ignitions are prevalent, but due to the discontinuous fuel structure and the less-productive nature of this ecosystem especially in the southern Rockies, fire spread is typically limited to a single or small group of trees. Since the 1980s, PJ woodlands in the southwest have experienced increases in the size of fires (Board et al. 2018), including several recent uncharacteristically large and high-severity fires that burned through PJ and adjacent forests in 2020-2025 (e.g., Pine Gulch (Colorado, 2020), Hermits Peak/Calf Canyon (New Mexico, 2022), Black Fire (New Mexico, 2022), Telegraph Fire (Arizona, 2021), Lee Fire (Colorado, 2025) (<https://inciweb.wildfire.gov/>)). This is largely driven by conditions conducive for canopy fire spread (i.e. drought and wind) becoming more common.

Post-fire recovery of PJ is expected to take a long time (Vankat 2014), driven by episodic cone production (5-7 years) and piñon seedling recruitment pulses that occur during cool and wet

years (Gray et al. 2006, Barger et al. 2009). With that said, Floyd et al. (2021), Woolet et al. (2023), and Phillips et al. (2024) have all observed a lack of tree regeneration, several decades following fire, prompting concerns whether these woodlands may be experiencing vegetation-type conversions or if this is a typical time-lag for tree recovery. In the Great Basin region, Miller et al. (2015) outlined ecological site and pre-fire vegetation composition as primary drivers of post-fire resilience, and that fire severity, post-fire weather, post-fire management (e.g. grazing), and monitoring and adaptive management are factors that may modify potential resilience pathways in shrubland and piñon-juniper woodlands. While the Great Basin PJ ecosystems have different species composition and structure, these factors can also be applied to the PJ woodlands of the Colorado Plateau. Additionally, biotic factors such as seed availability and dispersal, nurse plant availability, the developing vegetation, and available microbial communities are also likely to drive resilience (Floyd et al. 2021, Redmond et al. 2023, Woolet et al. 2023, and Phillips et al. 2024, Trimber et al. 2026). Collectively these elements can be considered bottlenecks of recovery (Wooten et al. 2022), or conditions that may influence whether tree regeneration is likely to occur.

If tree recruitment continues to fail, what are the long-term consequences? This question can be considered from different perspectives, such as loss of biodiversity and cultural resources, changes in ecosystem productivity, energy balance, or hydrological processes (Breshears et al. 2011). Here, we consider what vegetation change means for ecosystem evapotranspiration (ET). ET is the combined loss of water via transpiration and evaporation, and is largely driven by plant type, net radiation, vapor pressure deficit (VPD), and wind (Zhang et al. 2001). Wildfire alters each of these drivers primarily by the removal of vegetation. In the short-term, high-severity wildfire shifts vegetation from high-transpiration plants like trees to lower-transpiration

vegetation like grasses and forbs (Goeking and Tarboton 2020). Because trees can take so long to mature, this effect can last for decades, and is highly correlated with fire severity (Poon and Kinoshita 2018, Ma et al. 2020). With that said, reduced transpiration from tree loss can be counteracted by increases in evaporation, which can also feedback into decreased tree recruitment. After wildfire, the removal of tree canopy increases net radiation to the forest floor, increases VPD, and decreases surface roughness and resistance which increases wind speed, all of which increase soil evaporation (Goeking and Tarboton 2020). Many of these changes are interrelated, for example, increased wind can further raise VPD by drying out soils more quickly and removing moist air. Therefore, when assessing fire-induced ET change, other aspects of the landscape need to be considered in addition to vegetation.

As persistent PJ woodlands are experiencing wildfires that are greater in size and face climate conditions that may restrict post-fire tree recruitment, we are likely to see this system moving beyond the recruitment niche necessary for tree reestablishment across its range. However, tree species do not exist in isolation, therefore it is crucial to consider biotic interactions that can alleviate increased stress and inform management strategies for restoration. To increase our understanding of post-fire recovery of PJ woodlands, I have identified overarching bottlenecks that may identify important aspects of the recruitment niche for piñon pine following wildfire and novel post-fire environmental conditions: *1) proximity to seed source (Chapter 2), 2) the developing vegetation community and microsite conditions (Chapter 2 and 3), and 3) the soil microbial community (Chapter 3)*. Further, expanding from PJ systems to the broader southwestern US, I conducted a study to assess the *broad ecosystem effects of vegetation change on the hydrological cycle, focusing on evapotranspiration (Chapter 4)*. By identifying

the factors that constrain or promote tree recruitment, land managers can better target restoration efforts and guide post-fire regeneration toward desired ecosystem conditions.

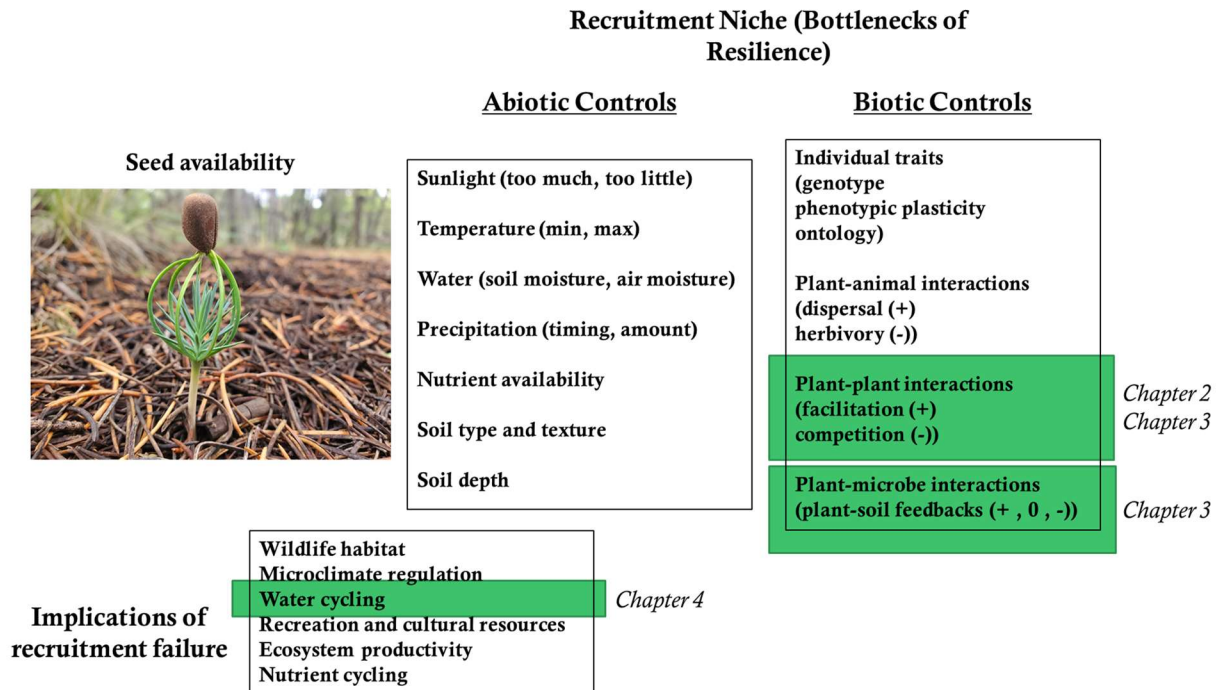


Figure 1. Conceptual diagram of abiotic and biotic factors that identify when and where seedlings are likely to germinate and survive. Assuming available seeds, species have a range of abiotic conditions that they are adapted to be successful under. For certain abiotic conditions, biotic interactions can control a species tolerance or intolerance of abiotic conditions. If recruitment does not occur, there are downstream effects on ecosystem services, a few which are listed. In italics are the chapters that investigate certain biotic controls (plant-plant interactions and plant-microbe interactions) and the consequence of vegetation type conversions on evapotranspiration.

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CHAPTER 2

Piñon pine and juniper seedling regeneration persists at burned edges but remains limited two decades after large wildfires

Abstract

Piñon-juniper woodlands, a prominent ecosystem in the southwest US, are undergoing significant ecosystem changes due to drought and fire. Concerns arise over lack of resilience, especially as this ecosystem experiences hotter and drier recovery conditions. To understand vegetation trajectories and to identify risk factors that may reduce tree seedling establishment, we examined three 25+ year old fires in western Colorado, USA and compared plant community recovery and tree establishment patterns in unburned, interior burned, and edge burned plots. Assessment included piñon and juniper seedling recovery and their microsite conditions, and plot structure, including percent cover of understory plant functional groups and fuel loading. We found that in burned plots, tree regeneration was highest in edge plots compared to interior plots. Seedlings were more often found under nurse objects, with more seedlings present under Gambel oak and logs compared to other nurse types. Our models indicated that piñon seedling presence was negatively associated with non-native plant cover and positively associated with the density of mature live piñon trees. Juniper seedling presence was positively associated with density of mature live juniper trees, as well as 1 hr and 10 hr fuels. Our findings suggest that recovery to a woodland structure may be prolonged, especially in large burned patches with limited seed sources and areas with high colonization of non-native plants.

Background

Across the western United States (US), climate change and past land management are driving larger and more severe wildfires (Parks and Abatzoglou 2020, Littell et al. 2016), altering post-fire recovery trajectories and limiting conifer regeneration (Davis et al. 2023). The combination of climate change and changing fire regimes impacts the resilience of many species and ecosystems (Johnstone et al. 2016). Ecological resilience is commonly thought of as the ability of an ecosystem to return to a similar functional state following a disturbance (Holling 1973). In this context, diminished resilience manifests as vegetation type conversion, such as a previously forested system growing post-disturbance as a shrubland or grassland (Coop et al. 2020, Falk et al. 2022, Guiterman et al. 2022). Diminished resilience may also arise as a change in species dominance while ecosystem structure is maintained (e.g. change in conifer species dominance or density but conifers still remain). Many dry, lower elevation forests and woodlands are at particular risk for vegetation-type conversion because these ecosystems are at the ecological limit of where trees can grow (Guiterman et al. 2022).

One such vegetation type is piñon pine and juniper (PJ) woodlands, which span over 40 million hectares across the southwestern US. PJ is the third most common forest cover type in the US (Romme et al. 2009) and holds the highest amount of old growth and mature forests and woodlands in the US (U.S. Forest Service 2024). PJ species composition and stand structure vary across its vast range, driven by seasonal precipitation patterns, temperature, and geomorphology (Romme et al. 2009). Across the west, there are 11 species of piñon and juniper, but in Colorado, the dominant tree species in PJ are two-needle piñon (*Pinus edulis* Engelm.) and Utah juniper (*Juniperus osteosperma* (Torr.) Little) in western Colorado or one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.) in southern Colorado. The understory of mature and intact

persistent woodlands is relatively discontinuous and consists of sparse shrub and perennial grass cover (Romme et al. 2009).

Although PJ woodlands provide an abundance of ecosystem benefits (Breshears et al. 2016), they are sometimes viewed negatively due to narratives of encroachment into rangelands, with management actions aimed at reducing tree abundance (e.g. Davies et al. 2011; Coates et al. 2017; Maestras et al. 2021). This perspective is relevant in regions where various piñon and juniper species, especially *P. monophylla* and *J. monosperma*, are expanding into deeper more productive soils, largely due to fire exclusion (Miller and Tausch 2001), and where expansion can displace habitat for species, like the Greater Sage Grouse. In other regions, including much of western Colorado, these woodlands have persisted for centuries, and the primary concern is not expansion but mortality, larger fires, and limited regeneration (Redmond et al. 2023).

Range-wide mortality of two-needle piñon pine is on the rise and is expected to be exacerbated by continued climate-driven ecosystem changes (Williams et al. 2010; Gaylord et al. 2013; McDowell et al. 2016; Shriver et al. 2022; Rodman et al. 2025). Some research suggests that prolonged drought in these already water-limited systems may lead to over 50% mortality of piñon pine by 2100 (McDowell et al. 2016). Of the piñon and juniper species, two-needle piñon and one-seed juniper are expected to be more affected by the intensifying conditions compared to the other PJ species (Noel et al. 2023). However, much of the research and projections of PJ reduction do not account for increases in wildfire activity and subsequent delayed regeneration (Shriver et al. 2022, Redmond et al. 2023, Rodman et al. 2025). Post-fire regeneration is critical to understand so we may recognize the potential for this woodland type to persist on the landscape in the upcoming years. While great steps have informed how woodlands recover and respond following drought-induced mortality events (e.g. Mueller et al. 2005, Redmond and

Barger 2013, Floyd et al. 2015, Redmond et al. 2015, Redmond et al. 2018), research investigating post-fire recovery in these systems is still in its infancy.

Fire is a naturally occurring phenomenon that has long influenced vegetation dynamics. However, its ecological role in PJ woodlands is less defined compared to other forest types. Unlike many pine species that have co-evolved with fire, piñon pines lack the structural and life-history traits typically associated with fire adaptation and can be considered “fire-avoiders” (Keeley 2012). Historic fire rotations within persistent PJ woodlands vary across the landscape, but in the Colorado Plateau, are generally long, occurring anywhere between 400 to 1,400 years (e.g., Floyd et al. 2004; Floyd et al. 2017; Kennard and Moore 2013), with some stands showing no evidence of large fire events (e.g., Kennard and Moore 2013). While wildfire ignitions are common in this region, the fuel structure and discontinuous understory (unlike PJ savannas and PJ shrublands) typically inhibit surface fire spread. Canopy fire spread usually only occurs during extremely hot and windy conditions (Romme et al. 2003). Surface and canopy fire tend to be absent on the shallow, rocky, and unproductive soils where mature and old growth woodlands are commonly found. On deeper, more productive soils that have more shrub cover, grass cover, and fine fuels, surface fire is more likely to spread, influencing the heterogeneous nature of many PJ stands with shrublands interspersed among woodlands (Miller et al. 2019).

The ecological role of fire in PJ woodlands, therefore, may be to help maintain uneven-aged stand structures and promote vertical and horizontal heterogeneity, features characteristic of many healthy woodlands (Huffman et al. 2009; Whitehair et al. 2024). Indeed, indigenous communities used fire in various ways, including to situate their home and villages, encourage ceremonial herbaceous plant growth, deter pests, and promote hunting (Jemez Mountains, NM; Roos et al. 2021). However, the removal of indigenous communities from the landscape, post-

colonial grazing practices, and climate change, have led to PJ woodlands in the southwestern US to experience increases in both the frequency and size of wildfires since the 1980s (Board et al. 2018). In PJ woodlands, the dry and windy weather that supports large fires, may also promote homogenous burn patterns due to the flammability of piñon and juniper trees, resulting in extensive high-severity patches (Floyd et al. 2004; McFarland et al. 2025).

Long-term post-fire studies have indicated that natural regeneration within large high-severity burn patches is quite rare. Floyd et al. (2021), Woolet et al. (2023), and Phillips et al. (2024) all report limited or absent two-needle piñon pine and Utah juniper tree regeneration more than 20 years after large fire events, suggesting a potential for vegetation-type conversion as climate becomes less suitable for these seedlings. In the Great Basin, Miller et al. (2014) identified ecological site characteristics and pre-fire vegetation composition as primary controls on post-fire resilience, or factors that may serve as useful indicators for recovery potential in PJ. Fire severity, post-fire weather, land management practices (e.g., grazing), and adaptive management strategies also influence resilience trajectories in PJ woodlands. Additionally, factors such as seed availability and dispersal, microclimate conditions, and the composition of the developing vegetation are likely to shape recovery outcomes, as supported by findings from other post-disturbance studies (Floyd et al. 2021; Redmond et al. 2023; Woolet et al. 2023; Phillips et al. 2024). Collectively, these elements represent potential “bottlenecks” to recovery (Wooten et al. 2022), or conditions that may constrain or enable future tree regeneration.

Seed production in neighboring unburned areas and dispersal of the seeds are required for seed-obligate tree species to reestablish into burned patches (Falk et al. 2022). For species that have large seeds, like piñon pine, animal-dispersal by birds and rodents is necessary to move seeds long distances from unburned woodlands to neighboring burned patches. Key bird

dispersers like Pinyon Jay (*Gymnorhinus cyanocephalus* Wied) and Clark's Nutcracker (*Nucifraga Columbiana* Wilson) have seen substantial declines in population, often linked to reductions in food availability (Boone et al. 2018, Schaming 2015). The reduction in food availability stems from persistent and intensifying drought in the western US (Williams et al. 2022) which has reduced piñon cone production (Zlotin and Parmenter 2008, Redmond et al. 2012) and frequency of cone masting events (Wion et al. 2019). Decreased seed production and seed dispersers limit the capacity of piñon to establish naturally, especially within fire footprints that are large in size. Juniper may have fewer seed-related constraints relative to piñon, as seeds are produced annually, can persist in the seedbank for several years (Chambers et al. 1999), and can be readily dispersed by birds and mammals (Salomonson 1978), including American Robin and other frugivores which may still use burned woodlands (Woolet et al. 2023).

If we ignore seed availability and dispersal limitations, abiotic conditions may limit the success for young trees to establish. There is growing understanding that while mature individuals occupy a larger climatic niche, juvenile climate niches may restrict the establishment or reestablishment of a species (Petrie et al. 2016, Kemp et al. 2019). This is especially true in burned areas that have high exposure of solar radiation due to the removal of the tree canopy (Von Arx et al. 2013, Holden et al. 2024). Biotic conditions, like nurse objects – plants or other landscape features that a seedling establishes underneath – can act as a buffer for harsh climatic conditions. Nurse objects create microclimates that shade seedlings from intense solar radiation and increase soil moisture available for the seedlings to use (Chambers et al. 1999; Pirtel et al. 2021, Redmond et al. 2023). Junipers tend to be less reliant on nurse objects and are often seen successful in interspace openings (Chambers et al. 1999). In disturbed PJ, Gambel oak (*Quercus gambelii* Nutt.) (Crockett and Hurteau 2022) has been shown to be a successful nurse plant for

two-needle piñon pine; other shrubs, like big sagebrush (*Artemisia tridentata* Nutt.) (Urza et al. 2019) could also be useful nurse plants as they are associated with increased *P. monophylla* seedling survival. Recent work in burned woodlands of the Great Basin by Reid (2024) show that any nurse object may be beneficial for planted *P. monophylla* seedlings. However, we lack an understanding of how two-needle piñon seedlings use other nurse objects that are available in burned patches. In all, this suggests that some amount of recovery may need to happen before site conditions are conducive for tree seedling establishment or that tree recovery may be more likely in locations that had low-severity fire and still contain pre-fire nurse objects.

Unlike native vegetation that can have facultative relationships with tree seedlings, non-native vegetation may inhibit tree seedling establishment by direct competition or by altering the biotic and abiotic environment (Lazaro-Lobo et al. 2021). In western dry forests and woodlands, one major concern is cheatgrass (*Bromus tectorum* L.), as it tends to quickly colonize disturbed patches due to increased availability of sunlight and nutrients, and due to their inherent resistance to warmer and drier climate (Kerns et al. 2020). Unfortunately, cheatgrass (and other non-native plants, especially those with rhizomatous root systems) are also linked to reduced piñon and juniper seedling establishment (Floyd et al. 2021; Phillips et al., 2024). Cheatgrass may inhibit tree seedling recruitment by utilizing water and other soil nutrients earlier in the growing season before native plants become active (Kerns et al. 2020). Cheatgrass may also alter the ectomycorrhizal community by reducing the abundance and colonization of beneficial ectomycorrhizal fungi which can cause a reduction in seedling biomass and resistance to drought (Trimber et al. 2026). Cheatgrass can alter the soil biotic environment (Reitstetter et al. 2022; Owen et al. 2013), further altering nutrient dynamics. Lastly, cheatgrass can change fire seasonality and frequency (Bradley et al. 2018) by drying out early in the season, its continuous

fuel structure, and its greater flammability (Fusco et al. 2019). Since frequent fires reset vegetation succession, sites with a high establishment of cheatgrass have a greater risk of converting to a non-native grassland state.

Post-wildfire recovery and resilience are rarely studied 25 or more years post-fire. In slow successional systems, like PJ woodlands, this time period is when an examination of vegetation trajectories can be assessed. Piñon and juniper trees are increasingly faced with interacting stressors such as increasing fire footprints, harsh climate, and non-native species establishment, which may influence patterns of post-fire regeneration. Our study aimed to investigate two-needle piñon pine and Utah juniper (hereafter piñon and juniper) seedling establishment in three 25-27 year old fires that burned PJ woodlands and investigate the roles that proximity to seed source and the developing vegetation have on tree seedling establishment. Specifically, this study had two main objectives: 1) identify and compare vegetation cover in edge and interior burned plots and in unburned reference plots, and compare native and non-native species establishment, 2) in the same plots, quantify piñon and juniper seedling regeneration and seedling microsite conditions and identify important biotic and abiotic variables that correlate with piñon and juniper seedling regeneration.

Methods

Site Selection

We identified three fires that burned piñon-juniper woodlands in western Colorado, USA between 1994 – 1996; the Disappointment Fire, Hatchet Fire, and Wray Fire (Table 1, Figure 1). Fires were selected based on having burned in predominantly two-needle piñon pine and Utah juniper with few ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) present. We estimate that woodlands had minimal pre-fire tree death caused by drought or bark beetle, as identified by

investigating burned snags and looking for beetle exit holes. Climate conditions (average annual precipitation and average annual temperature) are recorded from the nearest NOAA weather station from 1991 - 2020 (Wray – Paradox 2N station, Hatchet – Altenbern station, Disappointment – Yellow Jacket 2W station <https://www.ncei.noaa.gov/access/us-climate-normals/>).

Table 1. Fires selected for study with the fire duration (date the fire ignited and date the fire was contained), size of the fire (ha), percent classified as moderate/high severity (via dNBR fire severity imagery from Monitoring Trends in Burn Severity (Eidenshink et al. 2007 [https://www.mtbs.gov])), percent classified as low severity/unburned, and the land management agency (Bureau of Land Management (BLM), or United States Forest Service (USFS)).

Fire Name	Fire Duration (start and end date)	Size (ha)	% Moderate and High Severity	% Low Severity and Unburned	Land Mgmt Agency	Annual precipitation (cm)	Annual temperature (°C)
Wray	7/13/1994 – 7/18/1994	700.1	86%	14%	BLM	33.32	10.33
Hatchet	7/23/1996 – 9/17/1996	2,300.6	71%	28%	BLM	43.36	8.56
Disappointment	7/20/1996 – 8/3/1996	1,473.8	44%	50%	USFS	38.18	9.72

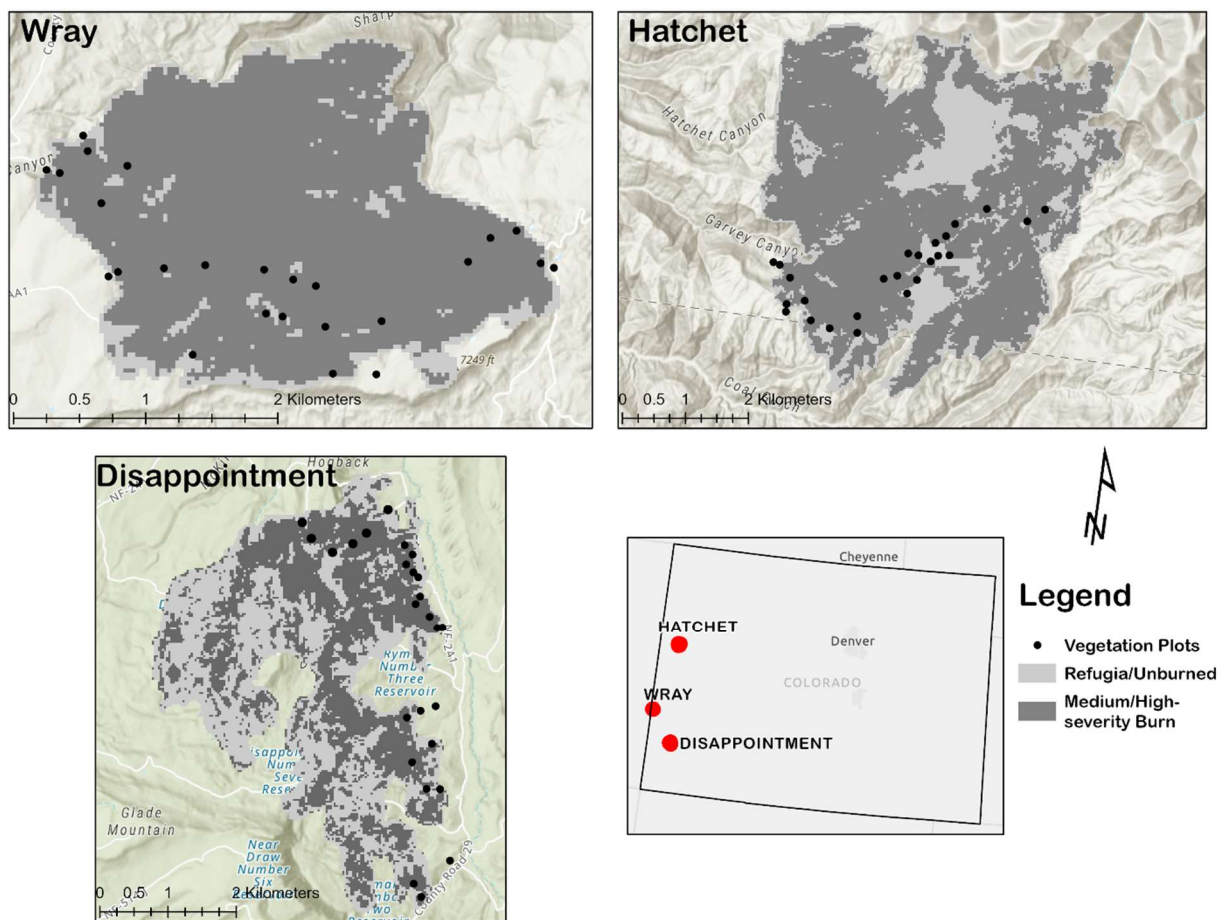


Figure 1. Map of the three fires included in this study and the locations for vegetation plots (black circles) in western Colorado, USA. Dark grey indicates regions that burned at moderate and high severity and light grey indicates areas of refugia (burned at low severity or unburned) within the fire according to dNBR fire severity imagery from Monitoring Trends in Burn Severity (Eidenshink et al. 2007 [<https://www.mtbs.gov>]) which was later confirmed in the field. Maps were created in ArcGIS Pro (ESRI, 2025).

All fires were natural ignitions, with Disappointment Fire reported as lightning ignited (National Interagency Fire Center 2024). Fire ignition date, containment date, area burned, and fire severity proportions are listed in Table 1. The ignition date for all fires indicated typical seasonality expected of this region. The Wray Fire seemed to exhibit the most extreme fire behavior of the fires studied, burning for five days and consuming over 700 hectares at overall moderate/high severity. The Hatchet Fire has large contiguous areas of moderate/high severity burn, with one large patch of low severity/unburned in the north-central region of the burn scar.

The Disappointment Fire had the highest amount of patchiness, with most of the fire burning at moderate/high severity on the eastern half of the fire, and low severity/unburned patches on the western half (Figure 1).

The Disappointment Fire and the Hatchet Fire both had no recorded post-fire treatments, based on U.S. Geological Survey Land Treatment Digital Library records (USGS LTDL; Pilliord and Welty 2013). About two-thirds of the Wray Fire was seeded by air in 1994 with a mostly native seed mix consisting of western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve), slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners), indian ricegrass (*Achnatherum hymenoides* (Roem. & Schult.) Barkworth), needle & thread grass (*Hesperostipa comata* (Trin. & Rupr.) Barkworth), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), galleta (*Pleuraphis* Torr.), sulphur buckwheat (*Eriogonum umbellatum* Torr.), Rocky Mountain penstemon (*Penstemon strictus* Benth.), winter rye (*Secale cereal* L.), and alsike clover (*Trifolium hybridum* L.).

Dominant soil types were Entisols, Mollisols, and Inceptisols in the Disappointment Fire, Entisols and Mollisols in the Hatchet Fire; and Mollisols, Inceptisols, and Aridisols in the Wray Fire (Soil Survey Staff, Natural Resources Conservation Service 2025; Table A1.1).

At each fire, we randomly selected 10-12 edge plots, 10-12 interior plots, and 5 unburned plots. Edge plots were randomly selected *a priori* via remote imagery and validated in the field; interior plots were selected in the field by walking towards the interior of the burned patch from the edge a random number of steps between 100-200. Edge plots were located within a burned patch, where the outer edge of the plot was within 2 m of an intact woodland; occasionally trees were present in the plot. Interior plots were fully within a burned patch. We aimed for interior plots to be 100 m or more away from an unburned edge or fire refugia. In some cases, most

notably within the Disappointment Fire, interior plots were located within 50 m of an unburned patch due to the heterogeneity of that fire. Unburned plots were either located near but outside of the fire perimeter or were located within the fire in patches of fire refugia (hereafter refugia). We define refugia as unburned or low severity burned islands within the fire perimeter (Meddens et al. 2018) which serve as live tree seed-sources and as refuge for fire-sensitive and forest-dependent wildlife (Robinson et al. 2014, Steenvoorden et al. 2019). Refugia showed no visible evidence of fire effects in remotely sensed imagery and in field assessments. The refugia patches selected exhibited overstory structure, understory vegetation structure, and fuel characteristics indistinguishable from unburned plots outside the fire perimeter. This is consistent with previous research done by our group which showed that PJ woodland refugia in this region (western Colorado) have comparable forest stand structure to unburned patches and fulfill a similar ecological role as unburned areas outside fires (Woolet et al. 2023).

Field Methods

We sampled all plots from May through July in 2023. We established a total of 76 circular 0.05 ha plots in interior ($n = 30$), edge ($n = 31$), and unburned ($n = 15$) areas by directing 12.5 m transects in the cardinal directions from plot center. At plot center, we recorded GPS coordinates, elevation, slope, and aspect. The distances to the nearest ten live piñon and juniper trees from plot center were measured using a rangefinder, if located outside of the plot, with 200 m the maximum distance measured (as limited by the rangefinder capabilities).

Along transects, substrate cover type (litter, rock, and soil) and vegetation cover were measured using line-point intercept at 0.5 m intervals along the four transects, totaling 96 measurements per plot. For vegetation cover, we identified intersections of the top three plants from breast height (1.3 m). For the herbaceous and woody plants that intersected the transect,

individuals were identified to genus or family, and where possible species. Downed woody fuels were assessed via Brown's transects (Brown 1974). Briefly, 1 hr (<0.6 cm diameter) fuels were counted along the first 6 m of each transect, and 10 hr (0.6 – 2.5 cm diameter) and 100 hr (2.5 – 8.0 cm diameter) fuels were counted along the entire length of each transect.

In the entire plot, natural tree regeneration was surveyed by recording the species, height, and diameter of all piñon and juniper seedlings. Microsite conditions at each tree seedling were estimated by noting the aspect, slope, and ground depression (present or not present) – which was defined as a dip in the soil where water could collect- as well as recording the type of nurse object the seedling is under (e.g. log, rock, plant species). When multiple nurse objects were present, the tallest (i.e. the nurse object that offers the most shading) was recorded. Coarse woody fuels (1000 hr; >7.62 cm) were measured by recording the diameter of each end and measuring the length that was within the plot. To assess pre-fire tree density in each plot, we recorded all live and dead tree species, and noted their age class (immature (<8 cm diameter) or mature) and mortality class (live, dead, partially dead). We counted all stumps in the plot, but species were not identified due to decay.

Data Analysis

We analyzed all data in R (version 4.5.1, R Core Team 2025) in R Studio (2025.05.1, Posit team 2025) using R package `tidyverse` (Wickham et al. 2019) for data manipulation and visualization.

Substrate characteristics and stand structure

We used linear regression and posthoc TukeyHSD pairwise comparisons (using `emmeans` (Lenth 2025) and `multcompView` (Graves et al. 2024)) to assess differences in percent surface substrate cover (rock, soil, and litter) in interior, edge, and unburned plots.

Mixed-effects models using `lme4` (Bates et al. 2015) package were used to assess differences in forest structure (stump ha^{-1} , dead juniper trees ha^{-1} , dead piñon trees ha^{-1} , live juniper trees ha^{-1} , live piñon trees ha^{-1} , total trees ha^{-1} (a sum of stumps, live, and dead trees), average distance to live juniper trees (m), and average distance to live piñon trees (m)). Treatment (unburned, edge, and interior) was the fixed effect for the models and fire (Wray, Hatchet, Disappointment) was the random effect for the model to account for potential differences across fires.

Vegetation cover and fuel structure of edge, interior, and unburned plots

Plant taxa were organized into vegetation groups based on growth forms: forbs, grasses, shrubs, and other plants (a combination of less-encountered genera such as sedges, rushes, and cacti). Plant taxa were also organized into native and non-native categories. Percent cover of vegetation groups were assessed by tallying the number of total line-point intercept hits per group and dividing by the total observation points (96). Since the top three plants were recorded at each observation point along the transect, percent cover had the potential to be up to 300%. Downed fine woody fuel (1 hr, 10 hr, and 100 hr) and coarse woody debris (1000 hr) loading were calculated using Brown (1974) equations.

Kruskal-Wallis tests were conducted to compare differences in percent cover of vegetation groups in edge, interior, and unburned plots and analysis of variance (ANOVA) tests were used to compare differences in downed woody fuel loading in edge, interior, and unburned plots. The `vegan` package (Dixon 2003) was used to evaluate differences in overall plot structure, including downed woody fuel loading and vegetation-group percent cover, among status categories (burned vs. unburned), treatment groups (edge, interior, and unburned), and among the three fires by calculating Bray–Curtis dissimilarity distances and visualizing with non-metric multidimensional scaling (NMDS). Permutational multivariate analysis of variance

(PERMANOVA) was conducted using the “adonis2” function to test for differences in Bray–Curtis dissimilarity distances among the three groups. The “envfit” function was used to assess which variables were strong predictors for driving differences in plot structure.

Seedling regeneration and microsite conditions in edge, interior, and unburned plots

Kruskal-Wallis tests were used to compare seedling densities (ha^{-1}) in edge versus interior versus unburned plots. Because pair-wise comparisons may not pick up differences in burned plots (due to the high number of seedlings in the unburned plots), we used Mann-Whitney U tests to compare seedling densities in edge versus interior plots.

To determine differences in nursed versus not nursed tree seedlings, the total number of piñon or juniper seedlings in each plot was summed and the proportion of piñon or juniper seedlings that were either nursed or not nursed were calculated. Two-tailed t-tests were used to test for differences in proportion of seedlings found under nursed object per plot *versus* proportion of seedlings not found under a nurse object per plot.

In burned plots (a combination of interior and edge), we used the `electivity` package (Quintans 2025) to calculate Ivlev’s Electivity Index (E) and Vanderploeg and Scavia’s Relativized Electivity (E^*) of piñon and juniper seedlings under the different nurse object types they were found under (Gambel oak, shrub, log/snag, rock, grass, other (in this case, “other” included plants within the genera *Opuntia* and *Heterotheca*), and none). E , introduced by Ivlev (1961), is commonly associated with animal foraging preferences. E , therefore, accounts for plot to plot differences and nurse type cover. E^* builds on Ivlev’s index by taking into account relative abundances of other resources within the plot. In combination, these two indices can describe optimal nurse object type by relating proportion of nurse object use to the availability of the nurse object in each plot. For piñon and juniper seedlings separately, we grouped the data by

each nurse object type, then calculated total seedling counts ("use") and mean percent cover of each nurse type ("availability"). Note that, while Gambel oak was grouped with percent shrub cover for vegetation analysis, it was grouped into its own category for nurse object electivity by subtracting the percent cover from the total percent shrub cover. While various shrub species were observed as nurse objects (e.g. *Amelanchier utahensis*, *Artemesia tridentata*, and *Cercocarpus montanus*), the individual species lacked the abundance to be included in the model on their own. We relativized "use" by calculating the proportion of total use and availability for each category within each treatment, producing proportional use (r) and availability (p) metrics. These proportions were used as inputs for the electivity index calculations, allowing us to assess whether seedling presence occurred more or less frequently than expected based on nurse object availability. We report E and E^* as these metrics best aligned with our study objectives (Lechowicz 1982). Both indices range from -1 (complete avoidance, or less seedling presence) to $+1$ (strong preference, or more seedling presence).

Important biotic and abiotic factors supporting or prohibiting seedling recovery

We employed the `tidymodels` package (Kuhn and Wickham 2020) to conduct random forest modeling, aiming to identify the key variables influencing seedling establishment across all plots (burned and unburned) and seedling establishment in burned plots. In total, we developed four random forest models, two for piñon seedling density (all plots and in only burned plots) and two for juniper seedling density (all plots and in only burned plots). Initial predictor variables included in the models were elevation, slope, folded aspect, stumps ha^{-1} , dead juniper ha^{-1} , dead piñon ha^{-1} , live juniper ha^{-1} , live piñon ha^{-1} , distance to unburned edge (spatially-calculated via burn severity metrics, as a proxy for distance to live seed source), percent cover of rock, soil, and litter, down woody fuel loading for the different size classes

(1000 hr, 100 hr, 10 hr, and 1 hr, measured in Mg ha^{-1}), percent cover of shrubs, grasses, forbs, and non-native plants, soil order type (Entisol, Inceptisol/Entisol, Inceptisol, Mollisol, Mollisol/Inceptisol, Rock, Entisol/Mollisol), depth to restrictive layer (0, 30, 33, 81, 94, 200 m), and surface soil texture (Gravelly clay loam, Clay loam, Stony clay loam, Loam, Unweathered bedrock, Gravelly loam). Before analysis, we transformed the aspect (in degrees) into folded aspect to estimate the heat load index using the following equation from McCune and Keon (2002): $\text{Folded Aspect} = |180 - |\text{Aspect} - 225||$. Higher folded aspect values indicate southwest slopes and greater heat load. To spatially calculate distances to unburned edge (because field measurements were limited to 200 m), we used burn severity `dnbr6` rasters from Monitoring Trends in Burn Severity (MTBS; Eidenshink et al. 2007 [<https://www.mtbs.gov>]) for each fire, and calculated the mean Euclidean distances of each pixel (30 m resolution) to unburned and low-severity pixels in R (Figure A1.1).

Prior to random forest analysis, we used the `corrr` package (Kuhn et al. 2022) to test for correlated variables to exclude from the analysis using $r > 0.7$ as the threshold. Soil and litter and grass and non-native plants were correlated. Litter and grass were removed from the predictor list as these variables had less explanatory power. The datasets were divided into training (75%) and testing (25%) sets. Model development was conducted on the training data and final performance was evaluated on the test set. To identify most informative predictors, we conducted forward feature selection using the “`ffs`” function from the `CAST` package (Meyer et al. 2026). This function iteratively adds predictor variables based on improvements in model performance based on root mean squared error (RMSE) with 5-fold cross validation. Using the best predictors, we followed the `tidymodels` framework for selection of hyperparameters. Models hyperparameters were tuned by testing “`mtry`” values of 2, 3, 4, and the number of “`tree`” values

of 250, 500 and 1000. Performance of hyperparameters were assessed with 5-fold cross-validation on the training set. The `mtry` parameter controls how much randomness is added to the decision tree creation process by controlling the number of input features a decision tree can consider at each split. The number of trees determines the number of decision trees that are combined to create the final prediction. The optimal models were selected based on their cross-validated performance, prioritizing models with higher R^2 and lower mean squared error (MSE) values. From the random forest model output, we visualized the effect and direction of each variable using partial dependence plots using the `iml` package (Molnar et al. 2018). Then, we calculated the Kendall's Tau correlation to determine significance of the variable's effect on seedling density. Kendall's Tau was used (instead of similar correlation test like Spearman's Rank), because this test tends to be more robust for small sample sizes and for data with ties.

Results

Substrate characteristics and stand structure

Substrate characteristics (% rock, soil, and litter) were similar in edge, interior, and unburned plots ($p > 0.05$; Table 2, Table A1.2).

Table 2. The mean (sd) percent cover of substrate types (% rock, soil, and litter) in burned interior, burned edge, and unburned plots.

	Substrate Characteristics		
	Rock	Soil	Litter
Unburned	8.0 (2.0)	25.9 (4.0)	64.8 (4.1)
Burned Edge	7.2 (1.4)	27.0 (2.8)	65.5 (2.9)
Burned Interior	4.5 (1.4)	30.3 (2.8)	64.9 (2.9)

For mixed models comparing stand structure variables, fire-to-fire variation was generally low relative to the residual variance across most of the models, indicating that variability occurred within fires (i.e. across treatments) rather than among fires (Figure 2, Table

A1.3). Unburned plots and reconstruction of burned plots indicate that study sites had (or still have) both piñon and juniper. Overall, fire significantly altered stand structure: burned treatments had higher number of stumps (edge: $p = 0.001$; interior: $p = 0.002$) and standing dead juniper trees (edge: $p = 0.026$; interior: $p = 0.004$) relative to unburned plots. In contrast, burned plots had fewer standing dead piñon trees (edge: $p < 0.001$; interior: $p = 0.001$), living juniper trees (edge: $p < 0.001$; interior: $p < 0.001$), living piñon trees (edge: $p < 0.001$; interior: $p < 0.001$), and total (living + dead) trees (edge: $p = 0.026$; interior: $p = 0.004$) relative to unburned plots. Distances to live piñon and juniper increased with burned treatments, with strongest effects in the interior burned plots (piñon: $p < 0.001$; juniper: $p < 0.001$). While burned plots had fewer standing dead piñon trees, this likely reflects differences in snag persistence, as dead piñon tend to fall within years while junipers remain standing for decades (personal observations). Therefore, many of the stumps recorded were likely piñon pine.

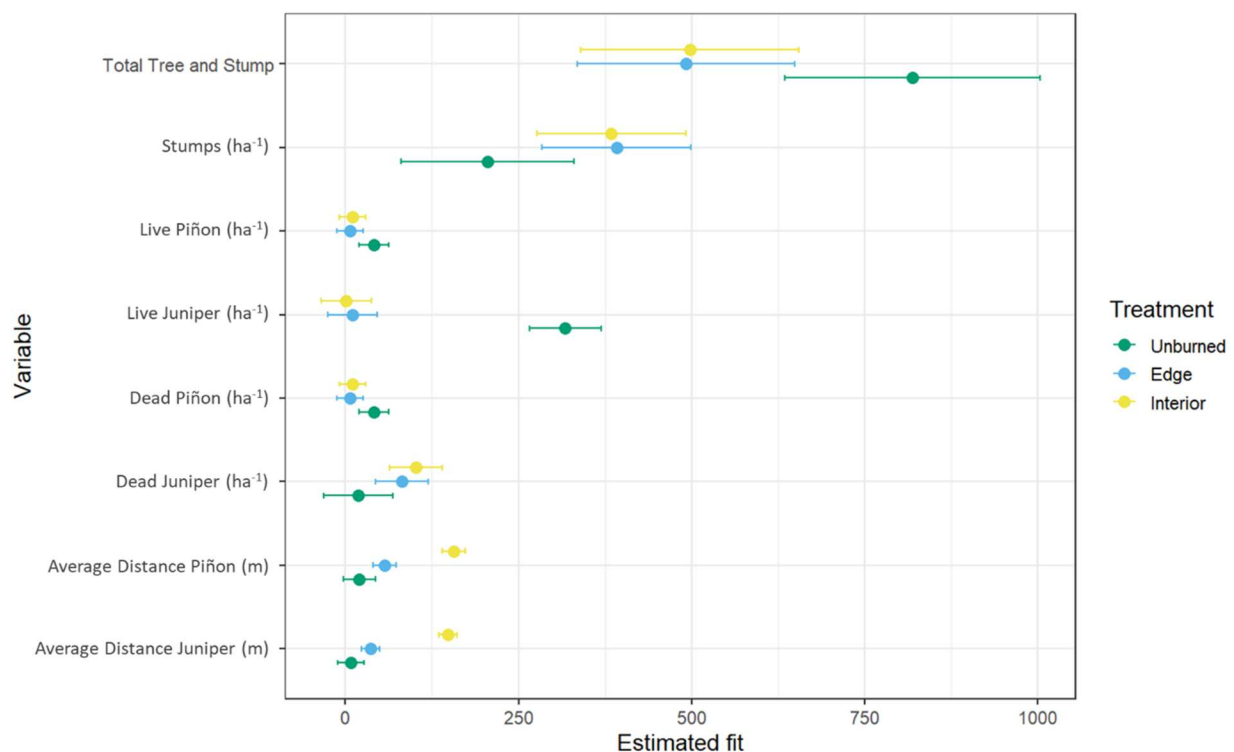


Figure 2. Graphical representation of mixed effects model for stand structure variables in unburned (green), edge burned (blue), and interior burned (yellow) with the model estimates and standard error.

Vegetation cover and fuel structure of edge, interior, and unburned plots

There were a total of 5,068 plant observations along the transects. Of the observations, 37% were grasses, 33% were shrubs, 27% were forbs, 1% were trees, and 0.6% were other. Additionally, 68% of the observations were native plants, 29% were non-native, and 3% were unknown. Edge and interior plots had less bareground and higher grass, forb, and shrub cover compared to unburned plots, though did not differ between interior versus edge plots ($p < 0.01$ for all; Figure 3, Table A1.4). There was no significant difference in percent cover of other ($p = 0.894$).

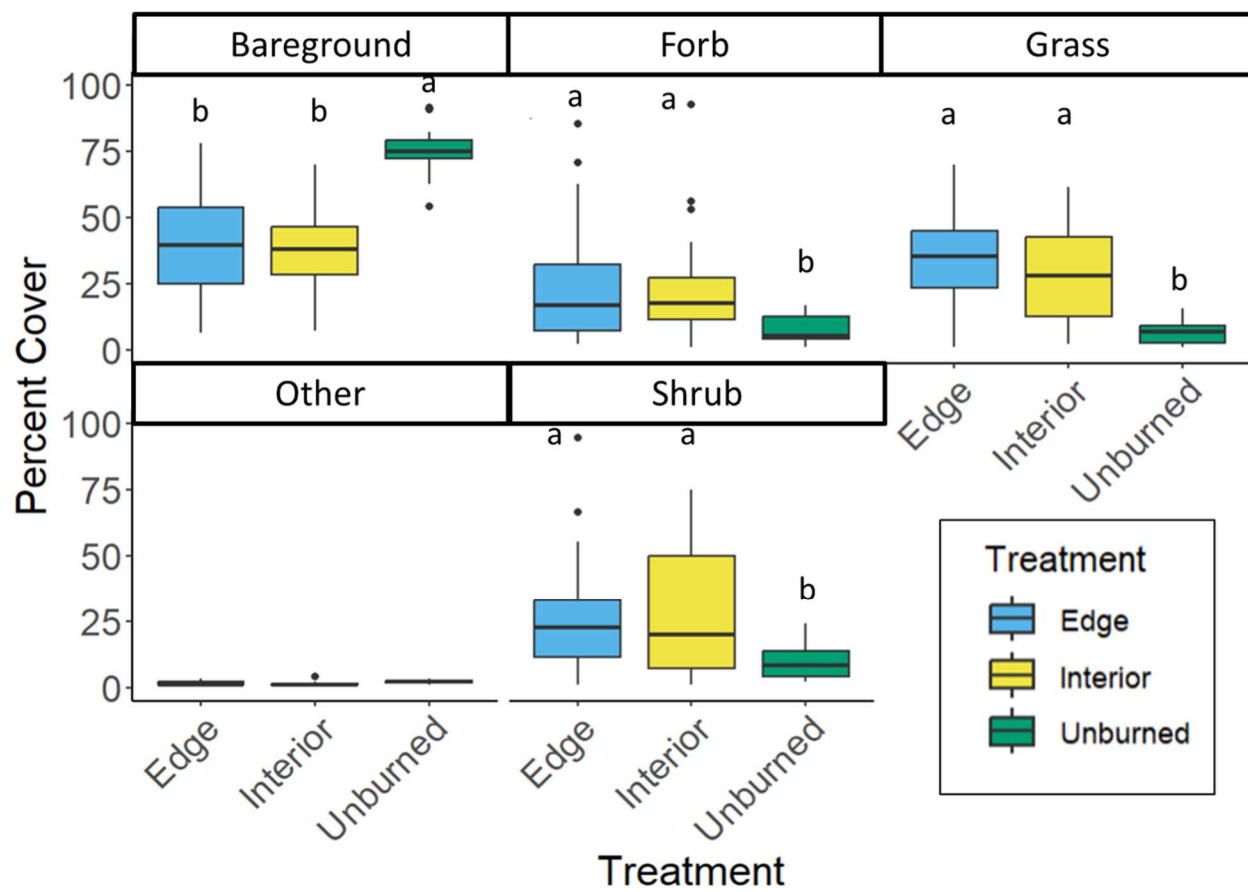


Figure 3. Boxplots representing differences in percent cover for the different treatments (blue = burned edge, yellow = burned interior, and green = unburned) across vegetation functional groups: percent bareground, grass, forb, shrub, and other.

There were no significant differences across treatments for 10 hr, 100 hr, and 1000 hr fuel loading ($p > 0.08$ for all; Table A1.5). Unburned plots had greater 1 hr fuels compared to edge and interior plots ($p < 0.001$).

NMDS plots of plot structure (1 hr, 10 hr, 100 hr, and 1000 hr fuel loading and percent cover of shrubs, grasses, and forbs) and subsequent statistics on the Bray-Curtis distances show significant differences in plot structure, with clustering within treatments, fires, and status (burned vs unburned) ($p = 0.001$ for all; Figure 4, Table A1.6). Variables that were strong drivers for differences in plots were 1 hr fuel loading, shrub cover, forb cover, grass cover, and 1000 hr fuel loading.

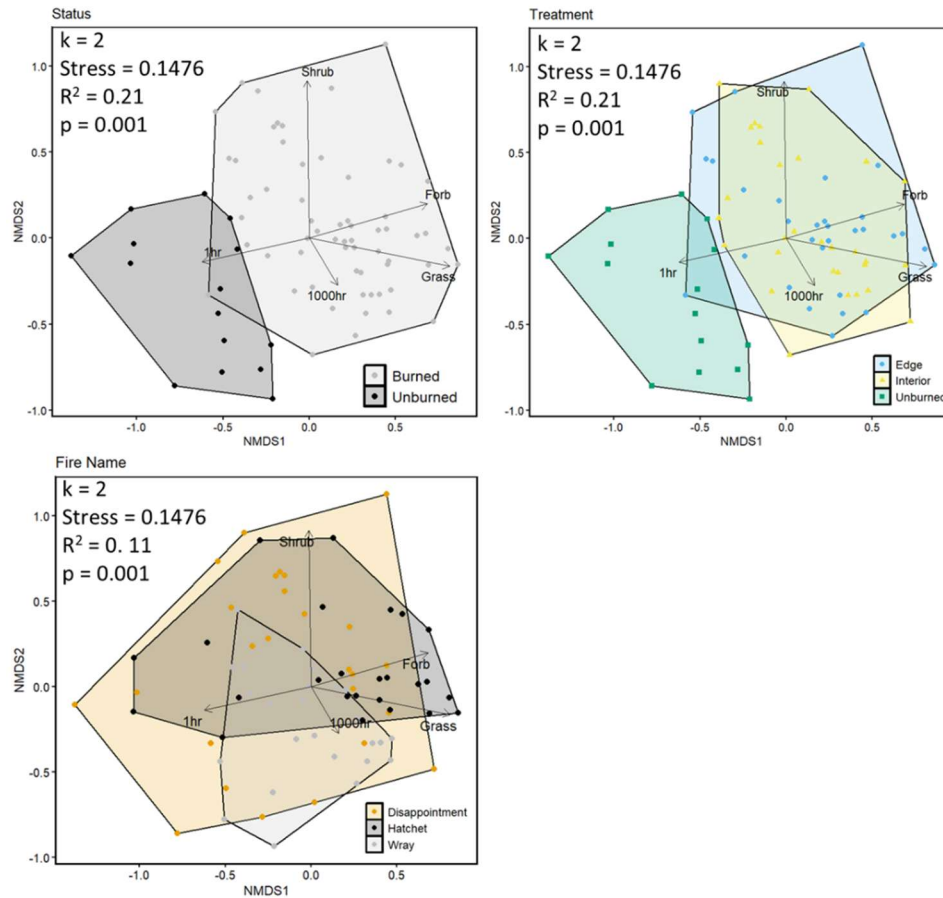


Figure 4. Non-metric Multidimensional Scaling (NMDS) plot of Bray-Curtis dissimilarity distances assessing overall plot structure, including downed woody fuel loading Mg ha^{-1} (1 hr, 10 hr, 100 hr, and 1000 hr) and percent cover of vegetation groups (shrub, grass, forb), for (a) status (grey = burned, black = unburned), (b) treatment type (blue = burned edge, yellow = burned interior, and green = unburned) and (c) fire (orange = Disappointment, black = Hatchet, and grey = Wray).

Non-native species establishment in edge, interior, and unburned plots

Percent cover of non-native plants ranged from 0 - 86.46% in edge plots, 0 – 87.5% in interior plots, and 0 – 6.25% in unburned plots. Percent cover of non-native plants was higher in edge and interior burned plots compared to unburned plots ($p < 0.001$; Table A1.4).

Seedling regeneration and microsite conditions in edge, interior, and unburned plots

Across all 76 plots, 33% lacked seedlings, 10% had only piñon present (at least one seedling), 16% had only juniper present (at least one seedling), and 41% had both piñon and juniper present. Across the 61 burned plots, 41% lacked seedlings, 10% had piñon-only regeneration, 20% had juniper-only regeneration, and 28% had both piñon and juniper present. Piñon and juniper seedling densities in edge plots (0 - 120 piñon seedlings ha^{-1} , 0-240 juniper seedlings ha^{-1}), interior plots (0 - 40 piñon seedlings ha^{-1} , 0 - 120 juniper seedlings ha^{-1}), and unburned plots (40 - 640 piñon seedlings ha^{-1} , 0 - 960 juniper seedlings ha^{-1}) were highest in unburned plots (Figure 5, Table A1.4). When comparing interior versus edge plots, piñon and juniper seedling densities were higher in edge plots compared to interior plots ($p = 0.01$ and $p = 0.001$, respectively).

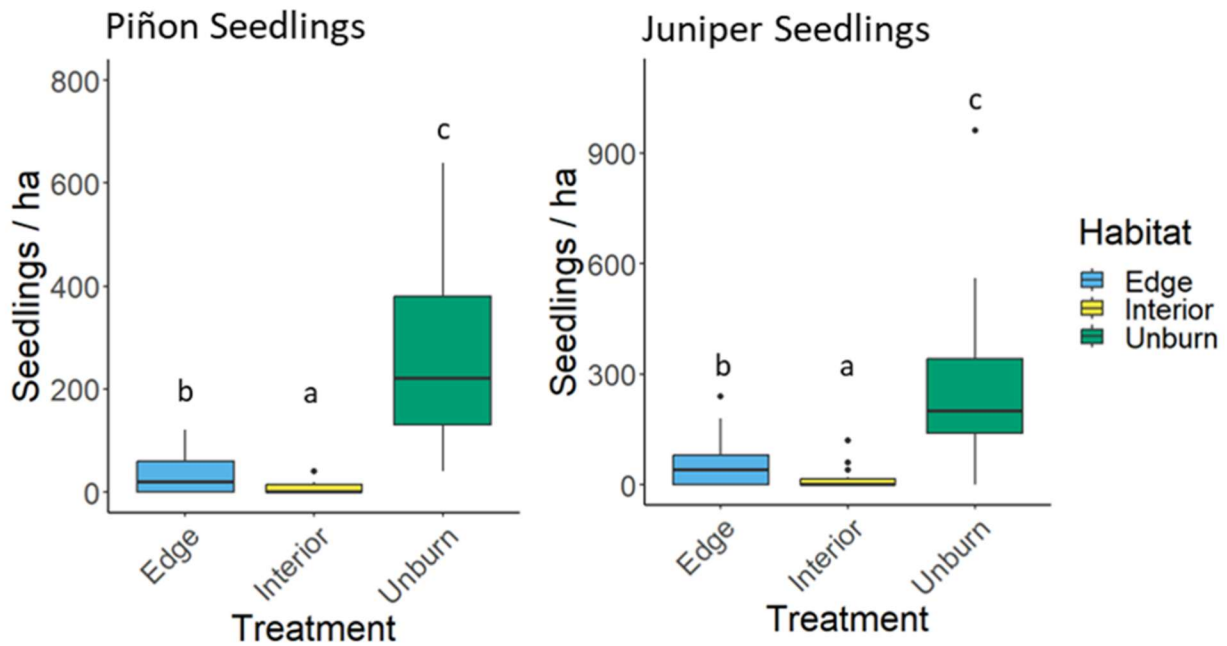


Figure 5. Piñon pine and juniper seedling densities (ha^{-1}) across all fires in edge burned (blue), interior burned (yellow), and unburned (green) plots. Letters indicate significant differences in seedling density across habitat types.

Across all plots, a higher proportion of piñon (85%) and juniper (75%) seedlings were found under nurse objects compared to not under a nurse ($p < 0.001$ for both; Table A1.7). *E* of piñon seedlings in burned plots revealed greater presence of seedlings under Gambel oak and nurse types in the other category, moderate presence under logs and rocks, and less presence under shrubs and bareground (Figure 6). *E* for juniper seedlings revealed more seedling presence under Gambel oak, neutral presence under shrubs, moderate presence under other and logs, and less presence under rocks and bareground. *E** values indicated that piñon seedlings had moderate presence under Gambel oak and other, less presence under rocks and shrubs, and nearly no presence in bareground. *E** for juniper seedlings revealed moderate presence under Gambel oak and other, and less seedling presence under for shrubs, rocks, and bareground.

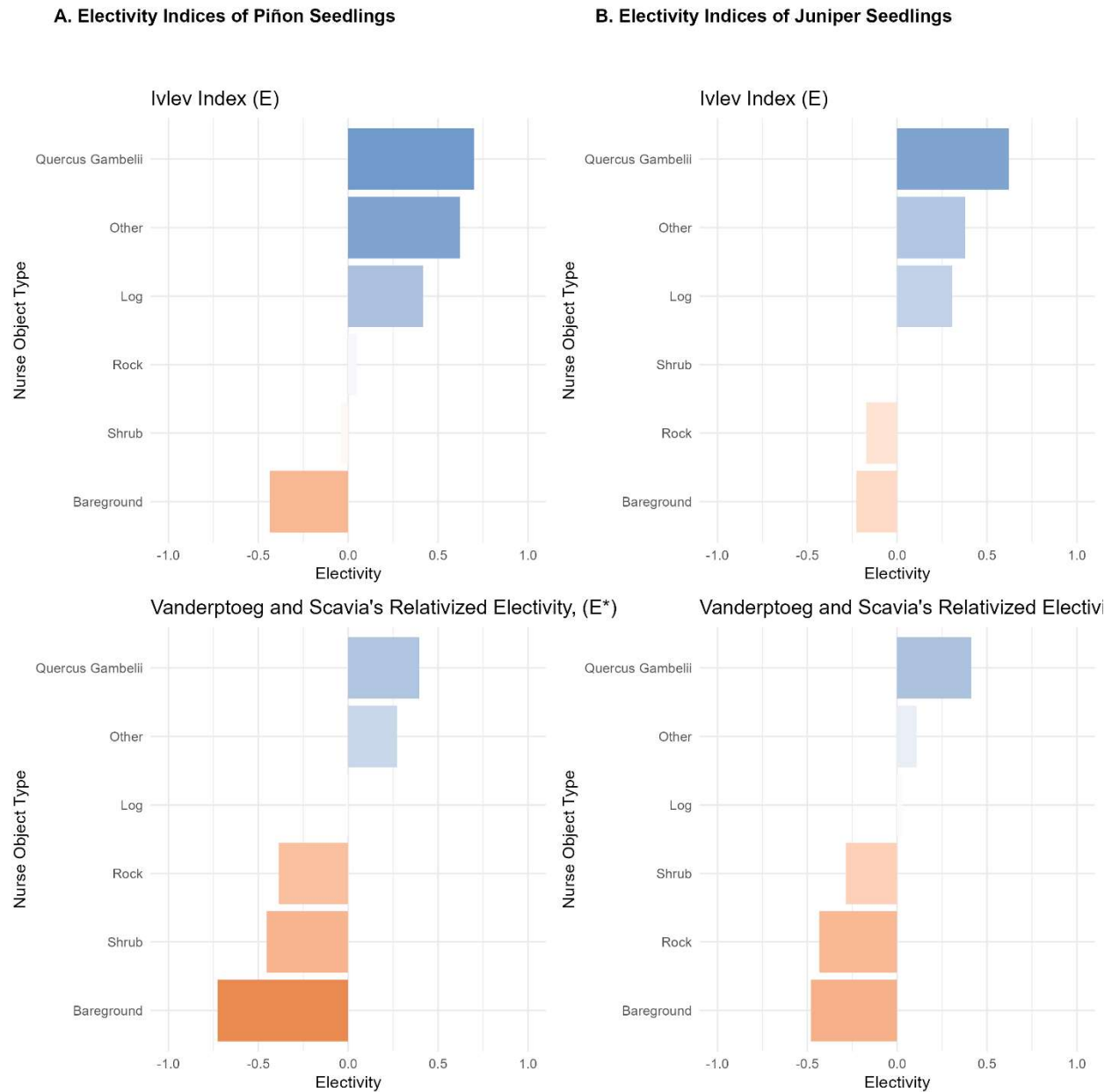


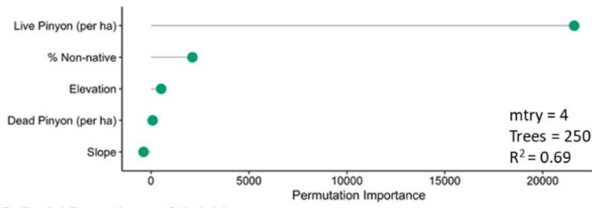
Figure 6. Electivity indices for piñon (a) and juniper (b) in burned plots. The top panel is a graphical representation of Ivlev's Electivity (E), and the bottom panel is the VS Relativized Electivity (E*). Blue coloring indicates greater seedling presence, while red coloring indicates less seedling presence.

Important biotic and abiotic factors associated with seedling density

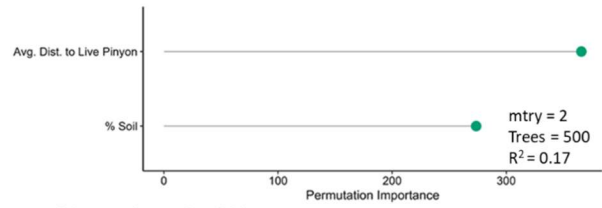
Final variables used in the random forest model for piñon seedlings across all plots were live mature piñon ha^{-1} (Permutation Importance (PI) = 21,612; Figure 7a), non-native plant cover (PI = 2,114), elevation (PI = 516), dead mature piñon ha^{-1} (PI = 81), and slope (PI = -383). The number of live mature piñon ha^{-1} was the most important predictor and had a PI value 10x that of the next most important variable (non-native plant cover). Partial dependence plots (Figure 7b) and Kendall's correlation analysis show that live mature piñon ha^{-1} ($\tau = 0.647$, $p < 0.001$) and dead mature piñon ha^{-1} ($\tau = 0.259$, $p = 0.009$) had significant positive influences on piñon seedling densities, while non-native plant cover ($\tau = -0.435$, $p < 0.001$) had a significant negative influence on seedling densities. Elevation and slope had a positive influence on seedling densities at mid-elevations (~2150 m) and at moderate (~20 degrees) slopes, although correlations were non-significant, likely due to the non-linear relationship.

Final variables used in the random forest model for piñon seedlings in burned-only plots were average distance to mature live piñon (PI = 366; Figure 7c) and exposed soil (PI = 274). Average distance to live mature piñon was the most important variable with PI value 1.3x higher than soil. Partial dependence plots (Figure 7d) and Kendall's correlation analysis show that average distance to live mature piñon had significant negative association with piñon seedling densities ha^{-1} ($\tau = -0.230$, $p = 0.023$) while soil was positively correlated with piñon seedlings especially at sites that had ~20% soil exposed, although this was non-significant ($\tau = 0.046$, $p = 0.644$), likely due to the non-linear relationship.

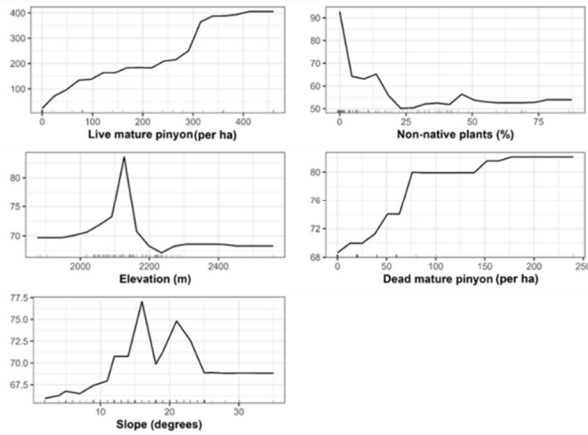
A. Variable Importance for Piñon Seedlings, All Plots



C. Variable Importance for Piñon Seedlings, Burned Plots



B. Partial Dependence of Variables



D. Partial Dependence of Variables

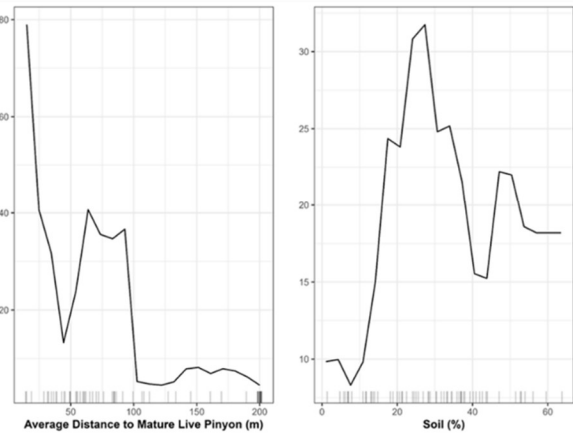


Figure 7. Results from random forest models investigating variable importance for driving piñon seedling density in (a) all plots and (c) burned plots. Model hyperparameters are listed on the figures. The lower panel are partial dependence plots showing the effect of each variable on the predicted piñon seedling density in (b) all plots and (d) burned only plots. The “rug” at the bottom of the partial dependence plots indicate sample distribution.

Final variables used in the random forest model for juniper seedlings across all plots were live mature juniper ha^{-1} (PI = 6,345; Figure 8a), 1 hr fuel loading (PI = 2,997), 10 hr fuel loading (PI = 2,255), distance to unburned edge (PI = 518), stumps ha^{-1} (PI = 198), loam surface texture (PI = 135), and dead mature juniper ha^{-1} (PI = 134). Live mature juniper ha^{-1} had the highest PI value and was 2.1 times that of the next most influential variable (1 hr fuel loading). Partial dependence plots (Figure 8b) and Kendall’s correlation show live mature juniper ha^{-1} ($\tau = 0.540$, $p < 0.001$), 1 hr fuel loading ($\tau = 0.414$, $p < 0.001$), and 10 hr fuel loading ($\tau = 0.254$, $p = 0.002$), all had significant positive associations with seedling density. Distance to unburned edge ($\tau = -0.380$, $p < 0.001$) was negatively and significantly associated with juniper seedling density. Stumps ha^{-1} was negatively associated with seedling density, although only marginally

significant ($\tau = -0.160$, $p = 0.060$). Loam surface texture, as a categorical variable, could not be assessed via Kendall's correlation.

Final variables used in the random forest model for juniper seedlings in burned-only plots were 1 hr fuel loading (PI = 851; Figure 8c), slope (PI = -1), and dead mature juniper ha^{-1} (PI = -14). One hr fuel loading was the most important variable with a PI value >8000x higher than slope and dead mature juniper ha^{-1} . Partial dependence plots (Figure 8d) and Kendall's correlation analysis show that 1 hr fuels had significant positive influences on juniper seedling densities ($\tau = 0.252$, $p = 0.009$).

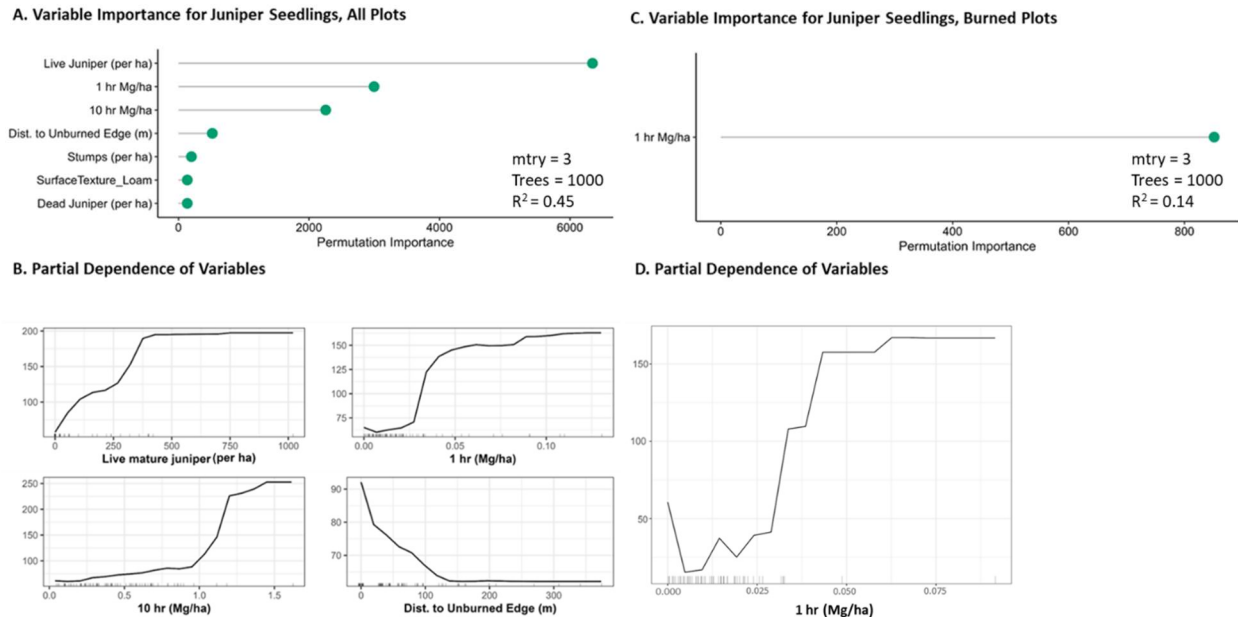


Figure 8. Results from random forest models investigating variable importance for driving juniper seedling density in (a) all plots and (c) burned plots. Model hyperparameters are listed on the figures. The lower panel are partial dependence plots showing the effect of each variable on the predicted juniper seedling density in (b) all plots and (d) burned only plots. The “rug” at the bottom of the partial dependence plots indicate sample distribution.

Discussion

In piñon-juniper (PJ) woodlands, like many slow successional systems, understanding post-fire vegetation dynamics over short time periods is challenging and thus few studies exist on

post-fire recovery in any PJ woodlands. These systems can exhibit decades of grass- and shrub-dominance following disturbance, which are a natural component of PJ systems. However, the increasing extent of high-severity patches under modern disturbance regimes may exceed historical patterns, and coupled with climatic constraints on tree seedling recruitment, may limit the re-establishment of woodland structure in some areas (Stevens-Rumann and Morgan 2019; Davis et al. 2023). We investigated vegetation patterns 25+ years after a fire, aiming to outline recovery trends and identify post-fire recovery trajectories, particularly of piñon and juniper trees. We found that nearly 30 years post-fire, the burned PJ woodlands studied have a greater percent cover of herbaceous, shrubs, and non-native plants and had fewer piñon and juniper seedlings compared to unburned reference plots. Importantly, our edge versus interior sampling design highlights strong spatial constraints on regeneration that are not captured in other studies. We show that, in burned patches, piñon and juniper seedlings were restricted to the edges of the fire perimeter. Our results also corroborate other research by showing that tree seedlings are less likely with high non-native plant cover. Lastly, in burned landscapes, both piñon and juniper seedlings have greater presence under Gambel oak relative to other available nurse objects. In all, our findings suggest that in some cases, recovery to a woodland structure may be prolonged, especially in large burned patches with limited seed sources, as well as areas with high colonization of non-native plants.

Piñon and juniper tree seedling establishment is more likely to occur closer to seed source

Regeneration patterns were strongly structured by location within the burned perimeter, with both piñon and juniper seedlings largely restricted to burned edges. Our random forest further expanded on this dynamic, where live mature tree density was the most important predictor for piñon and juniper seedling densities across all plots. Even in burned-only plots,

piñon seeding density decreased as distance to live mature piñon increased. Previous studies in Mesa Verde reported little two-needle piñon and Utah juniper seedling regeneration in the burned landscape (Floyd et al. 2021; Philips et al. 2024). However, those studies did not explicitly account for spatial position within the fire perimeters, with plots being located at least 100 m from an unburned edge (Philips et al. 2024) or without considering seed source proximity. Our findings suggest that incorporating distance to seed source and live tree density (if there is any) within burned landscapes is necessary to predict potential tree establishment. This is especially important when considering management activity like planting, which may be more critical and concentrated further into high severity burned patches when forest reestablishment is desired (Stevens-Rumann and Morgan 2019).

Our observed regeneration patterns contrast with the commonly assumed role of avian seed dispersers in facilitating piñon and juniper establishment across long distances, like other obligate-seeding species (Ligon 1978, Coop and Schoettle 2009, and Leirfallom et al. 2015). Instead, our findings align with many other western forest coniferous species, where regeneration is restricted to near the unburned edge (within ~100 m) in large burned patches (Davis et al. 2023). Limited tree regeneration on interior burn plots is likely driven by range-wide population declines of Pinyon Jay and other seed-dispersing birds (Boone et al. 2018; Schaming 2015), which may limit the number of seeds being moved from unburned to burned patches where they can be cached and later germinate (Gill et al. 2022). It is also possible that, as seed dispersing birds tend to cache seeds in the open (Van der Wall 2023), caching sites may be too harsh for young seedlings to survive (Petrie et al. 2016). In contrast, regeneration near unburned edges may indicate short-distance dispersal by gravity, rodents, or lagomorphs as the leading dispersal agents into burned patches (Chambers et al. 1999, Van der Wall 2023). Short-distance dispersal,

plus rodents often caching seedling under shrubs (Van der Wall 2023) may influence our greater observation of living seedlings (Wang and Corlett 2017).

The role of the developing vegetation on piñon and juniper seedling establishment

Nurse objects are widely considered important for piñon establishment, though juniper has traditionally been viewed as less dependent on them (Chambers et al. 1999). Nurse objects can provide both biotic and abiotic protections to seedlings, including reduced radiation and temperature stress, increased soil moisture, and protection from herbivory and trampling (Shemesh 2025). Recent work by Ried (2024) found that planted single-leaf piñon survival increased under nurse objects regardless of type. In contrast, our findings for two-needle piñon suggest that nurse object identity is important. In unburned woodlands, mature juniper trees are often the dominant nurse type for both piñon and juniper seedlings (Chambers et al. 1999; Redmond et al. 2013). In the absence of mature juniper, we found that both piñon and juniper seedlings occurred most frequently beneath Gambel oak, with lower presence under other shrubs and rocks. It is possible that rocks may not provide sufficient moisture retention or protection in our study region (Carlucci et al. 2011) and other shrubs may compete with seedlings for belowground resources or disrupt beneficial biotic interactions. For example, increased shrub cover has been associated with lower seedling densities in drought-impacted woodlands (McHugh and Gehring 2006). Overall, our findings highlight that the composition of nurse object types are important considerations when assessing site suitability for two-needle piñon and Utah juniper recruitment in burned woodlands of western Colorado.

The strong association between juniper seedlings and nurse objects was unexpected because juniper are generally considered more drought tolerant and less reliant on nurse plants (Chambers et al. 1999). Recent work in northern Arizona found high mortality of small one-seed

juniper and limited new recruitment from 2014–2023, suggesting that young juniper may be more sensitive to drought stress than previously recognized (Rodman et al. 2025), consistent with projections by Noel et al. (2023). Although the aforementioned studies focus on a different juniper species, the results align with our findings and raises the possibility that nurse plants may play a larger role for Utah juniper recruitment under increasingly stressful climatic conditions. Further, juniper seedling density increased with higher 1 hr and 10 hr fuel loading across our plots, with 1 hr fuel loading remaining the only significant predictor in burned-only models. These results suggest that fuel-related microsite conditions, potentially linked to litter accumulation, may also influence juniper establishment. However, the mechanisms underlying this relationship remain unclear, and additional sampling in areas with a gradient of fine-fuel loading is needed.

In addition to this, previous studies in Arizona report earlier establishment of one-seed and Utah juniper relative to piñon (Huffman et al. 2012), and recruitment projections for two-needle piñon and Utah juniper indicate that two-needle piñon is more likely to experience reduced recruitment under hotter and drier conditions, whereas Utah juniper is less likely to be impacted (Noel et al 2023). Combining these ideas, we would expect greater juniper seedling density compared to piñon seedlings in our field sites. Contrary to this expectation, we observed no clear temporal separation between piñon and juniper seedling establishment. Regional differences in climate, pre-fire woodland composition, or post-fire microsite availability may explain the contrasting patterns. It is also possible that abundance of nurse objects, especially Gambel oak, at our sites may have facilitated greater piñon recruitment. Huffman et al. (2012) reported shrub cover below 18%, suggesting fewer suitable microsites for the more drought-sensitive piñon.

Non-native plants inhibit woodland succession

Non-native plants were significantly higher in burned edge and interior plots compared to unburned plots, and we saw a significant and negative association with non-native plant cover and seedling densities, similar to others (Floyd et al. 2021, Phillips et al. 2023). Cheatgrass and other non-native plants can inhibit establishing trees by reducing their ability to germinate, survive, and grow. Non-native species like cheatgrass can monopolize nutrient and water resources (Kerns et al. 2020), hindering vegetation recovery, especially in dryland systems where resources are already scarce. Recent work also shows that cheatgrass can disrupt the beneficial relationships piñon have with ectomycorrhizal fungi, decreasing growth and their resilience to stress (Trimber et al. 2026).

Interestingly, we observed a negative correlation between non-native plant abundance and percent shrub cover (Figure A1.2), similar to findings by Floyd et al. (2021) in Mesa Verde. This may indicate another influence non-native grasses may have on the natural recovery of PJ ecosystems. While this relationship does not indicate causation, shrubs may suppress non-natives, or vice versa. For example, previous work has shown bunchgrasses can suppress invasive plants (Blank et al. 2020). Regardless of causation, this interaction suggests an additional pathway that non-native plants may influence recovery dynamics.

Study Limitations

Our study captures only a snapshot of the relationship seedlings have with different nurse object types and site conditions. It remains unclear how many seedlings initially germinated under certain conditions, what the survival rates are, and how long interactions (like the potentially facultative relationship with Gambel oak) may persist. Future research is needed on shrub-seedling dynamics by studying planted seedlings over longer time periods, empirically

testing seedlings' relationship with available nurse objects, particularly shrubs, and the longevity of the facilitative relationships. These future studies could also measure annual site characteristics, like soil moisture, temperature, and plant stress (via changes in biomass or plant respiration). Following Urza et al. (2019) and Sthultz (2006), these relationships should be tested at varying levels of stress (e.g. moisture, temperature, elevation precipitation variability, invasive species presence) to understand how these relationships may be maintained or utilized under future climate and site conditions.

While our sampling design captured clear spatial patterns in regeneration, a greater number of plots across a broader number of fire perimeters would improve our ability to generalize these results. For example, conducting a transect study assessing vegetation and tree seedling regeneration at consecutive distances from unburned edge (as in Chambers et al. 2016), would further elaborate spatial trends in piñon and juniper regeneration. Future work integrating longer temporal and refined spatial dynamics would improve our understanding of post-fire tree recruitment and vegetation recovery trajectories in this system.

Implications for Long-Term Recovery

Seedling presence near unburned edges demonstrates that woodland recovery is occurring, in some places. Naturally, expansion of regenerating areas will occur via in-filling, where seedlings regenerate closest to the edge, and as those seedlings mature and produce seeds, tree establishment will gradually work towards the interior of the high severity patch. However, tree establishment by infilling will take centuries to reach the center of some of the high severity patches, as modelled in different forest systems (Shive et al. 2018). Many PJ woodlands experience periods of expansion and within-stand infilling during cool wet years (Amme et al. 2020; Redmond et al. 2023). It is possible, therefore, that it is within these climate conditions

where we see regeneration within burned patches. Further, piñon can take nearly half a century to reach reproductive maturity (Ruel and Whitham 2002), thus recovery to a mature woodland may not occur for multiple centuries due to the episodic nature of seedling recruitment and the long delay for trees to reach sexual maturity. Large burned patches will ultimately require more time to recover and managers and scientists must continue to monitor these areas to truly understand the long-term recovery patterns in these landscapes. If more rapid recovery to woodlands is desired by managers, they may potentially need targeted management.

Conclusions

Piñon-juniper woodlands are a slow growing, yet critical ecosystem experiencing stress from changing climate, increased drought intensity (Noel et al. 2023) and increased size and frequency of fire (Board et al. 2018). This leads to concerns about PJ woodland persistence on the landscape following large disturbances. Here we demonstrate that while regeneration is occurring within 25+ year old fires, it is occurring at low densities with key mechanisms limiting regeneration. Regeneration of piñon and juniper seedlings is linked to proximity to nearby seed sources and is lower in areas of high non-native vegetation, both of which may prohibit seedlings from establishing. While PJ systems are inherently heterogeneous and are often interspersed with shrub and grasslands, the increasing size of high-severity burn patches may limit tree regeneration over ecologically meaningful timescales. Where accelerated woodland recovery is a specific management objective, interventions such as planting tree seedlings under Gambel oak and logs, especially in interior burn patches, and controlling invasive plant establishment by planting native perennial grasses and shrubs, may help facilitate recovery. In doing so, management action may balance the structural heterogeneity of woodlands, by promoting tree seedling recovery as well as native grasses and shrubs.

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CHAPTER 3

Nurse objects, not burn age or soil inoculation, drive outplanted *Pinus edulis* seedling survival in recent and old burned environments, western Colorado, USA

Summary:

- The resilience of conifer-dominated ecosystems, such as piñon-juniper (PJ) woodlands, is linked to several processes, including above- and below-ground biotic interactions, that may alter the recruitment niche of piñon pine. We investigate how soil biotic conditions influence piñon seedling height growth and survival through a common garden experiment.
- Inoculated piñon seedlings (grown in a mixture of field soil from an unburned woodland and sterile potting mix), and non-inoculated seedlings (grown in a sterile soil mixture), were planted into high-severity burned patches from a 3-year-old fire and a 27-year-old fire adjacent to different nurse objects.
- After 2 years of growth, piñon seedling survival was most influenced by nurse object type, with Gambel oak and logs having significantly higher survival. Inoculation had little influence on the fungal community of planted seedlings, but ectomycorrhizal fungi were present in both fire ages and the relative abundance of EMF influenced seedling survival.
- Biotic interactions, in particular planting seedlings under Gambel oak, can be used for increasing planted seedling survival outcomes. Inoculation with whole-soil inoculum

prior to planting does little to influence seedling survival and soil fungal communities next to planted seedlings seem to be driven by field soil community.

Introduction

Plants require, and are influenced by, biotic and abiotic factors which control seed production, dispersal, germination, and establishment (Grubb 1977). As the climate changes, and wildfires increase in size and severity in the western US (Mueller et al. 2020), there is a growing concern about the ability of trees to regenerate naturally (Stevens-Rumann et al. 2022; Davis et al. 2023). Many western conifer forests are struggling to regenerate naturally due to dispersal limitations (Stevens-Rumann and Morgan 2019), therefore many recent post-fire management decisions have focused on artificial reforestation by planting tree seedlings. There is high variability in tree seedling planting success, ranging from 16-100% survival, linked to regional differences in climate water deficit, drought, planting season, fire severity, and post-fire canopy cover (Rodman et al. 2024). Importantly, planted tree survival tends to be lower in hot and dry forests. Variability in planted seedling survival can also be influenced by biotic conditions that contribute to seedling health and survival which may be absent following wildfire (Ibanez et al. 2022). Defining biotic and abiotic conditions that support or inhibit seedling survival can offer valuable insight into the challenges of tree reestablishment, both naturally and artificially, and can be intentionally utilized to improve planting outcomes (Li et al. 2025). Doing so can inform actionable strategies in post-disturbance restoration (Larson et al. 2023).

To explore some of the biotic dynamics influencing planted seedling survival in a post-fire setting, we focus on *Pinus edulis* (two-needle piñon pine), a widespread foundation species across the southwestern United States withing piñon-juniper (PJ) woodlands. PJ is an ideal system for studying biotic interactions because piñon pine forms interactions across taxonomic

kingdoms that are associated with regeneration, seedling survival, and resistance to stress. Aboveground, piñon seedlings rely on nurse objects, such as trees, shrubs and other biotic and abiotic land features, that offers shade that reduces solar radiation and increases soil moisture (Chambers et al. 1999). In mature woodland stands, piñon seedlings are commonly found under juniper trees (Chambers et al. 1999; Redmond et al. 2018; Woollet and Stevens-Rumann, *in revision*). Belowground, piñon pine seedlings engage in mutualistic interactions with ectomycorrhizal fungi (EMF), which provide water and essential nutrients such as nitrogen and phosphorus in exchange for carbon (Gehring et al. 2017, Mueller et al. 2019, Owen et al. 2019, Gehring et al. 2020). EMF play a critical role in facilitating seedling growth, particularly under high-stress environmental conditions. Certain fungal genera, such as *Geopora*, have been linked to improved seedling performance during drought, with colonized seedlings exhibiting higher growth rates than those lacking these fungi (Gehring et al. 2017, Mueller et al. 2019).

Fire disrupts the biotic mutualisms available for seedlings compared to intact woodlands. After high-severity fire – fire that results in near-complete or complete mortality of the overstory tree community – vegetation dynamics are reset. In burned PJ in western Colorado, naturally regenerating piñon seedlings tend to be found living under Gambel oak (*Quercus gambelii*) (e.g. Woollet and Stevens-Rumann, *in revision*). While many potential nurse objects may exist in the post-fire environment (e.g. mountain mahogany (*Cercocarpus montanus*), Utah serviceberry (*Amelanchier utahensis*), Mormon tea (*Ephedra viridis*), standing or downed logs, and rocks), only Gambel oak has been tested to understand potential facilitation post-fire (Crocket and Hurteau 2022), although we lack an understanding of the mechanisms and temporal dynamics of these relationships. Facilitation of *Pinus monophylla* (single-leaf piñon pine) by *Artemisia tridentata* (Big sagebrush; Urza et al. 2019) and of *P. edulis* by *Fallugia paradoxa* (Apache

Plume, Sthulz et al. 2006) are other examples of shrub facilitation. However, the relationship is variable, shifting from facultative to competitive or neutral when environments conditions are less stressful (Sthulz et al. 2006) or when the tree seedling gets older (Urza et al. 2019).

Belowground, high-severity fire reduces EMF abundance and alters community structure due to soil heating and the loss of host species (Karst et al. 2014; Owen et al. 2019; Pulido-Chavez et al. 2021, Trimber et al. 2026). In some cases, high-severity fire can eliminate EMF entirely (Nelson et al. 2022). The duration of EMF depletion largely depends on ecosystem type, the size of high-severity fire patches, and the rate of vegetation recovery (Kałucka and Jagodzinski 2017). General trends across other ecosystem types indicate that following disturbance or environmental degradation, fungal saprotrophs dominate and EMF are in low abundance, and this ratio switches with forest development (Vivian et al. 2025). EMF may persist by surviving as spores, as they do in fire-adapted landscapes (Glassman et al. 2016); such spores or other biological legacies may not be present in "fire-avoidant" landscapes, like PJ (Keeley 2011). EMF may colonize by dispersing from refugial patches of live host trees, either aboveground as spores or belowground through hyphal exploration. However, dispersal in different ecosystems are likely limited to ~1km distances, as some studies have found decreasing EMF diversity with increasing distance from live trees (Peay et al. 2010) and decreased colonization rates of seedlings at further distances from fungal spore sources (Peay et al. 2012). Even so, surviving spores or access to rooting zones for inoculum (Markovchick et al. 2023) may still pose challenges for seedlings germinating in the increasingly large patches of contemporary high-severity wildfires, especially if there is a mismatch between the fungal community present and host-specificity.

To date, we do not understand if EMF communities are maintained in PJ woodlands post-fire, or for how long they may remain depleted (Andrews and Gehring 2020). A recent greenhouse study by Trimber et al. (2026) showed lower fungal colonization and different EMF communities when piñon is planted in soils that burned ~20 years ago, compared to unburned reference soils (Trimber et al. 2026). While they found EMF present in burned soils, the community was depleted of taxa associated with piñon seedling resistance to drought (Gehring et al. 2017). Specifically, colonization of *Rhizopogon* was greater on trees planted in burned soils compared to *Geopora* in the unburned soils (Trimber et al. 2026). Therefore, restoring mycorrhizal fungi from a nearby intact woodland, especially in regions experiencing climate stress, may be a key consideration for post-fire tree plantings (Andrews and Gehring 2020; Li et al. 2025).

A common way of introducing mycorrhizal fungi to a system is through inoculating tree seedlings in the greenhouse. A cost-effective method of doing so is by whole-soil inoculations (as opposed to single- or multi-species isolates), where field soil is mixed in with potting media to incorporate the naturally occurring microbiota. In selecting whole-soil inoculum, temporal factors need to be considered as mycorrhizal fungi associated with early-successional ecosystems, often found in commercially available products, tend to not be particularly beneficial to late-successional plant communities like trees (Koziol et al. 2018). However, tree seedlings also tend to have a different EMF composition than adult trees, forming associations with early-successional EMF that have less carbon demand and the ability to utilize inorganic nutrients (Kałucka and Jagodzin'ski 2017). With these considerations in mind, soils from intact woodlands (compared to commercially available products) are likely to have a diverse EMF

composition consisting of members that young trees can form associations with, as well as community members piñon have evolved to have associations with.

Using a whole-soil inoculum to restore mycorrhizal fungi and other beneficial microbes can also introduce other microbes that are neutral or harmful (van der Voorde et al. 2012). There is a growing concern that planting trees grown in greenhouses and nurseries may introduce pests and diseases into a system (e.g. Baird and Pope 2022). Although inoculation may seem promising, current research highlights many limitations in attributing seedling success to inoculation (Wubs et al. 2019), and that aspects of the field soil, including soil type and already-present soil microbial community members, have greater influences on seedling performance than inoculation (Wasyliw et al. 2022). Regardless, the limited experimental studies of tree inoculation in burned forests and woodlands in the southwestern US highlights the need for a deeper understanding of its potential to aid reforestation efforts (Neuenkamp et al. 2019), especially if EMF are not present in the burned system.

Here, we investigate how above and belowground biotic conditions in burned soils of two different ages influence planted piñon seedling survival. This study has three main objectives: 1) assess how inoculation, fire age, and nurse objects influence piñon seedling growth and survival, 2) assess the soil fungal community in the two fire ages and investigate how the community adjacent to planted seedlings changes, and 3) assess how dominant members of the soil fungal community influence seedling survival, with special focus on taxa classified as ectomycorrhizal. We hypothesize that: 1a) seedling survival and growth will be better in the old-burned site compared to the recently burned site due to a greater amount of time for above- and belowground recovery, 1b) certain nurse object types will increase seedling growth and survival; namely, objects that offer more shade, increased soil moisture, and greater microbial diversity (e.g.

Gambel oak, large shrubs, standing dead trees/logs) will improve seedling survival and growth more compared to objects that offer less shade and belowground interactions (grass, rocks) and, 1c) inoculated seedlings will have greater survival and growth compared to non-inoculated seedlings due to access to ectomycorrhizal fungi; 2a) soil samples from the old burn and recent burn will have a different fungal community structure; the old burn samples will have greater fungal richness and diversity metrics during the study period (Tikhonova and Kravchenko 2020), and have a higher relative abundance of ectomycorrhizal fungi, and 2b) soil adjacent to non-inoculated seedlings will have lower diversity metrics and lower relative abundance of EMF taxa compared to inoculated seedlings, and 3) certain fungal taxa present, such as taxa from the genera *Geopora* or *Tuber*, can help predict whether seedlings are alive in the next time point.

Materials and Methods

Greenhouse Methods

Field soil from an intact PJ woodland and piñon cones were collected September 2022. Field soil was collected from unburned PJ stands near planting sites. Surface litter as removed to expose the soil; we found minimal organic soil depth, therefore mostly mineral soil was collected to a depth of 30 cm beneath mature piñon trees. The soil was homogenized and sieved to 4 mm to remove roots and plant biomass and kept refrigerated until the planting pots were packed. Seeds were collected from the San Isabel National Forest near Salida, Colorado due to the lack of cones availably nearby planting sites.

Unopened green cones were stored at room temperature in a breathable container in a dark room for ~2 months until they dried and opened (Figure A2.1). Seeds were removed from opened cones and were stratified by soaking them in a water bath for 36 hours with the water replaced every four hours (including during the night) and then stored at 5°C for 40 days. Seed

viability was not conducted, but following stratification, seeds were germinated on wet paper towels and only successful germinants (via emergence of the radicle) were planted into Deepots. Prior to planting germinants, Deepots were packed with a soil mixture of 20:5:1 autoclaved potting mix: autoclaved Greensgrade (a coarse, inorganic soil amendment that increases drainage; Profile Products LLC, Buffalo Grove, IL): field soil (non-inoculated field soils were autoclaved, inoculated field soils were not autoclaved). Potting mix, Greensgrade, and field soil for the non-inoculated treatment, and potting mix and Greensgrade for the inoculated treatment, were autoclaved for 30 minutes in attempt to partially sterilize the soil mixtures. Seedlings were grown in the Plant Growth Facilities greenhouse at Colorado State University with supplemental lighting from Nov 2022 – June 2023. In the greenhouse, seedlings were watered until flowthrough every three days. In June 2023, seedlings were removed from the greenhouse and grown in outdoor conditions to harden trees until planting in Oct 2023. Vegetation where seedlings were hardened off were typical residential plants in Fort Collins, CO, including lilac (*Syringa spp.*), Siberian elm (*Ulmus pumila*), chokecherry (*Prunus spp.*), and rose (*Rosa spp.*). If rain did not occur within a week duration, seedlings were watered during this time period.

Planting Methods

Planting sites were within high-severity burned patches in fires that burned in 1996 (Hatchet Fire; “old”) and in 2020 (Pine Gulch Fire; “recent”; Figure 1). Research permits were received by the Grand Junction BLM Field Office, and sites were assessed for cultural resources before planting. Old and recent planting sites are comparable to each other by elevation, aspect, and slope. Planting sites were 45,569 m² and 69,127 m² in the old and recent fire, respectively. Sites were irregularly shaped, but maximum linear extent was about 220 x 350 m in the old fire and about 280 m x 270 m in the recent fire. Planting sites at the old and recent burned were

divided in half so that inoculated and non-inoculated seedlings were planted within the same site, but in different sections to keep treatments somewhat separated. A total of 300 piñon seedlings were planted; 150 were planted in the recent fire, and 150 were planted in the old fire (Figure 2). In each fire, 75 inoculated seedlings and 75 non-inoculated seedlings were planted under or adjacent to different nurse objects (15 seedlings at each nurse type: standing dead tree or downed log, Gambel oak (*Quercus gambelii*), Utah serviceberry (*Amelanchier utahensis*), and rock (old burn) or Russian wildrye (*Psathyrostachys junceus*; recent burn) and in the interspace (non-nursed). Heights and diameters of seedlings were measured after seedlings were planted.

All seedlings were planted on the north side of nurse objects. Tubex standard seedling protection tubes (made of polypropylene co-polymer, diameter ranging from 7 – 10.5 cm) were cut to 30.5 cm and were placed over the seedlings to prevent herbivory of the young trees. Labeled and flagged stakes were installed at each seedling. Planted seedlings were not provided water at planting and did not receive supplemental water after planting. In each planting site, five soil temperature and moisture sensors (HOBO mx2307) and five air temperature and relative humidity dataloggers (HOBO U23-002A) were deployed. At each site, soil dataloggers were deployed at a Utah serviceberry, near a rock, at a Gambel oak, and at two standing dead trees or logs. Dataloggers recorded measurements at 1-hr intervals. Hourly measurements at each logger were averaged to calculate daily average and were then averaged across recent burn and old burn (Figures 3). While we aimed to obtain measurements to track microclimate, some air loggers were screwed into standing logs or strapped to shrub growth, so were not paired with the soil loggers.

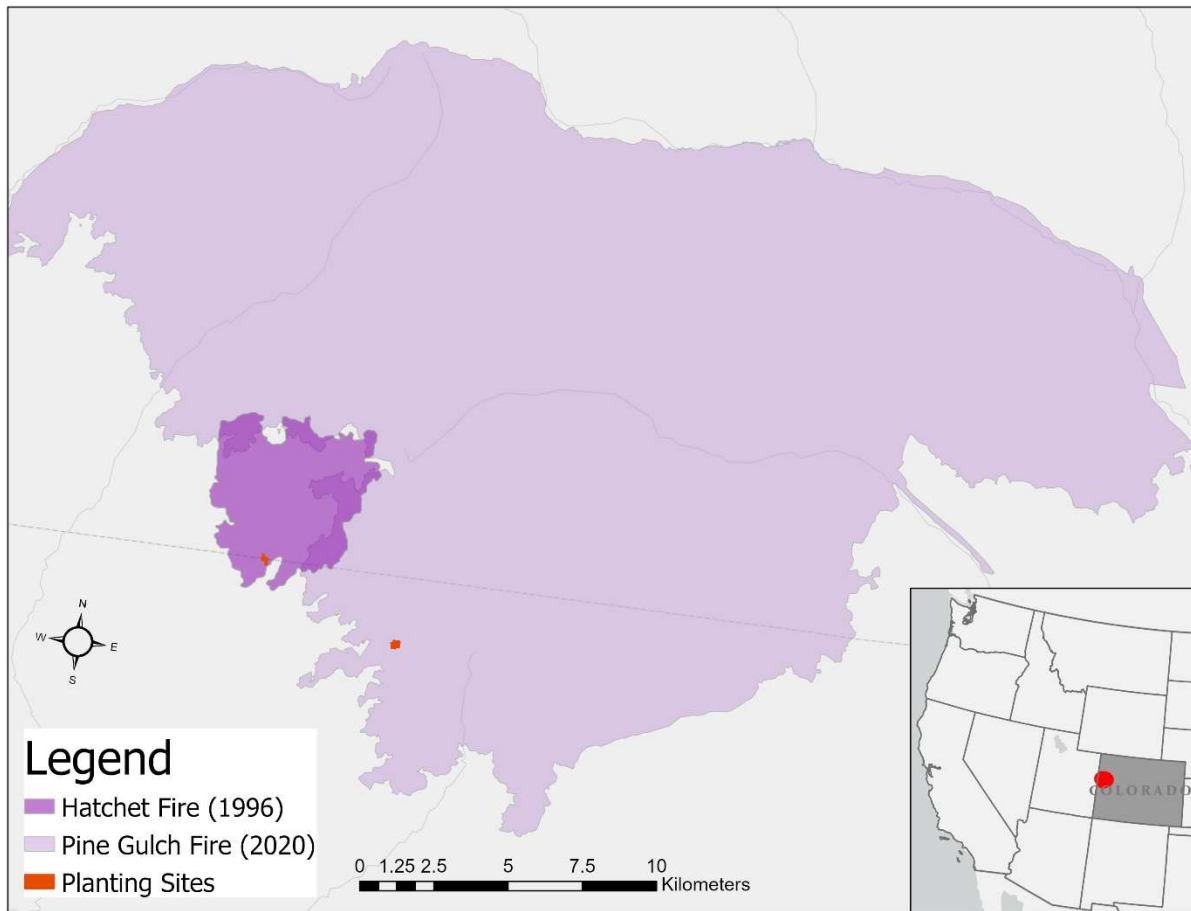


Figure 1. Piñon seedling planting sites within high-severity burned patches in an older burned fire (Purple, Hatchet Fire (1996) and a recently burned fire (Lavender, Pine Gulch Fire (2020) in Colorado, USA. Planting sites, outlined in red, were permitted by the Grand Junction BLM Field Office.

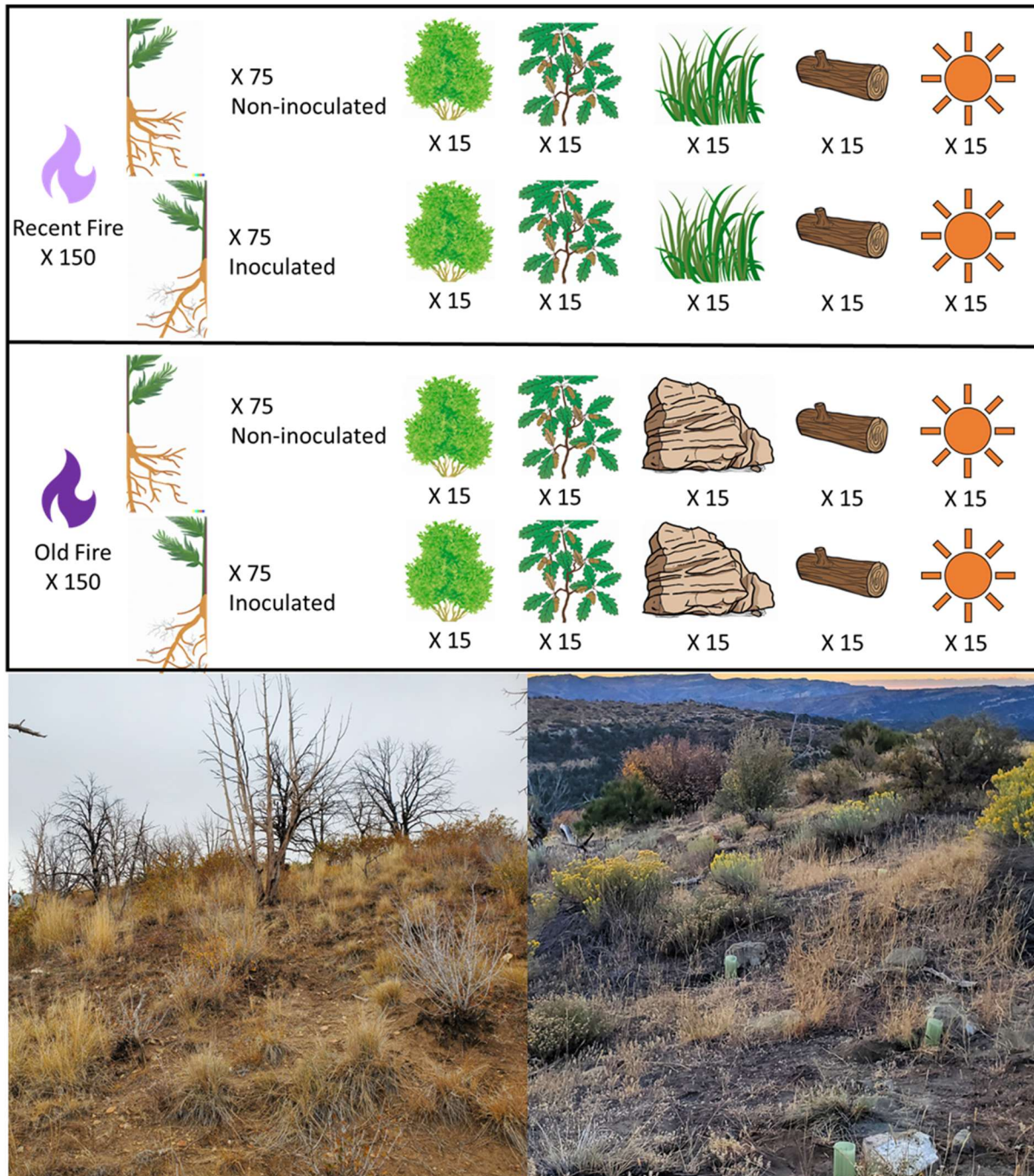


Figure 2. Planting schematic showing the number of seedlings planted in each treatment. A total of 300 seedlings were planted, with 150 in the recent burn and 150 in the old burn. Within each fire, 75 inoculated and 75 non-inoculated seedlings were planted beneath different nurse object types (15 seedlings per nurse object type). Photographs show the planting site in the recent fire (left) and the old fire (right). Recent fire lacks rocks, has standing dead trees, and smaller shrubs, while old fire has rocks present, down dead trees, and larger shrubs.

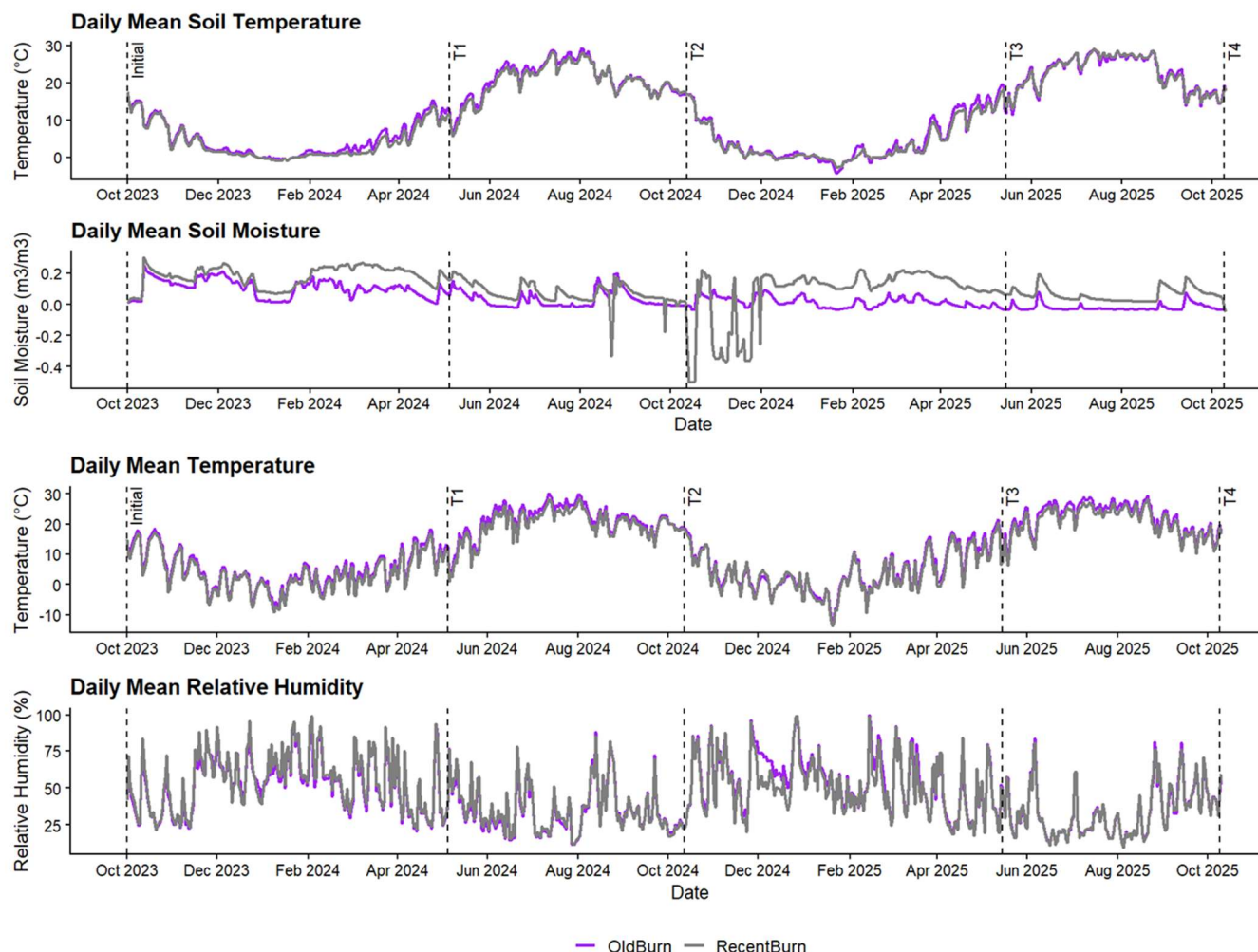


Figure 3. Daily mean soil temperature, soil moisture, air temperature, and relative humidity in the old (purple) and recent (grey) fire. Dashed horizontal lines indicate sample time points (initial, timepoint 1 (T1), T2, T3, and T4), when seedling survival and soil samples were collected.

Field Measurements

Bulk soil and soil microbial sampling

At planting, baseline soil samples were collected from the seedling soil (excess soil remaining in the seedling containers after plant growth to assess inoculation success), and from the field. For field samples, 10-cm depth x 5-cm diameter soil cores were collected at the planting location from a representative of each treatment (inoculated and non-inoculated; nurse

type; fire age) to understand baseline field soil fungal community. Since these soils do not exhibit obvious organic and mineral horizons, the soil cores were divided into upper (0-5 cm) and lower (5-10 cm) depths, put into labelled bags, and homogenized. A ~10 g sub-sample for microbial analysis was taken from each bag and put into a small labelled bag for microbial analysis. The remaining bulk soil sample and the microbial sub-sample were kept on ice in the field until being transferred to a -40°C freezer.

Soil cores were collected in the spring and fall for two years; 10-cm depth x 5 cm diameter soil cores were taken from a representative of each treatment (inoculated and non-inoculated; nurse type; fire age), collected at least 3 cm away from the seedling. While we hoped to obtain soil samples from the same seedling across the timepoints, if the seedling died, soil cores were taken from a randomly selected living seedling of the same treatment. Soil cores were divided into upper (0-5 cm) and lower (5-10 cm) depths, put into labelled bags, and homogenized. A ~10 g sub-sample was taken from each bag and put into a small, labelled bag for microbial analysis. The remaining bulk soil sample and the microbial sub-sample were kept on ice in the field until being transferred to a -40°C freezer.

Seedling measurements

Seedling survival and growth were recorded in the spring and fall of each year for two years. At each visit, seedlings were located, survival assessed, and heights of surviving seedlings measured. Visual assessment of seedling condition was performed to indicate an estimate of percent non-photosynthetic needles (as indicated by percent yellowing and brown needles).

At the end of the second growing season in fall 2025, final measurements were taken. Live seedlings were destructively sampled and removed from sites. Overall growth was

measured in the lab; if seedling exhibited multiple shoots, each shoot was measured and summed for cumulative growth.

Lab analyses

Soil chemical analysis

Bulk soil samples that were collected at Timepoint 0 were air-dried (after initial storage in freezer) and submitted to the Colorado State University Soil Testing Laboratory for analysis of chemical and physical characteristics, including pH, soluble salts, lime, organic matter, nitrate, phosphorus, potassium, sulfate content, total C, total N, and C:N (Table A2.1).

DNA extraction and amplicon sequencing

Soil DNA was extracted using a DNeasy PowerSoil Pro extraction kit (Qiagen) from 0.25 g of soil following manufacturer's instructions in the Dryland Ecology and Management Lab at Colorado State University. A blank extraction was included for every 24 soil samples as a negative control. DNA extracts were sent to the Colorado State University Next-Generation Sequencing Core for PCR amplification. A total of three separate sequencing runs were conducted across all samples, with Timepoints 0 – 2 on the first run, timepoint 3 on the second run, and Timepoint 4 on the third sequencing run (Table A2.2). PCR was performed in duplicate on DNA samples using Platinum II Hot Start Master Mix (Invitrogen) on a SimpliAmp thermocycler (ThermoFisher), targeting the ITS1 regions using ITS1-F (CTTGGTCATTTAGAGGAAGTAA; Smith et al. 2014) and ITS2 (GCTGCGTTCTTCATCGATGC; Bellemain et al. 2010) primers. The thermocycler program included initialization at 94°C for 2 min, 35 cycles of [94°C for 15 sec, 60°C for 15 sec and 68°C for 60 sec], 72°C for 10 min, and 4°C hold. After confirming amplification via gel electrophoresis, individual libraries were quantified using the Quant-iT PicoGreen dsDNA assay

kit (Invitrogen). Libraries were pooled in equimolar amounts by plate and then cleaned using AMPure XP beads (Beckman Coulter). Pooled libraries were quantified using the Qubit 1X ds DNA HS Assay kit on a Qubit 4 fluorometer (Invitrogen). The pools were combined in equimolar amounts into a final library. The final pooled library went through three quality and quantification steps: 1. Quantification on the Qubit 4 using the 1X ds DNA HS Assay kit 2. Checking the size distribution of the library using the High Sensitivity D1000 ScreenTape and Reagents (Agilent) on the Agilent 4150 TapeStation System and 3. qPCR quantification using the KAPA Illumina Quantification kit (Roche) on an Applied Biosystems QuantStudio 3 Real-Time PCR System. After quality and quantification steps were performed and library met standards, the library was sequenced with 15% phiX spike on an Illumina MiSeq v2 500-cycle (for timepoints 0-3) and on a MiSeq v2 Nano 500-cycle for timepoint 4.

Amplicon sequence processing

Sequence data were processed in R (version 4.4.2, R Core Team 2025) using R Studio (RStudio 2025.05.1, Posit Studio), following the *dada2* (1.34.0, Callahan et al. 2016) pipeline. The three sequencing datasets (from the four time points) were processed separately. Reads containing ambiguous bases were removed, primers were trimmed with Cutadapt (4.0, Martin 2011), and quality filtering was applied (maxEE = 2, truncQ = 2, minLen = 50). Only forward reads were used for downstream analyses due to low-quality reverse reads and improved performance for assembly (Pauvert et al. 2019). No samples (other than blanks) were discarded for low reads. Blank samples had low (<25) reads per sample, showing low contamination. Error rates were learned from the data and used to infer amplicon sequence variants (ASVs), which were assembled into a sequence table and screened for chimeras using the consensus method. Taxonomy was assigned to ASVs using the UNITE fungal reference database (general release,

February 2025, Abarenkov et al. 2024). The resulting ASV table, taxonomy, and sample metadata were combined into a phyloseq object for downstream analyses using the *phyloseq* package (McMurdie and Holmes 2013). Functional guilds were assigned using FUNGuild (Nguyen et al. 2016). Read counts filtered at each processing step are available in Table A.2.2.

Statistical Analysis

All statistics were conducted in R using R Studio. Data formatting, manipulation, and visualization were done using *tidyverse* (Wickham et al. 2019).

Seedling survival and height growth across planting conditions (1a/1b/1c)

First, to assess how inoculation, fire age, and nurse objects influence seedling survival, we used Chi-squared tests to assess differences in seedling survival across seedling treatment (non-inoculated *versus* inoculated soil) and fire age (old *versus* recent) and Kruskal-Wallis tests to assess differences in seedling survival across different nurse objects (shrub, native grass, log, rock, non-nurse). To assess how inoculation, fire age, and nurse objects influence seedling height growth, Mann-Whitney U tests were used to assess differences in the change in seedling height (height at final sampling - height at planting) by seedling treatment and by fire age and Kruskal-Wallis was used to assess differences in the change in seedling height across different nurse objects. Non-parametric tests were selected for these analyses due to data failing assumptions for normality and/or variances.

Fungal community across planting conditions (2a/2b)

Next, to assess fungal alpha and beta diversity, we separated samples by time point and soil layer, and filtered samples to retain only fungal taxa and to remove non-target sequences (mitochondria and chloroplasts) and taxa lacking phylum-level classification. ASVs present with fewer than one read across all samples were excluded. To control for differences in sequencing

depth, samples were rarefied to a common depth equal to the minimum library size using random subsampling without replacement. While rarefying may increase false positives in tests for species that are differentially abundant (McMurdie and Holmes 2014), it remains a useful tool for normalizing data and performs better than not normalizing or normalizing by proportion of sequences (Weiss et al. 2017).

Alpha diversity metrics were calculated using *phyloseq* and *vegan* (Dixon et al. 2003) R packages. We estimated Chao1 abundance, Shannon diversity, Simpson's Index, and Pielou's evenness. Shannon accounts for both the abundance and evenness of ASVs in the sample, and Chao1 accounts for unseen species that we are unable to detect in sequencing by considering rare ASVs (those with one or two reads) but not evenness. For each timepoint $\times$ soil layer combination, Wilcoxon rank-sum tests were used to assess whether alpha diversity differed between fire age classes and between treatments for Chao1 richness, Shannon diversity, Simpson diversity, and Pielou's evenness. Prior to hypothesis testing, assumptions of normality were evaluated using Shapiro–Wilk tests and visual inspection of distributions, and homogeneity of variances was assessed using Bartlett's tests. Because several diversity metrics violated parametric assumptions, non-parametric Wilcoxon rank-sum tests were used to compare diversity metrics between fire age classes and treatment groups.

Beta diversity was assessed using Bray-Curtis dissimilarities calculated from rarefied fungal community data. Analyses were performed separately for each timepoint and soil layer. Non-metric multidimensional scaling (NMDS) ordinations were used to visualize differences in community composition. Permutational multivariate analysis of variance (PERMANOVA) was used to test for effects of fire age and inoculation treatment on Bray-Curtis distances.

PERMANOVA was conducted using the `adonis2` function in the *vegan* package with 999 permutations.

To determine relative abundance of EMF at each time point, ASVs with zero total abundance were first removed from each phyloseq object (one phyloseq object for each sequencing run). Read counts within each sample were converted to relative abundances by dividing each ASV's read count by the total number of reads in that sample. To reduce noise from extremely rare taxa, ASVs with a mean relative abundance < 0.00001 across samples were excluded. The `melt` function was used on each phyloseq object to convert the object to a dataframe. Taxa were filtered from the dataframe by retaining guilds with “probable” and “highly probable” guild assignment classifications. From this filtered dataset, taxa classified as EMF were selected. Taxa that were assigned to multiple guilds were excluded to only retain EMF assignments (e.g. guild assignments like “Ectomycorrhizal-Endophyte-Plant Pathogen-[Plant Saprotroph]” were not used). For each sample, the relative abundances of each EMF-identified ASV were summed to obtain the total relative abundance of EMF. Samples were grouped by time point, fire age $\times$ inoculation treatment combination, and soil layer and the mean relative abundance of EMF was calculated. Mann-Whitney U tests were used to compare the relative abundance of EMF in inoculated versus non-inoculated seedlings before planting, and for assessing differences in old burn vs recent burn baseline soil. Differences in EMF relative abundance among fire age $\times$ inoculation treatment combinations were tested separately for each timepoint and soil layer using non-parametric Kruskal–Wallis tests. Similar methods were used for calculating relative abundances of pathogenic fungi and saprotrophic fungi.

To visualize EMF genera at each time point, phyloseq objects were processed similar to the above, where ASVs with zero abundance were removed, and read counts were transformed to

relative abundances within samples. Rare taxa (mean relative abundance < 0.00001) and taxa lacking confident guild assignments were excluded. The melt function was used to convert phyloseq object to a dataframe. Taxa classified as ectomycorrhizal fungi were retained. Relative abundances of EMF taxa were summed by genus within each sample to obtain genus-level relative abundance values.

Relative abundance of fungal guilds and influence on seedling survival (3)

Finally, to assess the influence of fungal community composition on seedling survival across timepoints, we used generalized linear models (GLMs) with a binomial distribution. Relative abundances of EMF, pathogenic/parasitic, and saprotrophic fungi were included as predictor variables, and seedling survival at the subsequent fall sampling was used as the response variable (i.e., fungal abundances measured at Time 0 and Time 1 were used to predict Time 2 survival, fungal abundances measured at Time 2 and Time 3 were used to predict Time 4 survival). Fall survival was analyzed because nearly all sampled seedlings survived the winter, resulting in uniformly high spring survival, whereas summer represented the primary mortality bottleneck (Table A2.2). Soil layers were modeled separately because fungal abundances in upper and lower soil horizons were likely correlated. To evaluate whether specific EMF genera were associated with seedling survival, we ran separate GLM models using the relative abundances of *Tuber*, *Geopora*, *Tomentella*, *Clavulina*, *Russula*, and *Rhizopogon* as predictors, each with their own model.

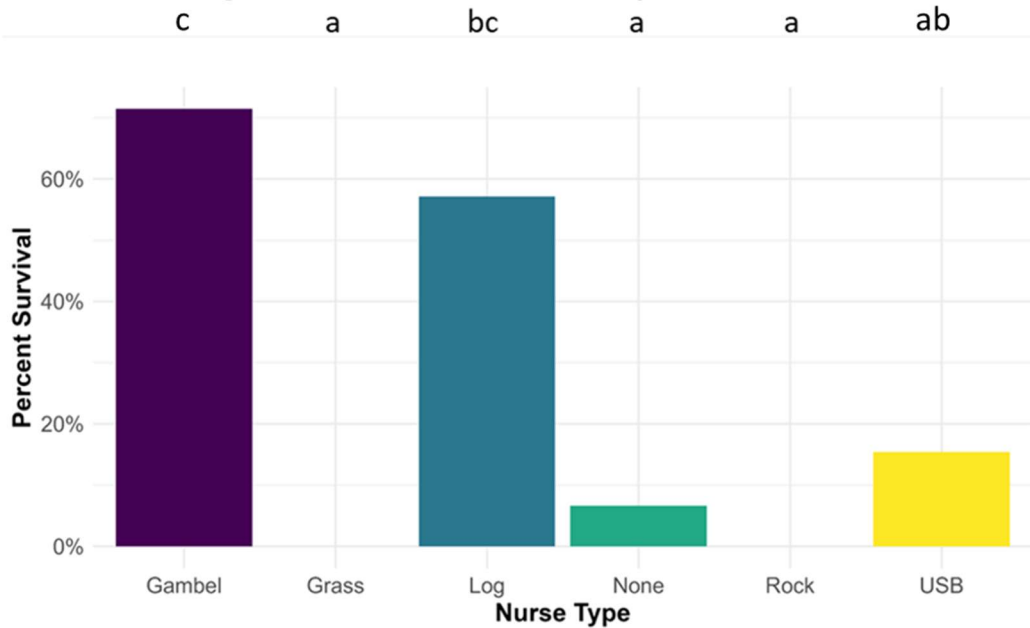
Results

Seedling survival and height growth across planting conditions (1a/1b/1c)

Total seedling survival after 2 years was 18%, with 50 live seedlings, 234 dead seedlings, and 16 seedlings unaccounted for (Table A2.3). The missing seedlings and tags may be attributed

to a combination of debris flow, herbivory, and human error. Missing seedlings were excluded from statistical analysis, allowing us to focus only on those with confirmed outcomes (alive or dead). In fall 2025, after the second growing season, there were more dead seedlings than live ones, regardless of treatment (inoculated (live = 28; dead = 224) and non-inoculated (live = 22; dead = 120)) or location (recent burn (live = 25; dead = 115) or old burn (live = 25; dead = 119)), with no significant associations between survival rates and treatment (inoculated vs. non-inoculated; $\chi^2 = 0.607$, $df = 1$, $p = 0.436$) or location (old burn vs. recent burn; $\chi^2 = 1.01 \times 10^{-30}$, $df = 1$, $p = 0.99$). Seedling survival was different under/adjacent to nurse objects ($\chi^2 = 58.44$, $df = 5$, $p\text{-value} < 0.001$), with Gambel oak and logs having significantly greater survival (Figure 4a). Seedling height growth was marginally higher in the inoculation treatment ($W = 387.5$, $p = 0.070$, Figure 4b), but was not different when comparing location ($W = 330$, $p = 0.555$) or nurse object type ($\chi^2 = 1.797$, $df = 2$, $p = 0.407$).

A. Percent seedling survival under different nurse objects



B. Change in seedling height (cm) by treatment

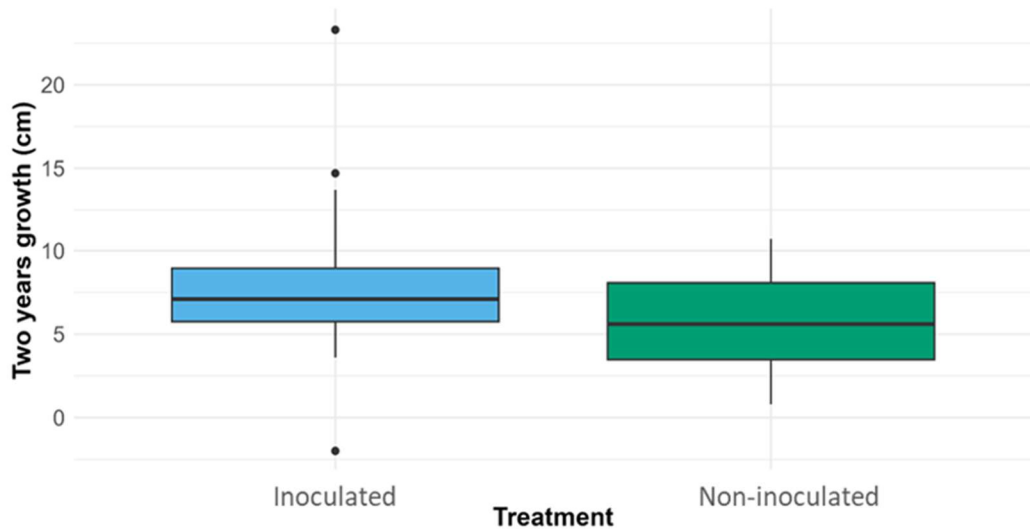


Figure 4. A) Percent piñon seedling survival across different nurse types in fall 2025 following two years of growth. Letters indicate significance groupings following Dunn's pairwise comparisons and bars are colored by nurse object type (dark blue = Gambel oak, blue-green = log, green = none, yellow = Utah serviceberry (USB).) There was no seedling survival at Timepoint 4 for seedlings planted under/adjacent to grass and rocks. B) Changes in seedling height (cm) from planting to Timepoint 4 of the inoculated (blue) and non-inoculated (green) seedlings. Inoculated seedlings had marginally more growth than non-inoculated seedlings.

Fungal community alpha and beta diversity across planting conditions (2a/2b)

Alpha diversity measures (Chao1, Shannon, Simpson, Pielou's) were not significantly different when comparing fire age (old burn versus recent burn) and inoculation treatment (inoculated vs non-inoculated) ($p > 0.05$ for all, Table A2.4, Figure A2.2). Differences in fungal community via Bray-Curtis dissimilarities were influenced by fire age at all time points and soil layers (PERMANOVA, $p < 0.05$ except for time 4, lower soil depth; Table 1, Figure 5).

Table 1. Permutational analysis of variance (PERMANOVA) results comparing the Bray-Curtis dissimilarity distances in samples at each timepoint (Time 0 – Time 4) by nurse object type, fire age and inoculation treatment, and separated by soil layer.

<i>Timepoint</i>	Soil Layer	<i>Fire Age</i>			<i>Treatment</i>		
		R ²	F	p-value	R ²	F	p-value
0	Top	0.169	3.481	0.001*			
	Lower	0.102	1.960	0.001*			
1	Top	0.167	3.602	0.001*	0.056	1.209	0.193
	Lower	0.081	1.595	0.004*	0.061	1.198	0.124
2	Top	0.146	2.727	0.001*	0.057	1.070	0.321
	Lower	0.109	1.873	0.001*	0.047	0.813	0.848
3	Top	0.127	2.398	0.001*	0.061	1.158	0.198
	Lower	0.130	2.401	0.001*	0.057	1.048	0.294
4	Top	0.118	1.351	0.01*	0.087	0.994	0.468
	Lower	0.111	1.244	0.064	0.090	1.013	0.447

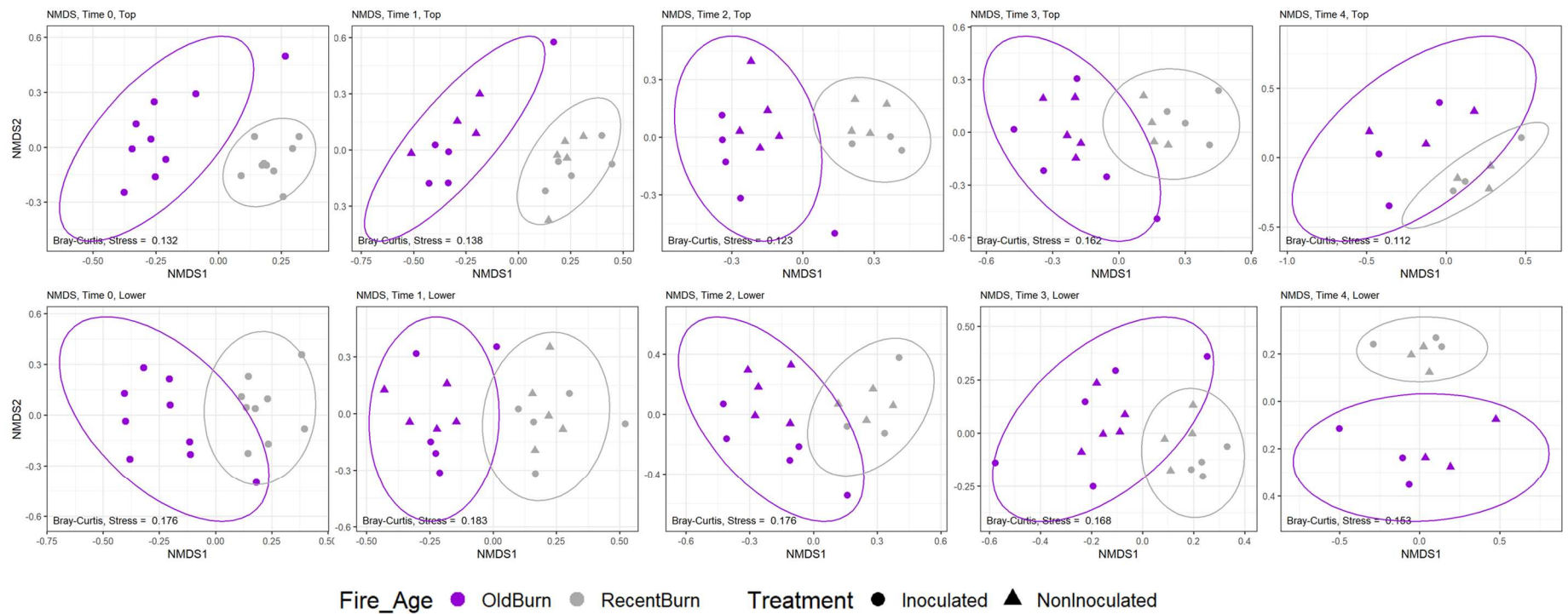


Figure 5. Non-metric multidimensional scaling (NMDS) ordination plot of the Bray-Curtis dissimilarity distances between the fungal (ITS2) communities of each sample at each time point and separated by soil layer (top = 0-5 cm and lower = 5-10 cm). Circles indicate inoculated samples and triangles indicate non-inoculated samples, colors indicate samples from the recent fire (grey) or old fire (purple).

Relative abundance of fungal guilds across planting conditions (2a/2b)

From the samples collected from seedling soils prior to planting, the inoculated treatment had significantly greater relative abundance of ectomycorrhizal fungi compared to the non-inoculated ($W = 100$, $p < 0.0001$; FIGURE 6). The EMF genus that was most prevalent in the inoculated samples was *Rhizopogon*, which was present in each inoculated sample collected, and contributed to an average of 15% of the fungal community (range 0.14% - 68.82%), followed by *Tuber* and *Geopora*, both contributing to an average of 1% of the fungal community across inoculated samples (Figure 6). EMF genera were present at very low abundance in the non-inoculated samples; *Tuber* was most abundant EMF genus, contributing to an average of 0.3% of the community.

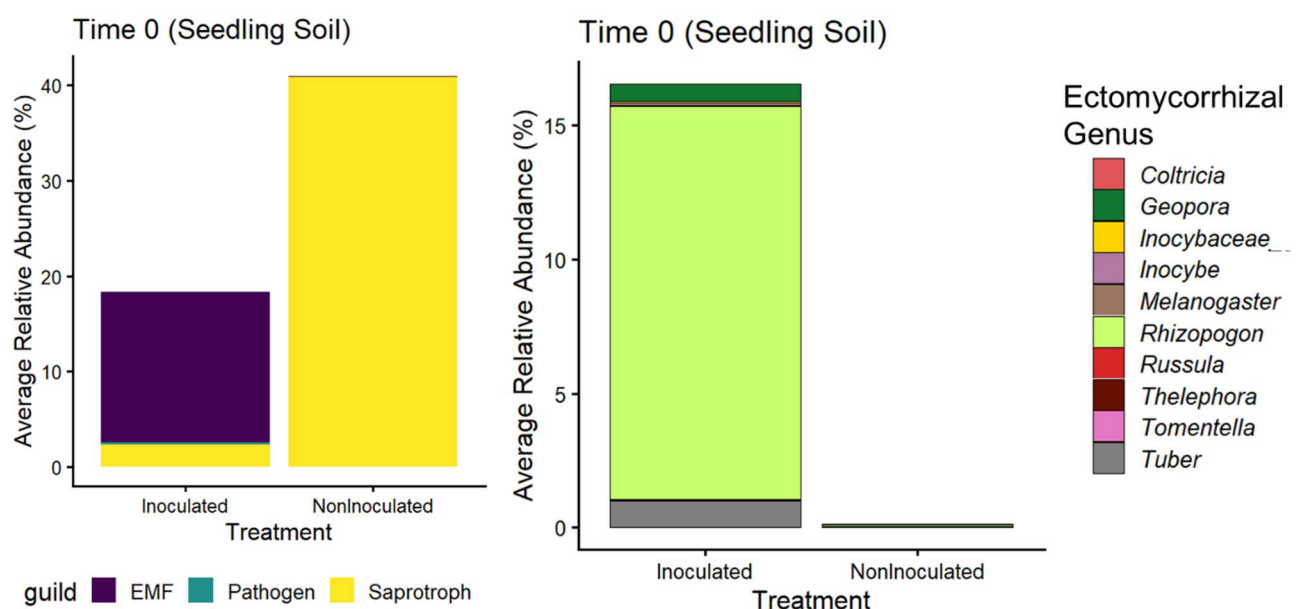


Figure 6. The left panel shows the average relative abundance of ectomycorrhizal (EMF; dark blue), pathogenic and parasitic (teal), and saprotrophic (yellow) guilds in the inoculated and non-inoculated treatment in the seedling soils collected prior to outplanting. The right panel shows the average relative abundance of EMF genera found in the two treatments.

In the baseline soil collected at Time 0, EMF relative abundances were not different between recent and old fires ($W = 55$, $p = 0.739$ top soil horizon; and $W = 48$, $p = 0.838$ in the

lower soil horizon, Figure 7, Table A2.5). Within each subsequent time point (Time 1 - Time 4), the relative abundance of EMF was not different among fire age $\times$ treatment combinations in either top or lower soil horizons ($p > 0.05$), indicating that inoculated seedlings did not have higher relative abundances of EMF.

Relative abundances of pathogenic and parasitic fungi were greater in the inoculated seedling soil than in the non-inoculated seedling soil ($W = 92$, $p = 0.002$). The relative abundance of pathogenic and parasitic fungi was greater in the old burn compared to the recent burn in the top-soil horizon ($W = 79$, $p = 0.029$) but was lower in the old burn compared to the recent burn in the lower-soil horizon ($W = 70$, $p = 0.043$, respectively) and did not follow consistent trends among fire age $\times$ treatment combinations. At subsequent timepoints, significant differences were found only in the top-soil horizon at Time 1 ($X^2 = 14.74$, $df = 3$, $p = 0.002$), where the old burn non-inoculated had greater and the recent burn non-inoculated had lower relative abundance of pathogenic fungi.

Relative abundance of saprotrophic fungi was greater in the non-inoculated seedling soil than the inoculated seedling soil ($W = 12$, $p = 0.003$). Relative abundance of saprotrophic fungi was greater in the recent burn compared to the old burn in the top soil horizon ($W = 11$, $p = 0.002$), but was not statistically different in the lower soil horizon ($W = 33$, $p = 0.356$). Relative abundance of saprotrophic fungi was not consistent among fire age $\times$ treatment combinations, with significant differences apparent only in the top soil horizon at Time 1 ($X^2 = 9.22$, $df = 3$, $p = 0.026$), and in the lower soil horizon at Time 2 ($X^2 = 8.57$, $df = 3$, $p = 0.036$). While pairwise comparisons did not pick up differences in Time 1, the means suggest recent burn had greater relative abundance of saprotrophic fungi compared to the old burn. At Time 2 in the lower soil

horizon, the old burn non-inoculated had lower relative abundance of saprotrophic fungi and the recent burn non-inoculated had greater.

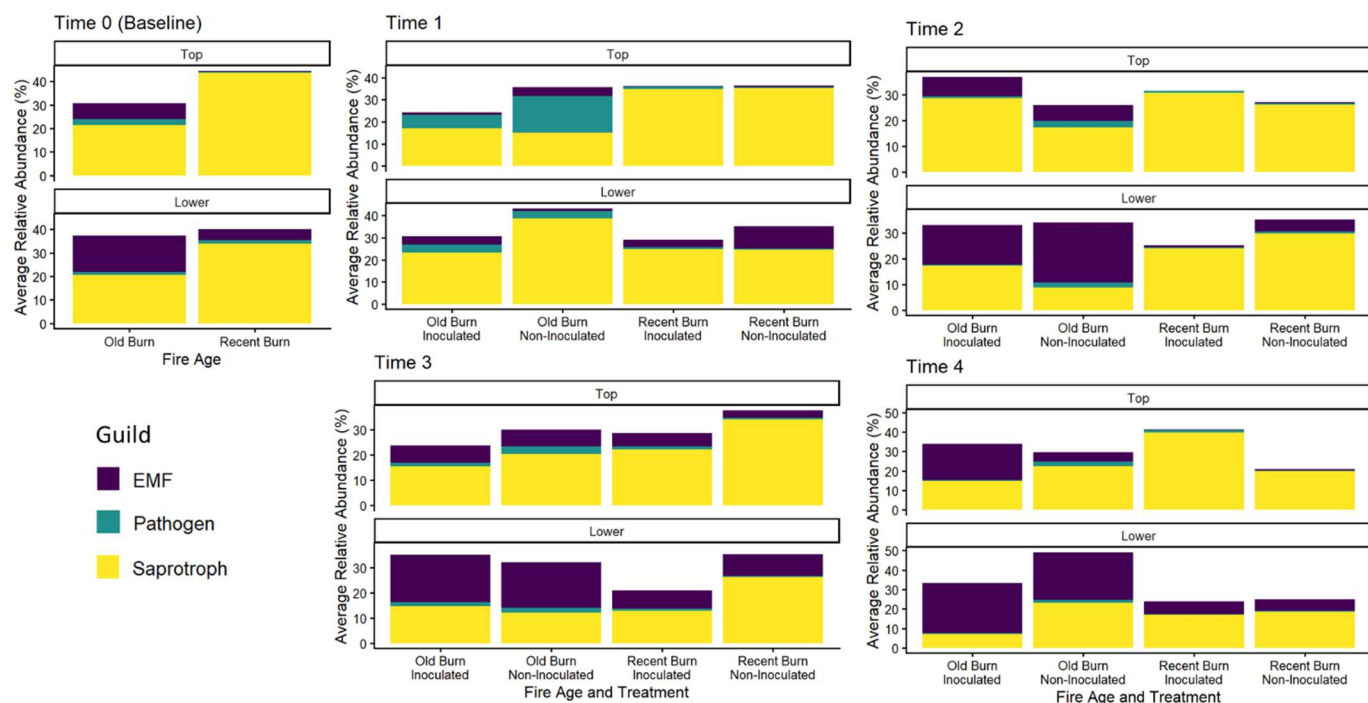


Figure 7. Average relative abundance of ectomycorrhizal (EMF; dark blue), pathogenic and parasitic (teal), and saprotrophic (yellow) guilds by fire age and treatment at each time point.

Relative abundance of ectomycorrhizal taxa across planting conditions (2a/2b)

Relative abundances of EMF genera were variable across treatment groups and over time (Figure 8). Most EMF genera overlapped across fire ages and inoculation treatments but varied in their relative abundance. Baseline genera most prevalent in the old burn were *Tuber*, *Tomentella*, and *Geopora*, whereas baseline genera most prevalent in the recent burn were *Clavulina* and *Russula*. The community composition of EMF genera near seedling roots differed between the inoculated and non-inoculated groups and dominant taxa shifted over time (Figure 8). At Time 1, the most prevalent genera in the old burn were *Polyozellus*, *Tuber* (inoculated), and *Geopora* (non-inoculated), and in the recent burn *Coltricia* (inoculated), *Tuber*, and

Clavulina (non-inoculated). At Time 2, most prevalent genera in the old burn was *Thelephora*, *Polyozellus* (inoculated), *Rhizopogon*, *Astreus* (non-inoculated), *Tuber*, *Geopora*, and *Melanogaster* (both treatments), and in the recent burn *Clavulina* (inoculated), *Tuber*, and *Russula* (non-inoculated). At Time 3, most prevalent genera in the old burn were *Polyozellus*, *Tomentella*, *Picoa* (inoculated), *Tuber*, *Astraeus*, *Geopora*, and *Melanogaster* (both treatments), and in the recent burn *Melanogaster*, *Astraeus*, *Tomentella* (inoculated), *Geopora*, *Tuber*, *Picoa* (non-inoculated), and *Inocybe* (both treatments). Lastly, at Time 4, most prevalent genera in the old burn was *Polyozellus*, *Thelephora*, *Genea*, *Rhizopogon* (inoculated), *Tuber* (non-inoculated), and *Geopora* (both treatments), and in the recent burn *Clavulina*, *Inocybe* (non-inoculated), and *Tuber* (both treatments).

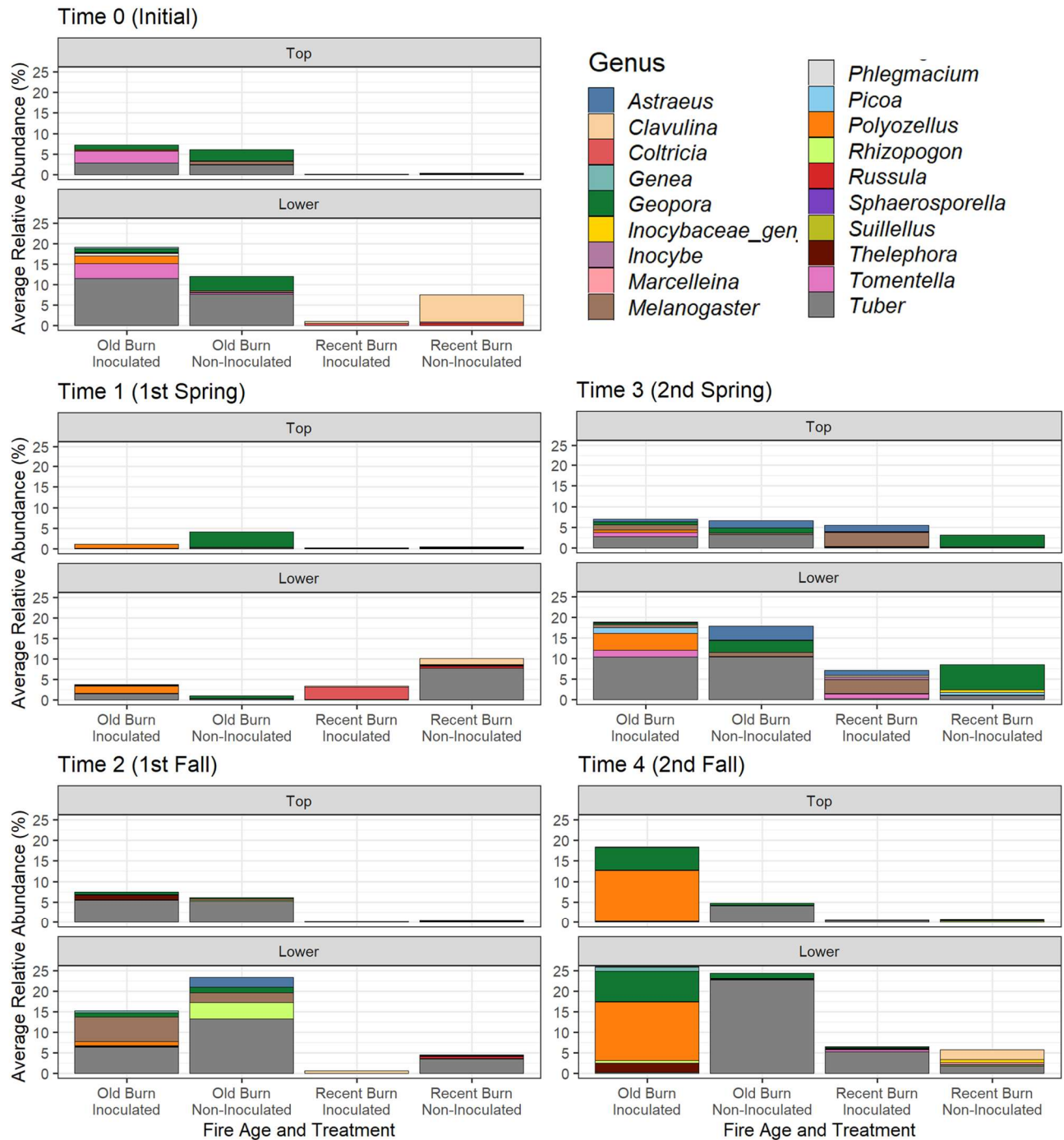


Figure 8. Average relative abundance of ectomycorrhizal fungi genera at each timepoint and across treatments. Bar is colored by genus, with colors noted in the legend. Note, that in the initial time 0, there are technically no “inoculated” or “non inoculated” samples. This time point, therefore, represents the spatial variability in the plot where inoculated and non-inoculated seedlings were planted.

Relative abundance of fungal guilds and influence on seedling survival (3)

When testing for the influence of the relative abundance of the different fungal guilds on seedling survival across timepoints, our models indicate that in the top soil horizon, a greater relative abundance of EMF is associated with seedling survival in the following fall ($p = 0.046$, Table 3), whereas the relative abundances of pathogens and saprotrophs do not significantly affect seedling survival. When looking at individual EMF genera, only *Tuber* had a marginally significant influence on seedling survival in the topsoil horizon (estimate = 9.68, std. error = 5.50, z -value = 1.76, $p = 0.0781$), while *Geopora*, *Tomentella*, *Clavulina*, *Russula*, and *Rhizopogon* were non-significant. All genera, besides *Tuber*, exhibited high estimates and standard errors, likely due to being zero-inflated. To account for this, we reran the models with a log transformation of the relative abundances with a pseudocount additive. Models were still not significant and had high estimates and standard errors.

Table 3. Output from general linear model (glm) with binomial regression testing the effect of the relative abundances of ectomycorrhizal fungi (EMF), pathogenic or parasitic fungi, and saprotrophic fungi the survival of planted seedlings at the subsequent fall.

	<i>Variable</i>	<i>Estimate</i>	<i>Std Error</i>	<i>z-value</i>	<i>p-value</i>
<i>Top (0-5 cm)</i>	Intercept	-0.537	0.857	-0.626	0.531
	EMF	8.549	4.290	1.993	0.046 *
	Pathogen/Parasite	0.057	4.833	0.012	0.991
	Saprotroph	-3.732	2.839	-1.315	0.189
<i>Lower (5 - 10 cm)</i>	Intercept	-0.596	0.702	-0.850	0.395
	EMF	2.727	1.818	1.500	0.134
	Pathogen/Parasite	-12.775	17.389	-0.735	0.463
	Saprotroph	-3.181	2.492	-1.277	0.202

Discussion

Biotic interactions, such as nurse objects and soil microbial communities, are influential components of ecosystems that can either alleviate or promote stress and dictate vegetation recovery response following wildfire. In this study, we examined how above- and below-ground biotic conditions influence planted piñon pine seedling survival and height growth. Surprisingly, seedling survival was not influenced by inoculation treatment or fire age, although inoculated seedlings exhibited greater height growth; survival was, however, greatest when seedlings were planted under Gambel oak and adjacent to logs. Fungal communities in recent burn and old burn soils exhibited different beta diversity, likely driven by the structure of fungal guilds where the old burn had a greater relative abundance of EMF taxa and the recent burn had more saprotrophic fungi. Greater seedling survival was seen in areas with higher relative abundances of EMF, but the relative abundance of specific EMF genera was not a significant predictor of seedling survival. These findings indicate that managers can use both above- and belowground biotic relationships when planting piñon pine in burned piñon-juniper landscapes.

Piñon seedling survival was most influenced by nurse object type

Seedling survival and seedling height growth were similar in the recent fire and the old fire, contrary to our hypothesis (1a). The condition that best supported piñon seedling survival in this experiment was planting seedlings under Gambel oak and adjacent to logs, aligning with our hypotheses (1b). However, the effectiveness of both nurse types was different in the two fire ages. In the recent fire, logs promoted much greater seedling survival compared to the old fire. In the old fire, Gambel oak promoted much greater seedling survival compared to the recent fire. This difference could be driven by a few mechanisms. First, the Gambel oak in the recent fire were shorter than in the old fire (average measured height in the new fire was 80 cm, median 72

cm, vs 148 cm mean, 166 cm median height in the old fire). Larger Gambel oak provide more shade than shorter oaks, which can influence microclimate conditions by less water loss and lower temperatures. Additionally, more litter cover and thicker leaf litter depth were observed accumulating under Gambel oak in the old fire compared to the recent fire, likely driven by time available to accumulate (27 years versus 3 years) and the amount of leaf litter produced from larger oaks. Litter cover contributes to greater soil moisture by providing a buffer from evaporation (Villegas et al. 2010), which is likely to increase seedling success. While soil moisture sensors indicated that the recent fire had greater soil moisture, moisture sensors were not measured beneath litter, therefore would not pick up on this microsite characteristic.

Orientation of the logs in recent and old fire were different, where logs in the recent fire were still standing, and logs in the old fire were downed. The difference in orientation may drive the differential influences logs had on seedlings in their respective fire. For example, when we planted the piñon seedlings near standing dead trees in the recent fire, dead tree roots on either side may have helped to limit water loss and provided a basin or depression for water to accumulate, increasing soil moisture available for seedlings (Marshall et al. 2023). It is also possible that the orientation of the standing log directed water flow to the base of trees, focusing the path of water movement and increasing soil moisture at the base of the tree. However, we are unable to find evidence in the literature to explain whether soil moisture is different between standing logs and downed logs, and the mechanisms that may drive this. What may be more telling is that in the old fire, the mean height of downed logs was 43 cm; therefore, downed logs may not provide much shade at peak radiation compared to seedlings nestled into the north-facing base of a standing tree. Regardless, while seedling survival was enhanced by planting at

the base of standing dead trees, dead trees will eventually fall, thus risking crushing or uprooting planted seedlings, making them a potentially less optimal nurse object for manual tree planting.

We saw little seedling survival in the open, in grass, and next to rocks, likely due to high exposure. Interestingly, US Forest Service tree planting guide lists stumps, rocks, and large down logs as the best site protection to sun exposure, but our study shows that these objects are not effective at increasing seedling survival (<https://www.fs.usda.gov/t-d/seedlings/planting/>).

Seedlings in the grass were generally found uprooted and trampled by grazing cows, therefore grazing highly influenced the survival of seedlings planted in grass. Utah serviceberry were also tall and spacious in the old burn, short in the recent burn, and had a high amount of litter collected underneath. We are uncertain why Utah serviceberry had low survival – *Tuber* was found in relatively high abundances under this nurse plant (Figure A2.3), and soil moisture was likely high. Future work may disentangle the mechanisms for why Utah serviceberry is not a good nurse object, exploring water and nutrient use and other plant-soil feedbacks which may inhibit or compete with young piñon seedlings.

Inoculation treatment did not increase seedling survival and had no observable influence on the soil fungal community

Inoculation, when initiated in the greenhouse, had no effect on outplanted seedling survival, and only a marginal effect on seedling growth, counter to our hypothesis (1c). Prior to planting, inoculated soils had a greater relative abundance of EMF compared to non-inoculated soils, with *Rhizopogon* as the most abundant EMF genus. Although *Rhizopogon* is commonly found in mature piñon stands (Andrews and Gehring 2020), its dominance here is consistent with expectations given its frequent association with young trees and low carbohydrate demand (Kałucka and Jagodziński 2017). Pathogenic and parasitic fungi accounted for 0.2 and 0.03% of

the inoculated and non-inoculated fungal communities, respectively, suggesting minimal introduction of harmful fungi upon planting; however, these levels did not appear to influence seedling survival over the course of the experiment. Non-inoculated soils supported a microbial community as well, although it was dominated by saprotrophic fungi. Taken together, the whole-soil inoculum successfully established seedlings with ectomycorrhizal fungi prior to outplanting, indicating that insufficient EMF colonization was not responsible for the lack of inoculation effect on seedling survival and growth.

While seedlings were successfully inoculated with EMF, these effects did not persist in the broader soil community after planting. The richness and diversity metrics, along with relative abundance of EMF, were not significantly different by inoculation treatment, contradicting our expectations (2b). While EMF community composition varied across subsequent sampling time points, this variability was mirrored in both inoculated and non-inoculated samples, suggesting that observed shifts were driven by seasonal fluctuations (Castaño et al. 2017) and spatial differences in soil cores rather than inoculation treatment. Had inoculation produced lasting effects, *Rhizopogon* – given its fast growth and colonization abilities (Molina and Trappe 1994) – should have remained at elevated abundances over time. Instead, *Rhizopogon* was consistently rare across all time points and treatments (including baseline samples), generally comprising less than 0.2% of the EMF community. The only exceptions were Time 2 in old burn non-inoculated samples and Time 4 in old burn inoculated samples, where this genus ranked among the top-five most abundant EMF taxa.

Consistent with this, fire age was the primary driver of differences in beta diversity across time points, aligning with our expectations, although alpha diversity metrics were not different across fire ages. Together, these results suggest that planting seedlings, regardless of

inoculation status, may have minimal influence on the surrounding soil microbial community (Menkis et al. 2007), contradicting our expectations (2b).

Ectomycorrhizal communities were present in the post-fire environment

Relative abundances of EMF were similar across fire ages and treatments, although the community members differed. Prevalent taxa in the old burn included *Tuber*, *Tomentella*, and *Geopora*, while *Clavulina* and *Russula* were more common in the recent burn. Soils collected from under mature piñon in Sunset Crater, AZ indicated that *Geopora* and *Rhizopogon* were the most abundant EMF associated with mature piñon woodland soil (Andrews and Gehring 2020). Other research in PJ woodlands in Arizona has previously identified *Tuber*, *Tomentella*, and *Russula* as other genera that commonly appear as piñon symbionts (Haskins and Gehring 2004, Gehring et al. 1998, and Hubert and Gehring 2008). Our models indicated that greater relative abundance of EMF, regardless of species, was related to survival to the next fall. This suggests that there is potential EMF inoculum for piñon pine present post-fire, even after just three years, which can influence seedling survival.

We note that relative abundances should not be conflated with absolute abundances (Alteio et al. 2021). Relative abundance reflects the proportion of a given taxon within the total microbial community in a sample, whereas absolute abundance refers to the total quantity of that taxon present. Consequently, a taxon may appear highly abundant in relative terms while still being low in absolute abundance. Relative abundances still provide valuable information on community structure, but should be interpreted with caution when comparing samples as differences may reflect compositional effects rather than true changes in total abundance.

With that said, the dominant EMF genera differed between sites in a way that appears counterintuitive; genera found in the recent fire (*Clavulina* and *Russula*) are typically associated

with later-succession soil communities, while genera found in the old fire (*Tuber*, *Tomentella*, and *Geopora*) are more characteristic of early-successional systems (Kalucka and Jagodzinski 2017, Fugimura et al. 2006). Outlined in Kalucka and Jagodzinski (2017), EMF genera associated with early-successional and disturbed systems tend to associate with younger trees, have low carbohydrate demand, exploit easy-access inorganic nutrients, and employ ruderal colonizing strategies characterized by rapid mycelial growth and dispersal through sexual spores. Conversely, late-successional EMF associate with older trees, have high carbohydrate demand and obtain nutrients from less accessible organic pools. Although dominant genera varied across sampling times, early-successional EMF (old: *Thelephoria*, *Rhizopogon*; recent: *Inocybe*, *Coltricia*; both fires: *Tuber*, *Tomentella*) appeared in both fire ages. Nevertheless, the old fire site consistently harbored more early-successional taxa, while the recent fire was more frequently dominated by late-successional species such as *Clavulina* and *Russula*.

Two notable exceptions were *Polyozellus*, found almost exclusively in the old fire and considered to be an indicator of old growth forests (Svantesson et al. 2021) and *Genea*, which is typically associated with *Quercus* species and may reflect the well-established Gambel oak present at that site (Smith et al. 2006). The unexpected presence of late-successional species in the recent fire may reflect genetic legacies in the soil, since DNA sequencing captures genetic information from both living and dead organisms. Alternatively, spores of these taxa may be persisting in the spore bank, and have not yet been outcompeted or displaced by other fungal taxa (Horton et al. 1998). Further, successional pathways for EMF may be different in different forest types, wet versus dry systems, and systems adapted to different fire regimes.

It is possible that the greater survival of seedlings in the old burn under Gambel oak was related to a higher abundance and diversity of EMF found in the samples collected under Gambel

oak (Figure A2.2). Our sampling design was not designed to thoroughly disentangle the EMF community differences between nurse objects (two samples per nurse object per fire at each timepoint). However, modifications of the mycorrhizal community by shrubs can contribute to nurse shrub effects through plant-soil feedbacks that shift nutrient cycling and change levels of pathogens and mutualists available to seedlings (Rodríguez-Echeverría et al. 2016), and Gambel oaks in particular share a portion of EMF taxa with piñon (Fernandez et al. *in review*). This provides argument for further investigation of nurse object biotic communities and their potential to act as piñon seedling inoculum of beneficial microbes – not just provide shade.

Study limitations and opportunities for future study

Prior to outplanting, the soil surrounding inoculated seedlings was dominated by *Rhizopogon* genus and lacked more beneficial taxa such as *Geopora* and *Tuber*. Seedlings were relatively well-watered prior to planting; this lack of stress conditions may have limited the development of beneficial relationships between seedlings and EMF. This may have also driven the lack of lasting effects for the inoculation treatment. Future research may induce stress or additional “seedling hardening” techniques at the greenhouse stage to influence the community selection of more beneficial microbes. Communities selected via stress treatments may also be compared to community members and associations formed under less stressful conditions.

EMF presence in the soil does not indicate root colonization of the host, thus assessing root colonization and comparing with fungal members found in the soil across treatments would better identify the likelihood of seedling success at different fire ages with different EMF community present. However, even where inoculation results in higher root colonization, improved survival and plant performance may not occur (Reid 2024; Maltz and Treseder 2015). Next steps in this research are identifying the fungal taxa and percent colonization of EMF on

piñon roots and determining whether differences exist across treatments. Lastly, since we did not sample dead seedlings, we do not know whether an absence or presence of certain fungi influence seedling mortality.

While Gambel oak seems to be a promising nurse object for piñon seedlings, more work needs to be done to understand mechanisms and limitations to their facilitative nature. What specifically about Gambel oak increases seedling survival compared to other shrubs, such as soil moisture or sun radiation to the young seedling? We also need to understand how long Gambel oak is beneficial – is this occurrence only for young piñon with shorter roots, or does the beneficial relationship persist to when piñon are older? Further, what are the environmental conditions – wet versus dry seasons or years – where Gambel oak is more beneficial? And lastly, while our work hinted at the potential for Gambel oak to provide inoculum to piñon seedlings, do Gambel oak and piñon share similar EMF communities, and are the EMF associated with increased piñon seedling survival and positive growth? Any of these questions will better help us to understand the limitations to Gambel oak as a preferential nurse object and whether this is a relationship that should be promoted by land managers.

Conclusion

Nurse objects played a key role in seedling survival, with seedlings planted under Gambel oak and adjacent to logs having highest survival rates, albeit still only ~70% and ~55%, respectively. While seedlings with inoculated soil had a significantly higher relative abundance of EMF prior to planting, the soil fungal communities next to planted seedlings were quickly overcome by the local soil communities, resulting in no sustained differences in EMF relative abundance across inoculation treatments or fire ages. Seedlings with a higher relative abundance of EMF were more likely to survive to the following fall, but specific EMF genera responsible

for survival were not identified. There is still much to understand regarding the biotic interactions that result in successful piñon seedling establishment post-fire. However, it is clear that planting seedlings under Gambel oak is most effective at supporting seedling survival, at least within the first two years.

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Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author contributions

Jamie Woolet: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision; **Camille Stevens-Rumann:** Conceptualization, Writing-editing draft, Supervision, Project administration, Funding acquisition; **Caroline Havrilla:** Funding acquisition, Resources, Writing – review & editing; **Michael Wilkins:** Conceptualization, Writing – review & editing; **Catherine Gehring:** Conceptualization, Writing – review & editing; **Gillian Trimber:** Writing – review & editing; **Michael Battaglia:** Writing – review & editing

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CHAPTER 4

Assessing evapotranspiration dynamics post-wildfire: a case study of vegetation type conversion

Abstract

The trajectory of forest recovery after wildfires significantly impacts long-term ecosystem processes and services, particularly through changes in vegetation type. While much post-fire hydrological research focuses on short-term impacts, such as flooding and erosion, the longer-term effects on evapotranspiration (ET) remain underexplored. This study investigates how fire severity and vegetation recovery influence ET rates following wildfire. Using remote sensing data products, we analyze wildfire and recovery patterns from six fires that occurred in 2002 to investigate how fire-induced vegetation change influences ET and ET:Precipitation in the short- (1-2 years after wildfires) and long-term (20-22 years after wildfire). Linear mixed effects models showed that pixel-level changes in dominant vegetation type causes greater departure in ET and ET:P both 1 and 20-years after wildfire. Overall, our Random Forest models show that while climate variables (i.e., temperature, max vapor pressure deficit, and precipitation) set the potential for ET, vegetation change, namely evergreen cover, dictate ET rates and ET departure from pre-fire rates to 1 and 20 year levels. This research enhances our understanding of how high-severity fires and subsequent vegetation shifts influences water dynamics over time, informing future management and restoration efforts.

Background

Vegetation cover types across the globe are shaped by and have evolved alongside particular climate and disturbance regimes. Disturbances, whether from insects, disease, fire, or human activity, interact with local and regional climate and topography to serve as major controls on vegetation dynamics and community assembly (White 1979, Thonicke et al. 2001). Among these, fire has played a particularly influential role over long timescales, shaping vegetation communities (Keeley et al. 2011). Fire strongly influences landscape vegetation structure and composition via characteristics of the fire regime. Any change in the regime - including frequency, severity, intensity, size, seasonality, or spatial heterogeneity - can profoundly affect post-fire vegetation trajectories (Johnstone et al. 2016).

Forested ecosystems in the western US are seeing substantial shifts in fire activity and behavior in response to a combination of fuel accumulation and fuel aridity. Fuel build-up are largely driven by historic fire suppression (Roos et al. 2020), removal of Indigenous people and Indigenous burning practices (Roos et al. 2021), introduction of agricultural grazing (Swetnam et al. 2016). Fuel aridity and flammability dynamics often attributed to hotter and drier climate (Parks and Abatzoglou 2020, Crimmins et al. 2025, Parks et al. 2025), reduced snowpack, and earlier snow melt (Balik et al. 2026). While size of wildfires is not necessarily unprecedented in many western forest types (Parks et al. 2025), fire behavior and burn severity? are. Specifically, fires that burn more severely (McClure et al. 2024) more heterogeneously (MacFarland et al. 2025), or more frequently (Turner et al. 2019) are linked to long-term ecosystem effects, such as reduced ability for conifer recruitment (Stevens-Rumann et al. 2019, Davis et al. 2023).

Forest cover types at different elevations and latitudes show different changes in their respective fire regimes. For example, wet mid- to high-elevation mixed conifer forests in the

Colorado Rockies, while adapted to large, infrequent high-severity wildfire, are burning more frequently than historically (Higuera et al. 2021). Short-interval reburning in *Pinus contorta* forests can inhibit post-fire recovery by consuming trees before they can produce an adequate crop of fire-adapted cones, leading to sparser forest regeneration (Turner et al. 2019). Dry, low-elevation *Pinus ponderosa* forests in the Southern Rockies are adapted to frequent low-severity or mixed-severity fires but are seeing increases in large high-severity wildfires (Singleton et al. 2019). Within large high-severity burn patches, conifer recruitment, especially in dry forests, is often limited to nearby seed sources (Chambers et al. 2016). Long term shifts to non-forests states are currently being observed, especially in large, burned patches (Woolman et al. 2022). In other dry forest types in the western US, such as piñon-juniper (PJ), historical fire regimes are quite variable due to the compositional and structural aspects of this vegetation type (Romme et al. 2009). However, in regions of PJ that are tree-dominated (i.e. persistent woodlands), fire is generally considered to be infrequent and high-severity, with fire spread driven by dry climate and windy conditions that promote canopy fire, as opposed to surface fuel-related drivers (Vankat 2013). Persistent PJ woodlands are experiencing regime shifts via increases in burned area, and in some regions, increases in burn frequency (Board et al. 2019). With increased area burned, we see decreased conifer recruitment within the interior of burned patches due to lack of surviving trees and increased distance to seed source (Woolet and Stevens-Rumann, *in revision*), as well as invasive grass establishment (Floyd et al. 2021, Philips et al. 2024, Woolet and Stevens-Rumann, *in revision*).

The close relationship between vegetation communities and fire regimes is further strained by a changing climate, which has led to hot and dry environmental conditions that are outside species adaptations (Coop et al. 2020, Guiterman et al. 2022). While seed-dispersal

limitations may physically inhibit seeds from reaching certain areas of a burned patch, anomalously hot and dry post-fire conditions increasingly limit the recruitment success of many tree species (Stevens-Rumann et al. 2018, Davis et al. 2019, Kemp et al. 2019). This trend is especially pronounced in forests that are at the boundary of their species range, such as dry low elevation forests and lower latitude forests (Davis et al. 2023). The compounded effects of altered fire regimes and climate can result in vegetation type conversions, defined as a lack of tree recruitment that leads to a fundamental shift in the dominant plant community (Guiterman et al. 2022). This has been observed across different forest types in the US, predominately in lower-elevation dry forests, where the post-fire plant community is dominated by persistent shifts to resprouting shrubs (ponderosa pine to Gambel oak; e.g., Coop et al. 2016, Rodman et al. 2020), or grasses (Douglas-fir to grass/steppe; e.g., Donato et al. 2016).

High-severity wildfire and alternative post-fire vegetation trajectories, especially forest loss, have significant implications for long-term ecosystem processes and ecosystem services (Hurteau et al. 2014, Breshears et al. 2011). One concern is how wildfires influence short- and long-term watershed hydrology (Moazeni and Cerda 2024). In the western US, most of the drinking water comes from forested systems (Liu et al. 2021), therefore fire-induced changes to the water budget, specifically, how much water from a burned landscape ultimately reaches headwater streams and downstream communities, is of particular concern. The water budget can be simplified as a balance of inputs (precipitation) and outputs (evapotranspiration [ET], sublimation, and discharge). ET is loss of water through soil evaporation (E) and plant transpiration (T). ET tends to increase with increasing abiotic factors like vapor pressure deficit (VPD), net radiation, and wind speed. ET is also highly influenced by plant type (Zhang et al. 2001), where differences in plant size, surface area, and water use strategies (anisohydry vs

isohydry; Poulos et al. 2021) can lead to increases or decreases in ecosystem ET. Persistent transitions from tree-dominated systems to shrub- or grass-dominated systems can cause shifts in ET dynamics (Montes-Helu et al. 2009, Goeking and Tarboton 2020, Collar et al. 2022, Collar et al. 2023). Additionally, transition from overstory- to understory-dominated vegetation can indirectly alter ET by influencing surface energy balance, such as net radiation and wind speed (Goeking and Tarboton 2020).

In the western US, fire affects ET at different temporal scales, with variability tied to fire severity and vegetation recovery patterns. ET tends to decrease immediately post-fire, (Poon and Kinoshita, 2018; Ma et al. 2020), with watersheds that have a higher proportion burned at high-severity exhibiting greater departures in ET compared to low-severity fire, relative to pre-fire rates. ET reduction can persist for 15 - 40 years, depending on how quickly vegetation returns to pre-fire vegetation functional types (Niemeyer et al. 2019, Ma et al. 2020), but may be permanently altered if vegetation conversion occurs (Collar et al. 2024). With that said, immediate ET responses are variable across the landscape; for example, dry forest types that become quickly dominated by resprouting shrubs can show an increase in ET rates compared to pre-fire conditions due to the density they regenerate and their water use strategies (Poulos et al. 2021). Despite the growing recognition that vegetation trajectories can shift post-fire from their historical state, there is still a lack of understanding on how these shifts alter ET at multidecadal timescales, and whether these long-term changes in ET can be directly linked to vegetation shifts.

Changes in ET after fire, when compared to pre-fire conditions, are influenced by fire severity, vegetation type and functional traits, and plant cover. As ET plays a vital role in regulating water retention within ecosystems and influences downstream water yield (Brown et

al. 2005, Collar et al. 2022), it is essential to predict how large, high-severity fires and potential conversion will alter long-term ET. Persistent or long-term vegetation shifts can fundamentally change how water is used and processed within ecosystems, and changes in ET can in turn influence vegetation recovery and successional trajectories due to altering soil moisture and how water is stored or lost. The objectives of this study are to 1) illustrate short- and long-term changes in monthly and annual ET and ET:precipitation from 20-year-old fires and 2) determine the driving causes of these changes. We hypothesize that ET will be reduced in the short term but will recover to near pre-fire levels where tree regeneration is substantial. We further expect that site-specific factors, including topography (slope and heat load index) and fire severity, will strongly influence post-fire ET rates. This study contributes to a growing understanding of the long-term effects of wildfire on ecosystem water use by explicitly linking ET dynamics to post-fire vegetation change. The results will help inform forest restoration strategies, improve representation of post-fire processes in hydrological models, and enhance predictions of watershed response following wildfire.

Methods

Study area

Monitoring Trends in Burn Severity (MTBS, <https://www.mtbs.gov/>) was used to select 20+ year old large (>25,000 hectares) fires that occurred in Colorado, New Mexico, Arizona, and Utah between 2000 - 2002. This resulted in six wildfires from 2002, including Hayman, Missionary Ridge, Ponil Complex, Rattle Complex, Rodeo-Chediski, and Sanford (Table 1, Figure 1). Before the fires, all regions were predominantly evergreen forest with patches of shrubland; Missionary Ridge, the highest elevation forest included in this study, was mostly evergreen, but also had deciduous and mixed-forest present (Figure 2). All fires burned at a

range of severities, and all ignited in late-May to mid-June, showing typical seasonality for the southwest.

Table 1. Fires selected for this study with the location, ignition date, area burned, and the percent of the fire that burned at high severity (dNBR4), moderate severity (dNBR 2 and dNBR3), and low severity (dNBR 1).

Fire	Location	Ignition Date	Area Burned (hectares)	% High Severity	% Moderate Severity	% Low Severity
Hayman	Colorado	06-08-2002	52,373	36%	29%	18%
Missionary Ridge	Colorado	06-09-2002	27,891	21%	37%	13%
Ponil Complex	New Mexico	06-08-2002	36,051	26%	29%	24%
Rattle Complex	Utah	06-20-2002	35,368	17%	52%	1%
Rodeo-Chediski	Arizona	06-18-2002	186,873	33%	.44%	14%
Sanford	Utah	05-31-2002	33,125	15%	37%	30%

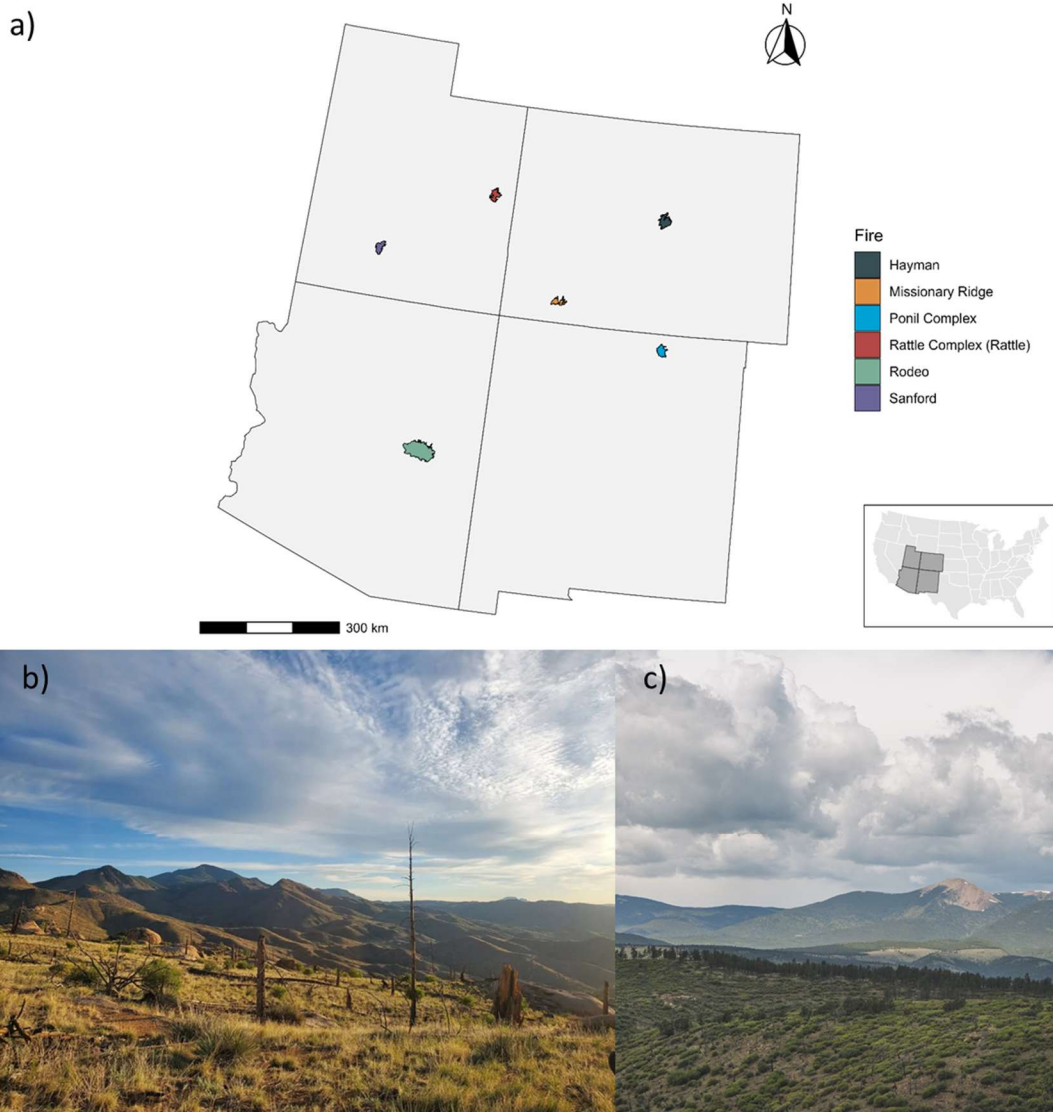


Figure 1. a) Location of the 2002 fires included in this study (grey = Hayman, orange = Missionary Ridge, blue = Ponil, red = Rattle, green = Rodeo-Chediski, purple = Sanford). b) Hayman Fire 20-years post-fire (photo credit: Jamie Woollet) and c) Ponil Fire 20-years post-fire (photo credit: Alex Smilor).

Spatial data acquisition

Fire perimeter shapefiles and dNBR6 fire severity rasters were downloaded from MTBS (Eidenshink et al. 2007). DNBR6 is derived from the differenced normalized burn ratio (dNBR), classifying burn severity into categorical classes (1 = unburned/low severity, 2 = low severity, 3 = moderate severity, 4 = high severity, 5 = increased greenness, and 6 = non-processed area).

DNBR is calculated by

$$dNBR = NBR_{pre-fire} - NBR_{post-fire}$$

where, normalized burn ratio (NBR) is calculated by

$$NBR = \frac{NIR - SWIR}{NIR + SWIR}$$

Here, green vegetation has a high reflectance of near-infrared (NIR) light, and strongly absorbs short-wave infrared (SWIR; Key and Benson 2006). This results in low NBR values and high dNBR values for areas that burned at high-severity.

OpenET SSEBop Monthly Evapotranspiration v2.0 (OpenET, Melton et al. 2021) data were downloaded using Google Earth Engine for the periods Jan 2000 – Dec 2001 (pre-fire), Jan 2003 – Dec 2004 (1-year post-fire), and Jan 2022 – Dec 2024 (20-years post-fire). The SSEBop model estimates actual ET (AET) by using satellite measurements of land surface temperature combined with reference evapotranspiration from gridded climate data to estimate how much water is being lost from the land surface (Senay et al. 2022). The model also uses vegetation information, such as the Normalized Difference Vegetation Index (NDVI), long-term average maximum air temperature, and net radiation to help improve the estimates (https://developers.google.com/earth-engine/datasets/catalog/OpenET_SSEBOP_CONUS_GRIDMET_MONTHLY_v2_0#description). SSEBop model was selected (as opposed to other available datasets like ECOSTRESS) because it has been shown to provide comparable pre- and post-fire ET estimates as eddy covariance flux towers (Poon and Kinoshita 2019, Collar et al. 2024) and is readily usable with minimal pre-processing steps (i.e. does not require cloud filtering).

Climate monthlies (precipitation (ppt), mean temperature (tmean), max vapor pressure deficit (vpdmax)) from all months within years 2000-2001 (pre-fire), 2003-2004 (1-year post-fire), 2022-2024 (20-years post-fire) were downloaded from Parameter-elevation Regressions on

Independent Slopes Model (PRISM, PRISM Group, Oregon State University, <https://prism.oregonstate.edu>, accessed 16 Dec 2025) using the PRISM api package *prism* (Hart and Bell 2015) in R. PRISM estimates climate conditions by combining measurements from weather stations with elevation, coastal effect, temperature inversions, and terrain barriers. Climate normals (20-year mean) for annual precipitation, mean temperature, max vapor pressure deficit, were also downloaded.

National Land Cover Database (NLCD) annual land cover rasters were downloaded from the Multi-Resolution Land Characteristics Consortium (USGS 2024) for years 2001 (pre-fire), 2003 (1-year post-fire), and 2023 (20-years post-fire). NLCD provides broad land cover from Landsat satellite imagery and other supplemental datasets, producing 30-m resolution rasters that classify land into standard categories.

Elevation datasets were accessed and downloaded on open topography (USGS 2021). USDA soil texture classes (OpenLandMap, Heigl 2018) were downloaded through Google Earth Engine. A full list of data, data sources, data download dates, initial resolution, and pre-processing steps can be found in Table 2.

Table 2. Spatial data sets used in analysis, including the variable, years (if applicable), data source, the source resolution, and the spatial pre-processing steps. All data were reprojected to Lambert Conformal Conic coordinate reference system based on NAD83 (lat1 = 31°, lat2 = 40°, lat0 = 37°, lon0 = -109°) and were either aggregated or resampled to match the ET grid (~1 km). Full pre-processing details can be found in the SI.

Variable	Years	Source	Source Resolution	Date Accessed	Pre-processing (summary)
Monthly ET	2000, 2001, 2003, 2004, 2022, 2023, 2024	OpenET SSEBop	1000 m	Nov 5, 2025	Reprojected to analysis CRS; cropped and masked to fire perimeters
Fire Severity (dNBR6)	2002	MTBS	30 m	July 27, 2025	Reprojected; aggregated to

					analysis grid; cropped and masked
Climate monthlies (Precipitation, mean temperature, max vapor pressure deficit)	2000, 2001, 2003, 2004, 2022, 2023, 2024	PRISM	~4 km	Nov 12, 2025	Resampled to analysis grid (bilinear); cropped and masked
Climate normals (precipitation, mean temperature, max vapor pressure deficit)	20-year mean	PRISM	~4 km	Nov 12, 2025	Resampled to analysis grid (bilinear); cropped and masked; used to compute climate anomalies (z- score)
NLCD land cover	2001, 2003, 2023	MRLC / USGS	30 m	Nov 14, 2025	Reprojected; aggregated to proportional cover at analysis grid; cropped and masked
Elevation	—	OpenTopography DEM	30 m	March 6, 2026	Reprojected; aggregated to mean elevation at analysis grid
Soil texture	—	OpenLandMap Soil Texture Class (USDA)	250 m	March 5, 2026	Reprojected; aggregated to proportional cover at analysis grid
Heat load index (HLI)	—	Derived from DEM	30 m	—	Calculated from DEM (spatialEco package); reprojected and aggregated to analysis grid

Spatial data pre-processing

All spatial pre-processing steps were conducted in R (R version 4.5.1) using the *terra* (Hijmans et al. 2023) and *tidyverse* (Wickham 2017) packages. A summary of the pre-processing steps can be found in Table 2.

For each ET raster (one for each month of the seven years), data were projected to a Lambert Conformal Conic coordinate reference system based on NAD83 ($\text{lat1} = 31^\circ$, $\text{lat2} = 40^\circ$, $\text{lat0} = 37^\circ$, $\text{lon0} = -109^\circ$), selected to minimize spatial distortion across the southwestern United States. Fire perimeter polygons were projected to the same coordinate reference system to ensure spatial alignment. Each monthly ET raster was cropped to the spatial extent of each fire perimeter and masked to retain only grid cells located fully within the fire perimeter. Monthly climate rasters (monthly ppt, monthly tmean, monthly vpdmax; one for each month of the seven years) were downscaled from their native ~ 4 km resolution to a 1 km grid by resampling each raster to match the spatial resolution, extent, and coordinate reference system of the corresponding monthly ET raster. Resampling was performed using bilinear interpolation. Bilinear interpolation calculates values of a grid location by taking the weighted average of the four neighboring cells, which is useful for working with continuous datasets. Downscaled monthly climate rasters were cropped to individual fire perimeters and masked to retain only grid cells entirely within the fire perimeter, similar to the steps conducted for ET. Preprocessing steps were applied consistently across all ET and PRISM rasters.

Annual NLCD rasters were processed separately for each fire perimeter. For each fire, NLCD rasters were cropped to the fire boundary in their native coordinate reference system and then reprojected to match the coordinate system of a reference ET raster. NLCD rasters were spatially aggregated to match the ET grid resolution. Aggregation was performed by calculating

the proportion of underlying NLCD pixels belonging to each land cover class, using an aggregation factor computed by taking the resolution of ET raster divided by the resolution of the NLCD raster. Following aggregation, proportion of each vegetation class layers were resampled to align exactly with the ET grid and masked to the fire boundary using bilinear interpolation because the aggregated rasters now contain a continuous proportion metric. The resulting raster stack represents pixel-level proportion land cover composition. Fire severity and soil texture rasters were similarly processed as NLCD, resulting in a raster stack of the proportion of each dNBR6 severity classes within each pixel and a raster stack of proportion of soil texture classes in each pixel.

DEM rasters were processed similar to the above, except with resampling being calculated with nearest neighbor. The final raster included the mean elevation calculated for each pixel, masked to each fire perimeter. From the original DEM rasters, slope and heat load index (HLI) were calculated using the *spatialEco* package (Evans and Ram 2021). HLI is calculated following McCune and Heon (2002). After calculating slope and HLI, rasters were similarly reprojected, aggregated, and resampled to obtain mean slope and HLI per pixel for each fire.

Data processing

ET trends for each month of the calendar year were assessed for each fire perimeter. The mean ET value of each ET raster file (each representing a single month) was calculated across all non-missing pixels within the fire boundary. Because each raster pixel represents $1,000 \text{ m}^2$, the resulting values correspond to mean ET per $1,000 \text{ m}^2$ for each calendar month. Monthly trends for ET:P were similarly calculated by dividing monthly ET rasters by corresponding monthly precipitation rasters and then calculating the mean ET:P value across all non-missing pixels within each fire perimeter. If a date had 0 mm of precipitation, a small pseudocount

(0.0000000001) was input, so that ET was not divided by zero. Dataframes were created from the ET and ET:P rasters for each fire, which were merged, retaining reference coordinates for data alignment. Mean monthly values pre-fire (Jan 2000 – Dec 2001), 1-year post-fire (Jan 2003 – Dec 2004), and 20-year post-fire (Jan 2022– Dec 2024) timeframes were calculated.

Annual ET was calculated by aggregating monthly ET rasters and summing pixel-level monthly values for each year for the entire year. Mean annual ET was calculated for pre-fire (2000 – 2001; $n = 24$ months), 1-year post-fire (2003 – 2004; $n = 24$ months), and 20-year post-fire (2022 – 2024; $n = 24$ months), by averaging annual ET rasters within each period. ET departures were computed as the difference between pre-fire mean annual ET and post-fire mean annual ET for both post-fire intervals.

Mean annual precipitation, t_{mean} , and vpd_{max} were calculated for the same time periods as ET. Monthly precipitation was summed to annual totals and averaged within each time period, while t_{mean} and vpd_{max} were averaged within each period. The ratio of annual ET to annual precipitation (ET:P) was calculated for each time period. Annual ET:P ratios greater than 1 indicate that there is more evaporation than precipitation received in a system, while less than 1 indicates that precipitation exceeds evaporation. Proportion of total precipitation received as summer precipitation (proportion summer precipitation) was calculated as the ratio of total precipitation occurring during the summer months (June - September) to total annual precipitation for each time period.

Long-term climate anomalies were calculated for precipitation, t_{mean} , and vpd_{max} from 20-year averages from PRISM. Climate anomalies for each pixel were expressed as z-scores by subtracting the long-term mean from the pre-fire, 1-year post-fire, and 20-year post-fire means and dividing by the long-term standard deviation.

Derived raster layers were converted to pixel-level dataframes retaining x–y coordinates and cell values. Dataframes were merged by spatial coordinates to create a final metadata file for each fire.

Data analysis

Mann-Whitney U tests were used to compare annual average ET and annual average ET:P between pre-fire (2000 – 2001) and 1-year post-fire (2003 – 2004), and between pre-fire (2000 – 2001) and 20-years post-fire (2022 – 2024), to assess whether mean annual ET within each fire recovered to pre-fire rates.

Vegetation composition was summarized for each pixel using fractional cover of major vegetation classes (deciduous forest, evergreen forest, mixed forest, shrub, and grass) at pre-fire (2001), 1-year post-fire (2023), and 20-years post-fire (2023) time points. For each pixel and timestep, the dominant vegetation class was defined as the class with the highest fractional cover. Vegetation transitions were characterized by comparing dominant vegetation classes across time. Binary variables were created to indicate whether a pixel's dominant vegetation class changed from pre-fire to 1-year post-fire and from pre-fire to 20-years post-fire. To evaluate the relationship between vegetation change and ET response, linear mixed-effects models were fit using the *lme4* package (Bates et al. 2015) with ET departure and ET:P departure as response variables at 1-year (2003-2004) and 20-years post-fire (2022-2024). Vegetation change (change vs no change) was included as a fixed effect, and fire name was included as a random effect to account for non-independence among pixels within the same fire.

ET is influenced by many other site-specific variables and the mixed-effects models focused on broad vegetation categories, Random Forest models were employed to examine variable associations with annual average ET, ET:P, and ET departure at the pixel level pre-fire

(2000–2001), 1-year post-fire (2003–2004), and 20-year post-fire (2022–2024) across all fires. R packages used for Random Forest analysis were *ranger* (Wright and Ziegler 2017), *spatialRF* (Benito 2025), *caret* (Kuhn 2008), and *CAST* (Meyer et al. 2025). The dataset included 5,534 pixels, each representing a sample point, with 480 - 2,610 pixels per fire. Variables included in each model are located in Tables A3.2-4. Climate and vegetation variables are grouped by timeframe, so the pre-fire model uses climate variables from 2000-2001 and landcover variables from 2001, the 1-year post-fire model uses climate variables from 2003-2004 and land cover variables from 2003, and the 20-year post-fire model uses climate variables from 2022-2024 and vegetation variables from 2023. For ET departure, we calculate the change in vegetation cover of each category by subtracting 1-year post-fire or 20-years post-fire cover from pre-fire vegetation cover; therefore, negative values indicate gains in cover, while positive values indicate losses in cover.

To reduce multicollinearity, variance inflation factors (VIFs) were calculated and variables exceeding a threshold of 10 were removed prior to modeling. Variables identified were removed from the global variable list. To account for spatial autocorrelation, spatial cross-validation was implemented following Meyer et al. (2019). Pixel coordinates were grouped into 30 spatial clusters using k-means clustering, and these clusters were used to define spatial folds. This resulted in approximately equal-sized spatial partitions of the data (with roughly 184 pixels per fold). In spatial cross validation, models are iteratively trained on $k - 1$ spatial folds, and tested on the remaining held-out fold, ensuring that the training and testing data are spatially independent. All model selection and tuning procedures were conducted using repeated spatial cross-validation (30 folds, 5 repeats). Forward feature selection (FFS; Meyer et al. 2018) was applied within this framework to identify predictors that improved model performance and was

conducted using a fixed set of hyperparameters prior to full model training. FFS starts by fitting models using all combinations of two predictor variables and progressively adds variables that improve model performance based on cross-validated RMSE. Variables that do not improve performance are dropped.

Model hyperparameters were tuned using a grid search over *mtry* values of 2–5 and minimum node size values of 20, 40, and 60, using the “maxstat” split rule. Tuning was conducted using repeated spatial cross-validation (30 folds, 5 repeats) based on the same spatial partitions described above. The final Random Forest model was fit using 1000 trees and the optimal hyperparameters identified during tuning. Geographic coordinates were not included as predictors, but spatial autocorrelation was accounted for by enforcing spatial separation between training and testing data through spatial cross-validation (Meyer et al. 2019), which reduces overoptimistic estimates of model performance. Final model performance was evaluated using spatial cross-validation, where models were iteratively trained on spatially independent subsets and evaluated on held-out folds.

To visualize variable effects on ET, ET:P, and ET departure, we plot the Accumulated Local Effects (ALE) using R package *iml* (Molnar et al. 2018) which quantifies the average local effect of each predictor on model predictions, while also accounting for potential correlation among predictors. While our variable selection aims to reduce correlation by calculating VIFs, certain variables may still be ecologically correlated (e.g. fire severity and post-fire vegetation).

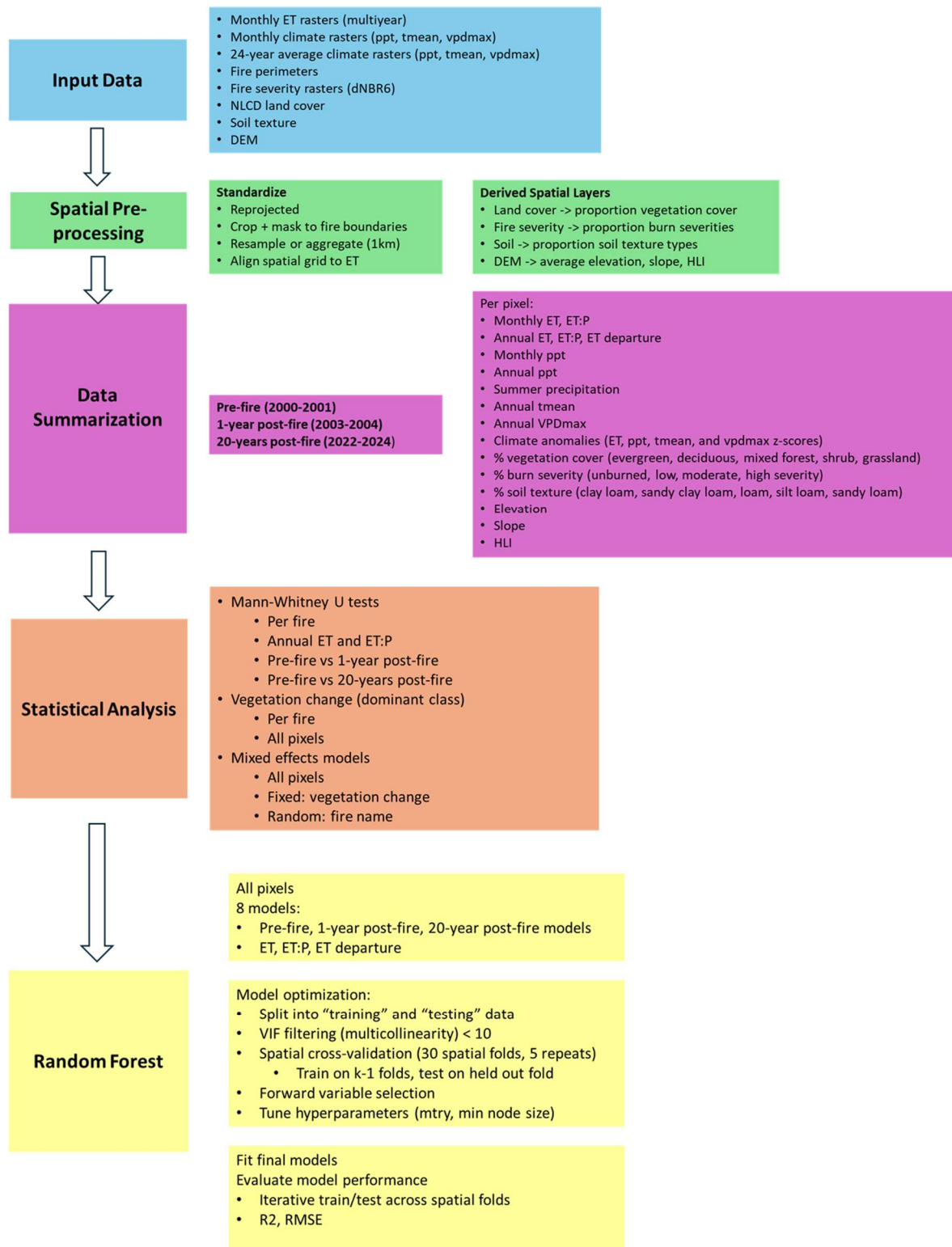


Figure 2. Flow chart summarizing methodological steps regarding data (blue), pre-processing steps (green), data summarization (purple), statistical analyses conducted (orange), and random forest modeling (yellow).

Results

Vegetation changes 1 year and 22 years after wildfires

Before 2002, pre-fire vegetation was predominantly evergreen forest within each fire perimeter (Table A3.1, Figure 3). Hayman, Ponil, Rodeo-Chediski, Sanford, and Rattle were mostly evergreen (67 – 82%), with moderate amounts of shrub cover (6 – 27%). Missionary Ridge, the highest elevation fire included in this study, was comprised of mixed forest, deciduous forest, and evergreen forest. One-year after the fires, forest composition shifted to grass cover (33 – 69%), retaining 21-36% evergreen forest in each fire perimeter. Twenty years after the fires, shrub cover (40-63%) and evergreen cover (28-58%) were the dominant cover types in Hayman, Ponil, Rodeo-Chediski, Sanford, and Rattle, showing gain in shrub cover and reduction of evergreen cover compared to pre-fire. Twenty years post-fire, Missionary Ridge Fire retained or recovered evergreen and deciduous forest cover, but had a reduction in mixed forest and gain in shrub cover.

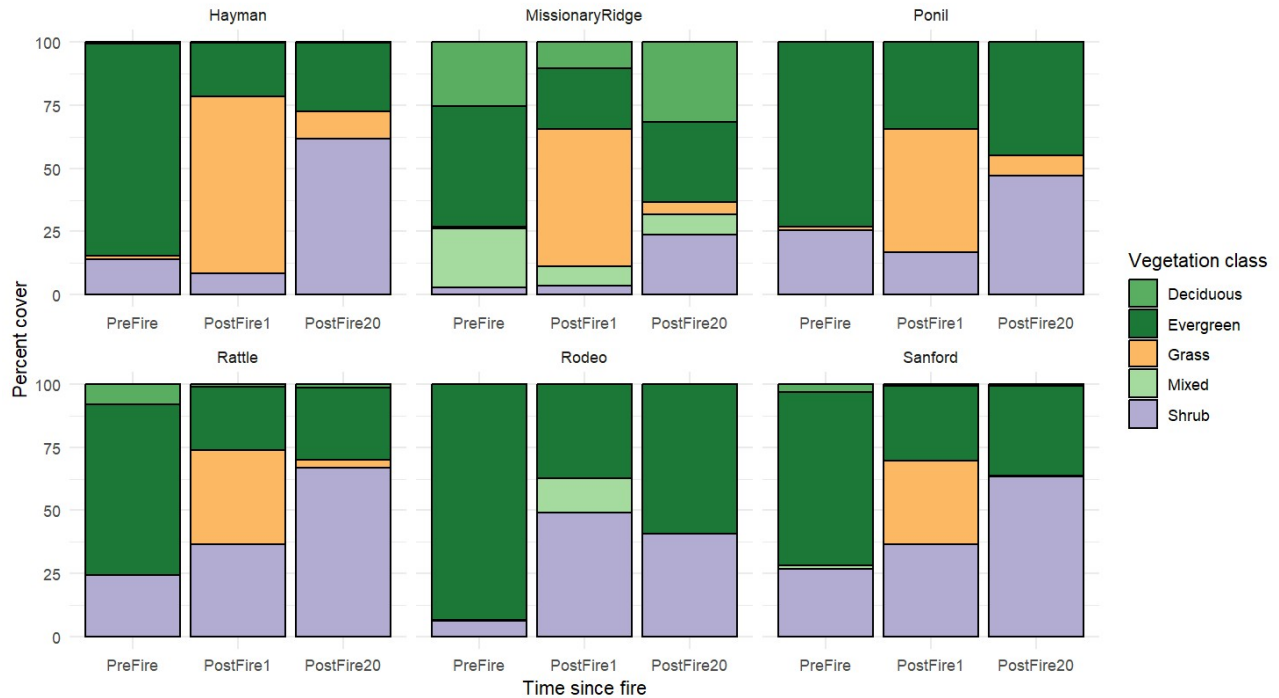


Figure 3. Stacked bar plots showing the percent cover (y-axis) of dominant vegetation classes (Deciduous Forest = medium green, Evergreen Forest = dark green, Grassland/Herbaceous = orange, Mixed Forest = light green, Shrub = purple) at the three time scales, pre-fire (2001), 1-year post-fire (2003), and 20-years post-fire (2023). Figure excludes minorly occurring vegetation classes: developed open space, developed low-intensity, woody wetlands. Full vegetation cover percentages can be viewed in Table A3.1.

Across all fires, vegetation composition shifted dramatically immediately after fire, followed by only partial recovery after 20 years (Figure 4). Pre-fire landscapes were dominated by evergreen forest type (90%), which was vastly reduced 1-year after the fires. One-year after fires, burned areas were dominated by shrub (34%), grass (31%), with 31% remaining evergreen. After 20-years, evergreen forests partially recovered to 46% of the area, but shrub cover remained dominant with 50% of pixels, indicating persistent post-fire changes in vegetation structure.

Transition patterns revealed consistent vegetation trajectories. Evergreen pixels frequently converted to shrub (35%) or grass (29%) immediately after fire, with only 34% remaining evergreen. Grass represented a transient state, with 78% of grass pixels at one-year

post-fire transitioning to shrub after 20 years. In contrast, shrubs were highly persistent, with 65% pixels remaining shrub and 35% transitioning to evergreen after 20 years.

Long-term comparisons showed incomplete recovery of forested systems: ~50% of pre-fire evergreen pixels returned to evergreen after 20 years, while the remaining half transitioned to shrub.

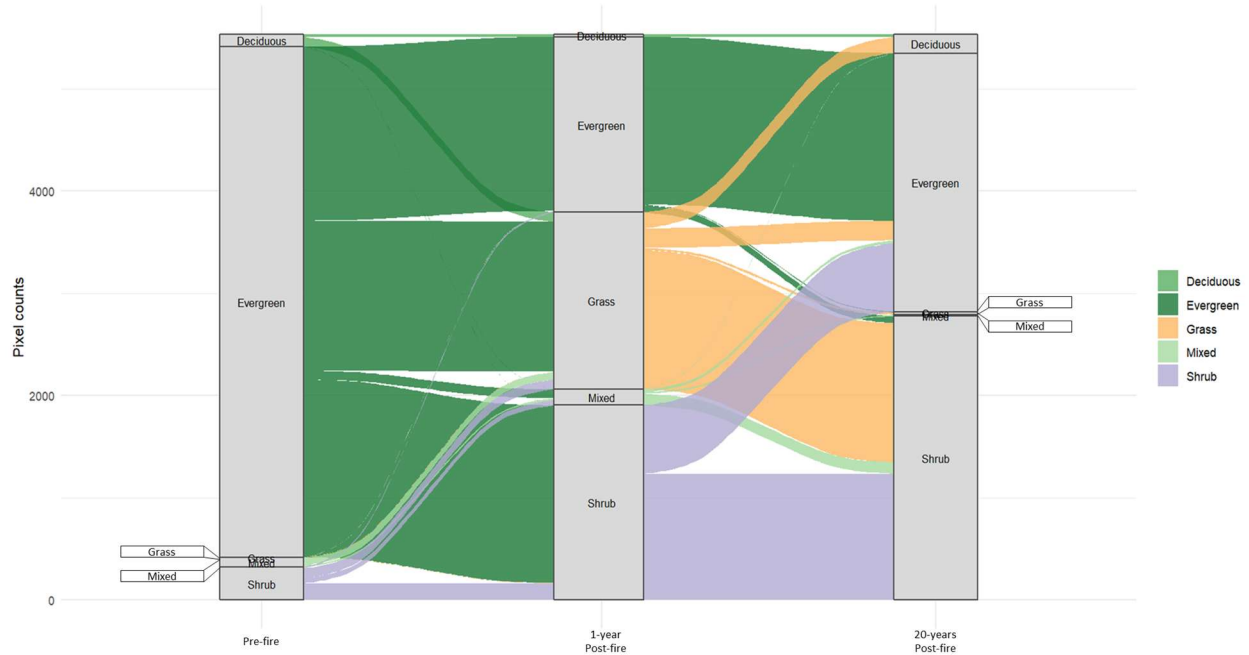


Figure 4. Pixel to pixel changes in dominant vegetation cover (Deciduous Forest = medium green, Evergreen Forest = dark green, Grassland/Herbaceous = orange, Mixed forest = light green, Shrub = purple) at the three time scales, pre-fire, 1-year post-fire, and 20-years post-fire. Aluvial plot was made using *ggalluvial* package (Brunson 2020).

Annual trends in ET and ET:P

Annual average ET was significantly decreased in all fires after one year and remained negatively departed after 20 years in all but the Ponil fire (Table 3). In all the fires, pre-fire ET exceeded the amount of precipitation that regions experienced (Table 3). One-year post-fire, ET:P was significantly decreased in all fires except Ponil, indicating that annual precipitation exceeded evaporation, shifting the water balance of these regions. After 20 years, although ET:P

showed trends towards recovery, it was still significantly less than pre-fire conditions. Monthly trends are plotted in Figure A3.1; ET rates tend to follow similar seasonal patterns, with reductions in monthly ET prevalent 1-year post-fire in the summer months. Precipitation across the timepoints are relatively variable; different fires reflect different seasonal wetness, where Missionary Ridge has winter and fall precipitation, Hayman and Ponil have relatively wet summers and dry winters, and Rattle, Rodeo and Sanford have dry summers and wet fall and winters. ET:P is especially high in months where there is little to no precipitation. ET:P seems higher pre-fire in May and June for Rattle. ET:P was especially high 20 years post-fire in April (Ponil) and May (Missionary Ridge and Sanford).

Table 3. Mean annual evapotranspiration (ET) (mm/year) and mean annual ET:P pre-fire, 1-year (2003-2004) and 20-years (2020-2023) after wildfires, and the z-value and p-value from Mann-Whitney U tests comparing the means in pre-fire to the different post-fire timeframes. Note that ET and ET:P values are not normalized by area and are meant to compare across timeframes, not necessarily across fires.

	Fire	Pre-fire	1-year post-fire	z-value	p-value	20-years post-fire	z-value	p-value
ET	Hayman	593.50 (94.94)	341.37 (124.65)	-30.48	<0.001	477.47 (125.92)	-18.53	<0.001
	Missionary Ridge	854.29 (109.09)	667.91 (128.97)	-19.72	<0.001	823.82 (121.07)	-4.12	<0.001
	Ponil	644.87 (78.01)	488.12 (92.45)	-23.20	<0.001	637.60 (90.00)	-0.85	0.394
	Rattle	589.69 (126.72)	385.65 (129.20)	-21.52	<0.001	517.85 (124.67)	-9.31	<0.001
	Rodeo	803.86 (140.94)	465.22 (136.44)	NA	<0.001	765.00 (151.58)	-8.82	<0.001
	Sanford	517.28 (140.35)	349.92 (103.95)	-18.61	<0.001	435.34 (89.02)	-9.85	<0.001
ET:P	Hayman	1.35 (0.25)	0.71 (0.28)	-31.31	<0.001	1.00 (0.28)	-22.23	<0.001
	Missionary Ridge	1.29 (0.24)	0.95 (0.23)	-19.09	<0.001	1.23 (0.27)	-3.43	<0.001
	Ponil	1.52 (0.19)	1.08 (0.20)	-25.69	<0.001	1.41 (0.19)	-8.48	<0.001
	Rattle	1.36 (0.22)	0.83 (0.23)	-26.20	<0.001	1.21 (0.23)	-11.18	<0.001
	Rodeo	1.72 (0.25)	0.99 (0.25)	NA	<0.001	1.68 (0.29)	-6.44	<0.001
	Sanford	1.02 (0.22)	0.67 (0.20)	-21.18	<0.001	0.90 (0.19)	-9.19	<0.001

Linear mixed effect model results of vegetation change on ET departure and ET:P departure

Shifts in dominant vegetation had significant effects on ET departure and ET:P departure 1-year and 20-years post-fire. After one year, pixels that experienced a vegetation change had an annual ET departure ~138 mm greater than pixels that retained their pre-fire vegetation (SE = 2.50, $t = 54.96$, R^2 [fixed effects] = 0.26, R^2 [full model] = 0.52). Even in the absence of vegetation change, 1-year post-fire ET was significantly different relative to pre-fire (intercept = 126.92 mm, SE = 26.97, $t = 54.96$), indicating that post-fire effects on ET were widespread but were amplified by vegetation change after one year. Variation among fires accounted for a substantial portion of the total variance, especially 1-year post-fire, as indicated by the large difference between fixed effects and full model R^2 values.

After twenty years, baseline ET departure was not significantly different from zero (intercept = 3.46 mm, SE = 11.28, $t = 0.31$, R^2 [fixed effects] = 0.25, R^2 [full model] = 0.33). However, pixels that had vegetation change showed substantially higher ET departures (~103 mm; SE = 2.35, $t = 43.95$). In contrast to the 1-year response, variation attributed to differences among fires was much smaller after 20 years.

A similar pattern was observed for ET:P departure. One-year post-fire, ET:P departure was significantly elevated even without vegetation change ($t = 5.13$), and increased by an additional 0.28 for pixels with vegetation change ($t = 50.65$). After 20 years, baseline ET:P departure was not significantly different from zero ($t = 0.74$), but remained significantly higher in pixels that had vegetation change ($t = 37.33$). As with ET, fire-to-fire variation was more pronounced in the short-term and diminished over longer time-scales.

Table 4. Linear mixed effects model results for the effect vegetation change has on ET departure (pre-fire – post-fire) and ET:P departure 1-year and 20-years after wildfires. Models were formatted as *Response ~ veg_change (1 | Fire)*. Fire name was used as a random effect to control for differences in fires. In all models, the number of observations (pixels) = 5534 and the number of groups = 6.

Model	Response	Fixed Effect	Estimate	Std. Error	t value	Random Effect	Variance (SD)
1-yr ET departure	ET_depart_1yr	Intercept (veg_change_1yr=FALSE)	126.92	26.97	4.71	fire (Intercept)	4335 (65.84)
		veg_change_1yr=TRUE	137.57	2.50	54.96	Residual	7673 (87.60)
20-yr ET departure	ET_depart_20yr	Intercept (veg_chang_20yr=FALSE)	3.46	11.28	0.31	fire (Intercept)	743 (27.27)
		veg_change_20yr=TRUE	103.36	2.35	43.95	Residual	7046 (83.94)
1-yr ET:P departure	ET_P_depart_1yr	Intercept (veg_change_1yr=FALSE)	0.32	0.06	5.13	fire (Intercept)	0.02 (0.15)
		veg_change_1yr=TRUE	0.28	0.01	50.65	Residual	0.04 (0.20)
20-yr ET:P departure	ET_P_depart_20yr	Intercept (veg_chang_20yr=FALSE)	0.03	0.04	0.74	fire (Intercept)	0.01 (0.09)
		veg_change_20yr=TRUE	0.22	0.01	37.33	Residual	0.04 (0.21)

Random Forest models assessing variables associated with ET

The model assessing variable importance for contributing to ET pre-fire had an R^2 of 0.55 and RMSE of 114.92, using 1000 trees, mtry of 4, and 20 nodes. ALE plots show the directionality and magnitude of the important variables (Figure 5). Differences in ALE y-axis ranges indicate that some variables have stronger effects on ET than others, with greater vertical extent reflecting stronger effects on model predictions. Climate variables were the strongest drivers of ET pre-fire. Increases in annual mean precipitation (Permutation Importance (PI) = 145.37) and annual mean temperature (PI = 113.69) were generally associated with higher ET, although the positive influence of annual temperature drops after 10 C°. A lower proportion of annual precipitation received in the summer (proportion summer precipitation, PI = 109.04) influences higher ET, with ET vastly decreasing when summer precipitation is greater than 40%

of the annual rain. Vegetation and topographic variables also contributed, with greater proportion cover of evergreen forest (PI = 80.30), greater proportion of mixed forest (PI = 64.776) and steeper slopes (PI = 59.02) corresponding to increased ET, although slope exhibited a more moderate effect size. A higher proportion of loam (PI = 65.58) was generally associated with lower ET, with a sharp increase only as pixels approached 100% loam; however, this relationship was relatively weak, as indicated by a limited ALE range (approximately -20 to 20).

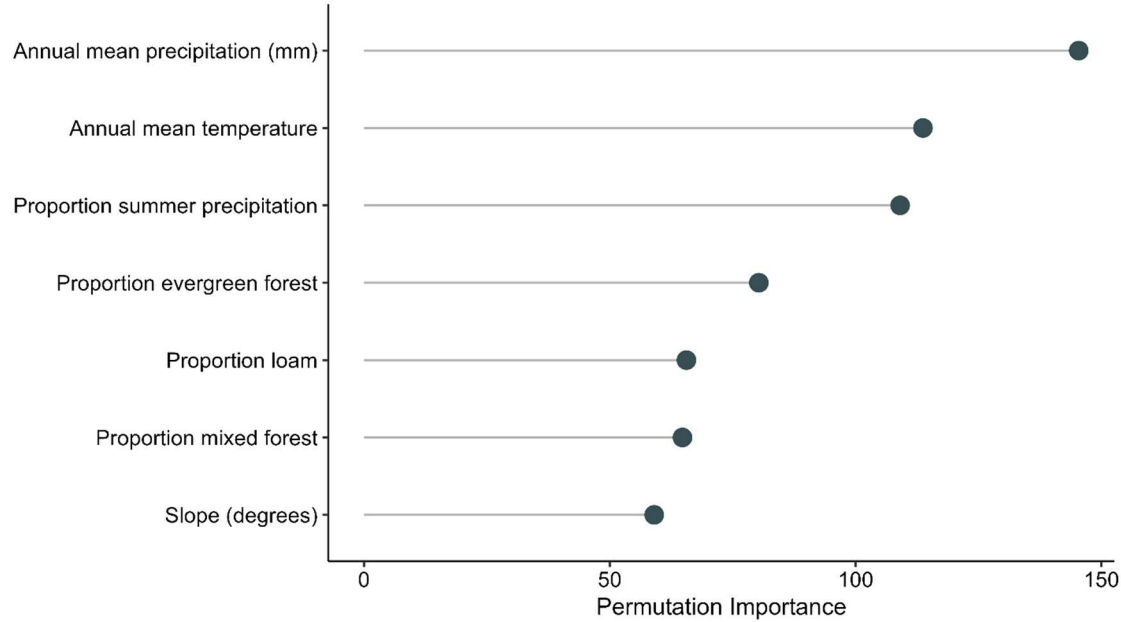
At 1-year post-fire, model performance metrics were moderately strong, with a $R^2 = 0.62$ and RMSE = 94.39, using 1000 trees, mtry of 3, and minimum node size of 20 (Figure 6).

Annual mean precipitation (PI = 111.85) and proportion cover of evergreen forest (PI = 108.96) showed the strongest positive associations with ET. Moderate positive relationships with ET were also observed proportion summer precipitation (PI = 86.21), reflecting an opposite trend from pre-fire. Proportion loam (PI = 58.56), slope (PI = 47.29) and increasing greenness (dNBR class 5, PI = 44.84) all had weak positive associations with ET. Lastly, proportion burned at low severity (dNBR class 1, PI = 34.78) also had a weak negative association with ET.

At 20-years post-fire, model performance was moderate, with performance metrics reflecting $R^2 = 0.65$ and RMSE = 112.90, using 1000 trees, mtry of 5, and minimum node size of 20 (Figure 7). Climate variables again dominated, with annual mean temperature (importance = 166.35) and annual mean precipitation (importance = 117.478) showing strong positive associations with ET. Evergreen forest cover (importance = 102.91) was also an important positive predictor. Similar to the pre-fire model, proportion summer precipitation (importance = 93.75), was negatively associated with ET. Other vegetation variables (proportion deciduous forest, importance = 46.04; proportion mixed forest, importance = 41.46), as well as slope (importance = 53.00), were also positively associated with ET. Burn severity variables

(increasing greenness (importance = 37.33), proportion burned at low severity (dNBR class 1; importance = 35.14), and proportion burned at mod-high severity (dNBR class 3; importance = 33.22) and proportion sandy clay loam (importance = 14.321) were associated with reduced ET, although these relationships were relatively weak.

A. ET Variable Importance, Pre-fire



B. ET ALE Plots, Pre-fire

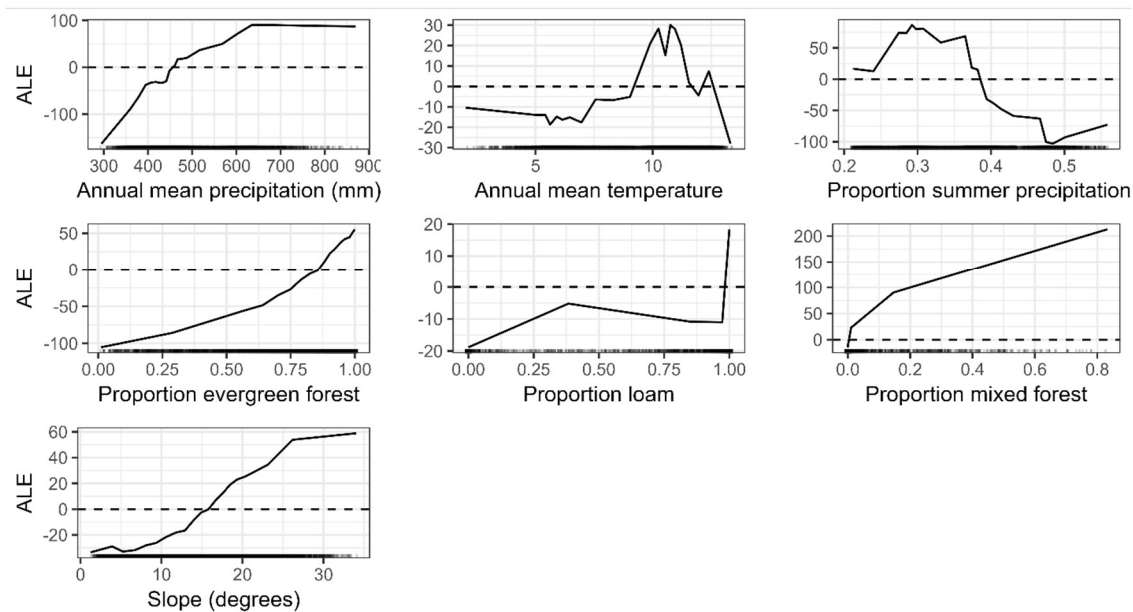
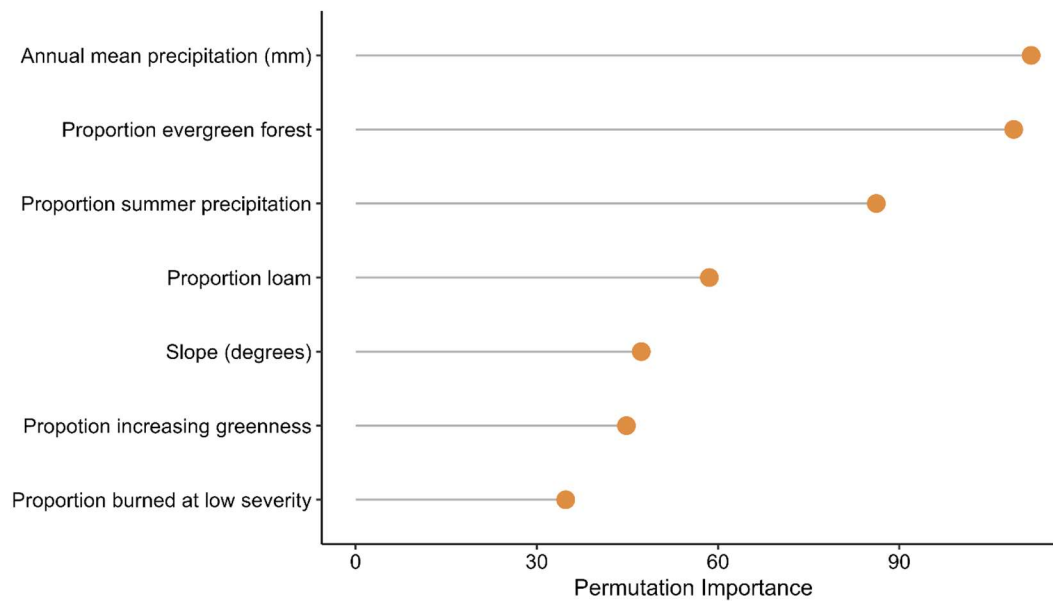


Figure 5. Variable importance (A.) and accumulated local effects (ALE) plots (B) depicting the average marginal effect of each predictor on evapotranspiration (ET) before the 2002 wildfires. The horizontal dotted line at $y = 0$ indicates no effect. Positive values correspond to increases in ET, while negative values indicate decreases in ET. Rug marks denote the distribution of observed predictor values, with sparsely populated regions indicating higher uncertainty in model estimates. Also note the differences in y-scale for the variables. Variables that reach a higher magnitude (i.e. 100 or 200, compared to 10 or 50), have greater influences on the response.

A. ET Variable Importance, 1-year post-fire



B. ET ALE Plots, 1-year post-fire

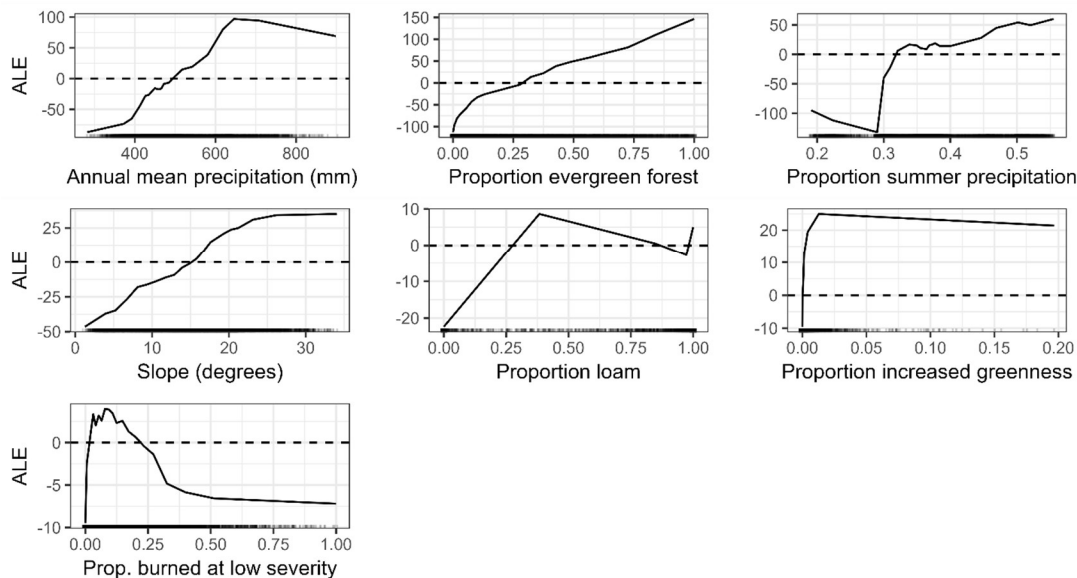
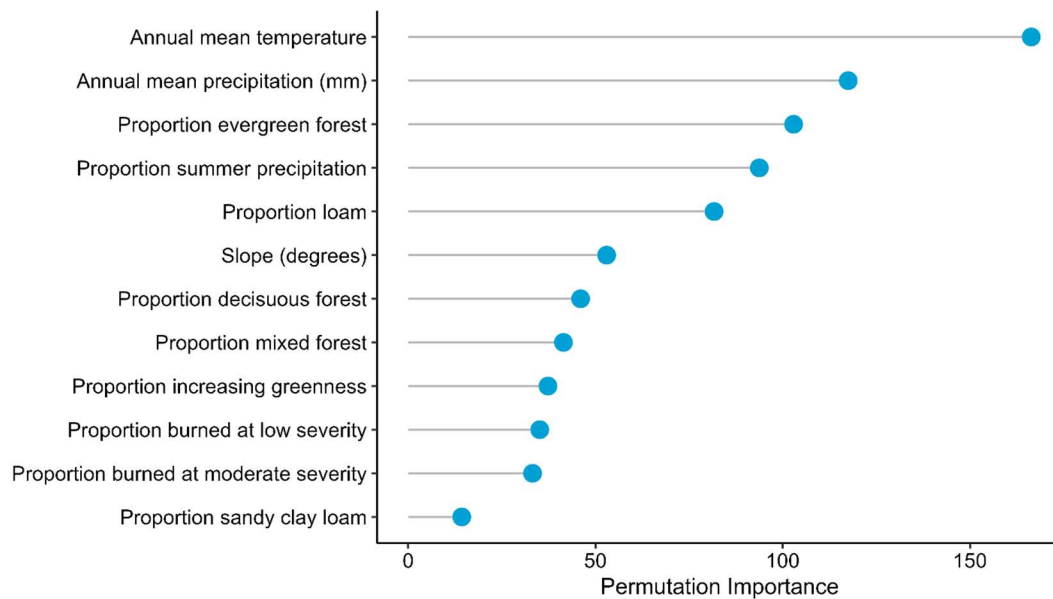


Figure 6. Variable importance (A.) and accumulated local effects (ALE) plots (B) depicting the average marginal effect of each predictor on evapotranspiration (ET) 1 and 2 years after the 2002 fires. The horizontal dotted line at $y = 0$ indicates no effect. Positive values correspond to increases in ET, while negative values indicate decreases in ET. Rug marks denote the distribution of observed predictor values, with sparsely populated regions indicating higher uncertainty in model estimates. Also note the differences in y-scale for the variables. Variables that reach a higher magnitude (i.e. 100 or 200, compared to 10 or 50), have greater influences on the response.

A. ET Variable Importance, 20-years post-fire



B. ET ALE Plots, 20-years post-fire

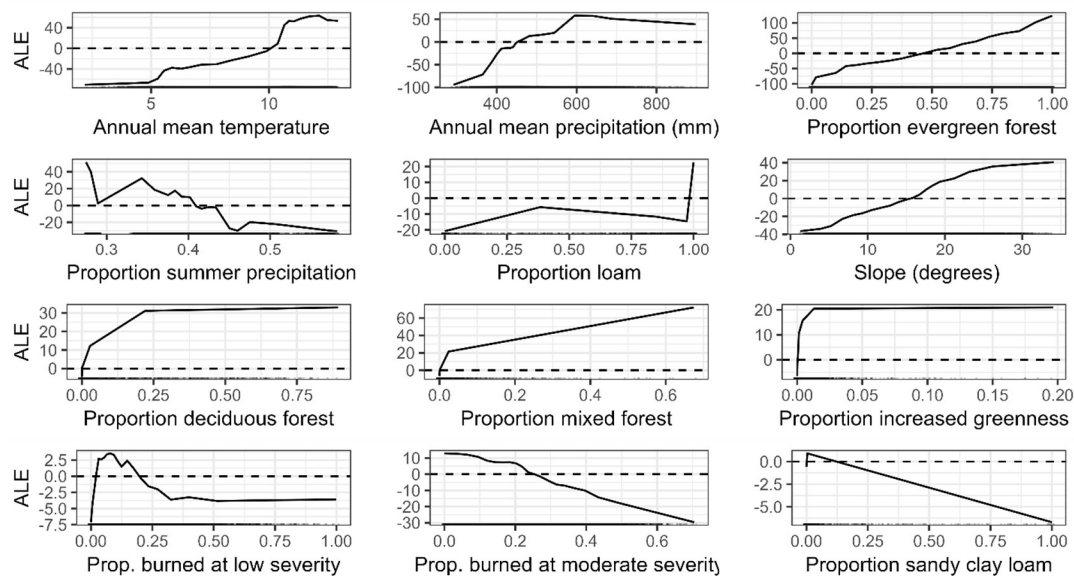


Figure 7. Variable importance (A.) and accumulated local effects (ALE) plots (B) depicting the average marginal effect of each predictor on evapotranspiration (ET) 20-22 years after the 2002 fires. The horizontal dotted line at $y = 0$ indicates no effect. Positive values correspond to increases in ET, while negative values indicate decreases in ET. Rug marks denote the distribution of observed predictor values, with sparsely populated regions indicating higher uncertainty in model estimates. Also note the differences in y-scale for the variables. Variables that reach a higher magnitude (i.e. 100 or 200, compared to 10 or 50), have greater influences on the response.

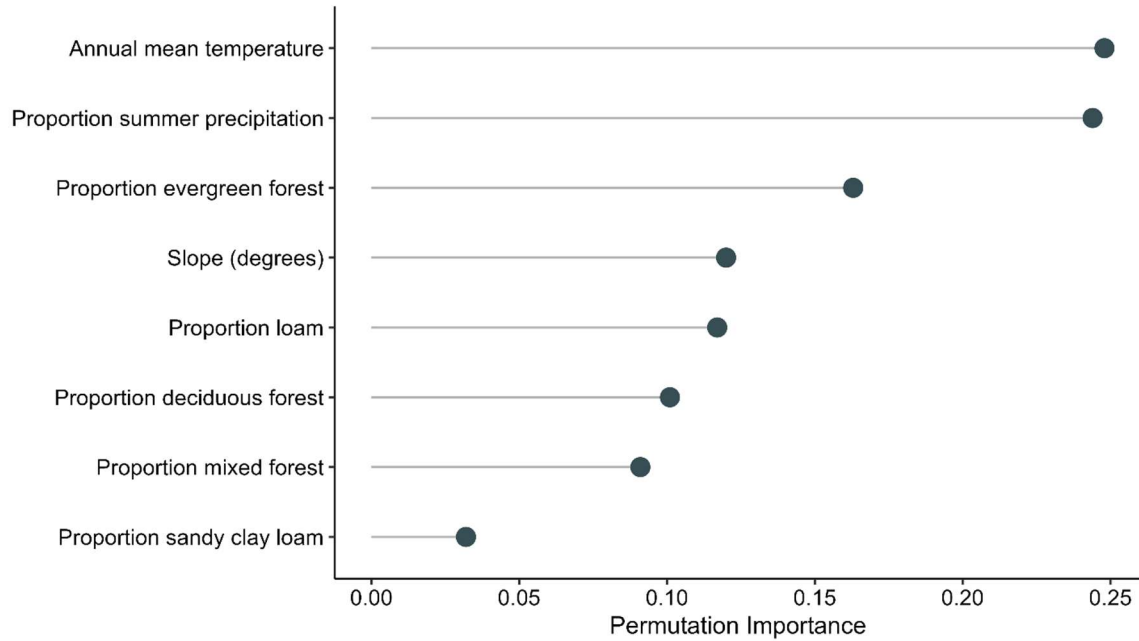
Random Forest models assessing variables associated with ET:P

The random forest model predicting pre-fire ET:P explained moderate variance ($R^2 = 0.56$ and $RMSE = 0.22$), using 1000 trees, mtry of 4, and minimum node size of 20 (Figure 8). Temperature and vegetation structure were the primary drivers of ET:P. Increases in annual mean temperature ($PI = 0.25$), proportion summer precipitation ($PI = 0.24$), proportion of evergreen forest ($PI = 0.16$), slope (importance = 0.132), proportion of loam soil ($PI = 0.12$), and proportion of mixed forest ($PI = 0.09$) were associated with greater ET:P. In contrast, greater proportion of deciduous forest ($PI = 0.10$) and proportion of sandy clay loam were associated with reductions in ET:P, although these relationships were relatively weak compared to other variables.

At 1-year post-fire, model performance was relatively weak ($R^2 = 0.35$ and $RMSE = 0.22$), using 1000 trees, mtry of 4, and minimum node size of 60 (Figure 9). ET:P remained positively associated with greater proportions of evergreen forest ($PI = 0.22$), higher annual mean temperature ($PI = 0.14$), and greater annual mean VPDmax ($PI = 0.13$).

At 20-years post-fire, model performance was strong ($R^2 = 0.77$ and $RMSE = 0.19$), using 1000 trees, mtry of 3, and minimum node size of 20 (Figure 10). Increases in annual mean temperature ($PI = 0.43$), proportion summer precipitation ($PI = 0.23$), proportion of evergreen forest ($PI = 0.21$) were the most influential variables and resulted in the greatest positive effects on ET:P. ET:P was also positively associated with proportion of deciduous forest ($PI = 0.13$), slope ($PI = 0.11$), proportion increased greenness (dNBR class 5; $PI = 0.07$), although these variables, especially deciduous forest and increasing greenness, had relatively weak effects.

A. ET:P Variable Importance, Pre-fire



B. ET:P ALE Plots, Pre-fire

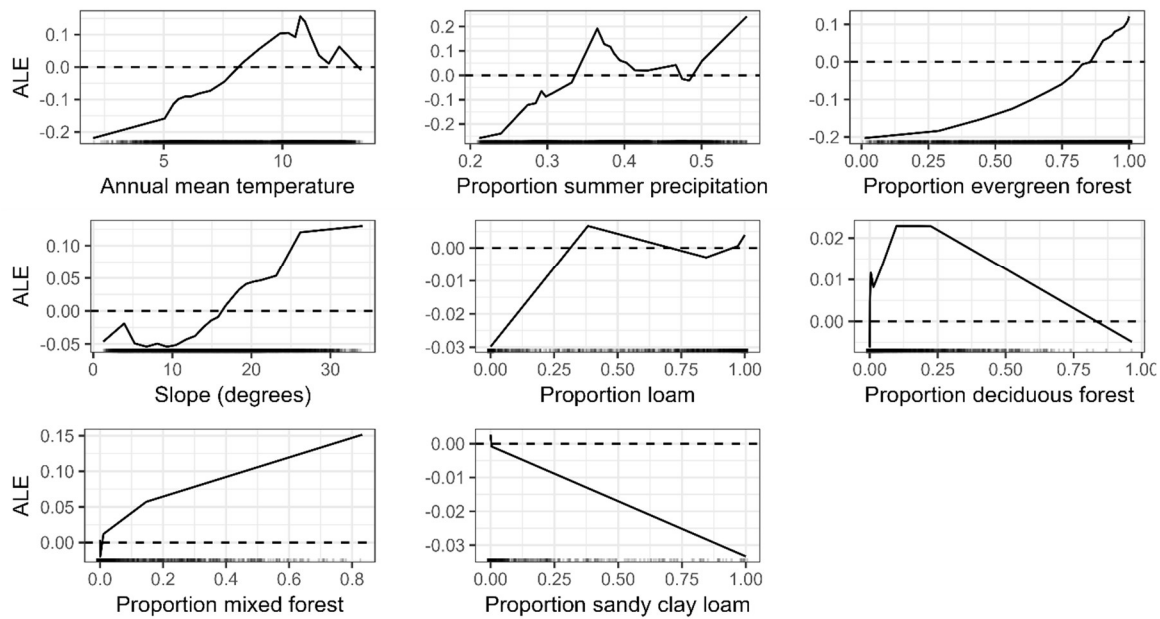
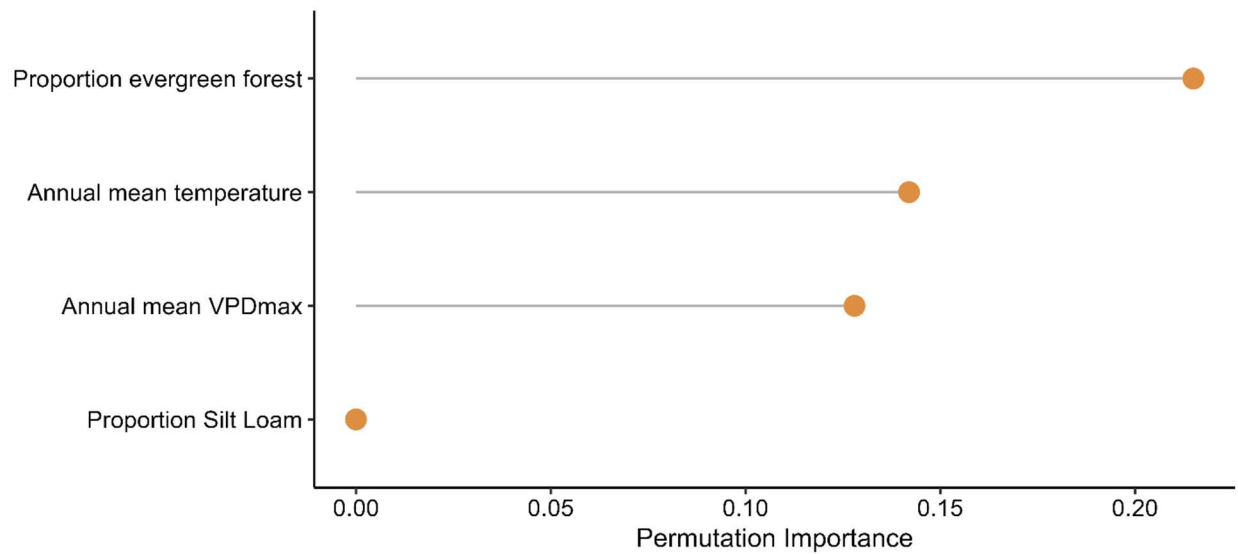


Figure 8. Variable importance (A.) and accumulated local effects (ALE) plots (B) depicting the average marginal effect of each predictor on evapotranspiration:precipitation (ET:P) one and two years before the 2002 fires. The horizontal dotted line at $y = 0$ indicates no effect. Positive values correspond to increases in ET:P, while negative values indicate decreases in ET:P. Rug marks denote the distribution of observed predictor values, with sparsely populated regions indicating higher uncertainty in model estimates. Also note the differences in y-scale for the variables.

A. ET:P Variable Importance, 1-year post-fire



B. ET:P ALE Plots, 1-year post-fire

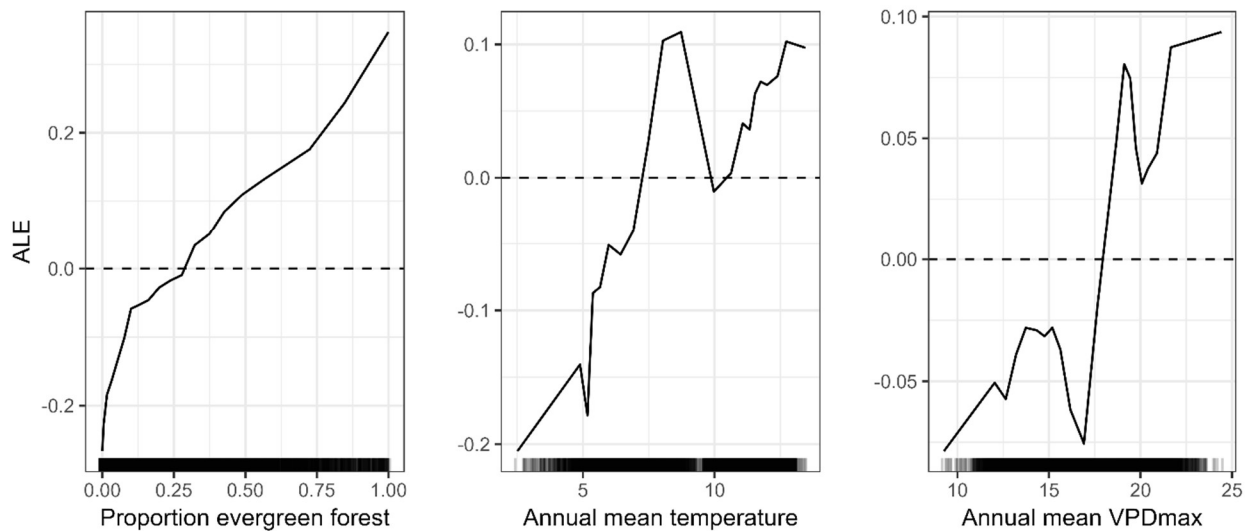
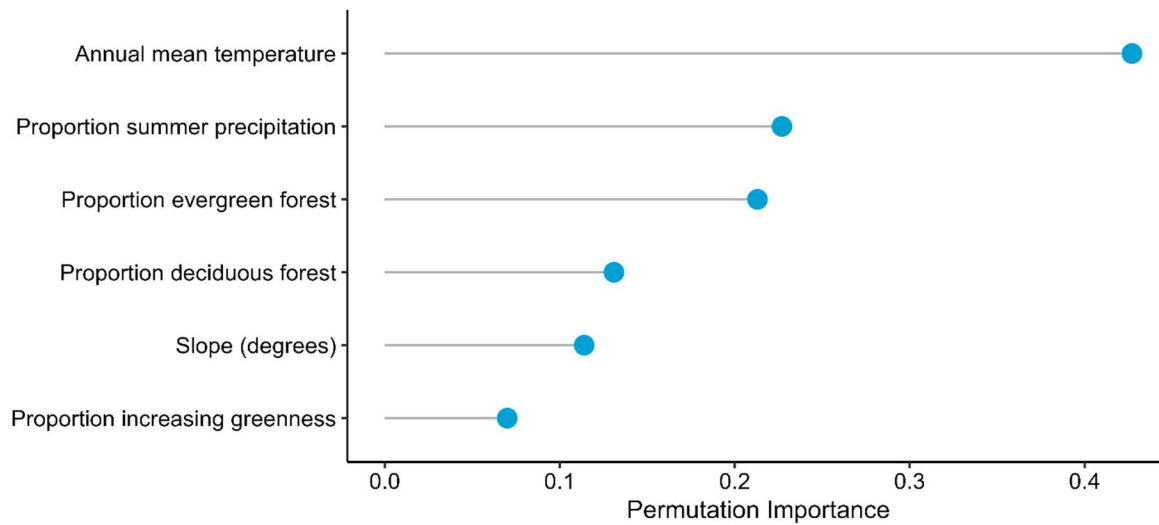


Figure 9. Variable importance (A.) and accumulated local effects (ALE) plots (B) depicting the average marginal effect of each predictor on evapotranspiration:precipitation (ET:P) one and two years *after* the 2002 fires. The horizontal dotted line at $y = 0$ indicates no effect. Positive values correspond to increases in ET:P, while negative values indicate decreases in ET:P. Rug marks denote the distribution of observed predictor values, with sparsely populated regions indicating higher uncertainty in model estimates. Also note the differences in y-scale for the variables.

A. ET:P Variable Importance, 20-years post-fire



B. ET:P ALE Plots, 20-years post-fire

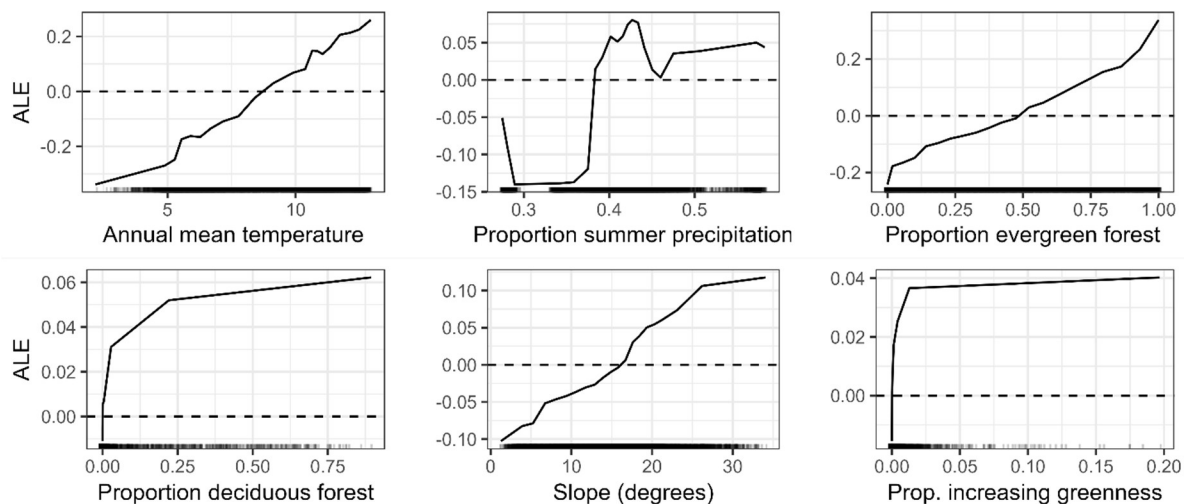


Figure 10. Variable importance (A.) and accumulated local effects (ALE) plots (B) depicting the average marginal effect of each predictor on evapotranspiration:precipitation (ET:P) 20 and 21 years after the 2002 fires. The horizontal dotted line at $y = 0$ indicates no effect. Positive values correspond to increases in ET:P, while negative values indicate decreases in ET:P. Rug marks denote the distribution of observed predictor values, with sparsely populated regions indicating higher uncertainty in model estimates. Also note the differences in y-scale for the variables.

Random Forest models assessing variables associated with ET departure

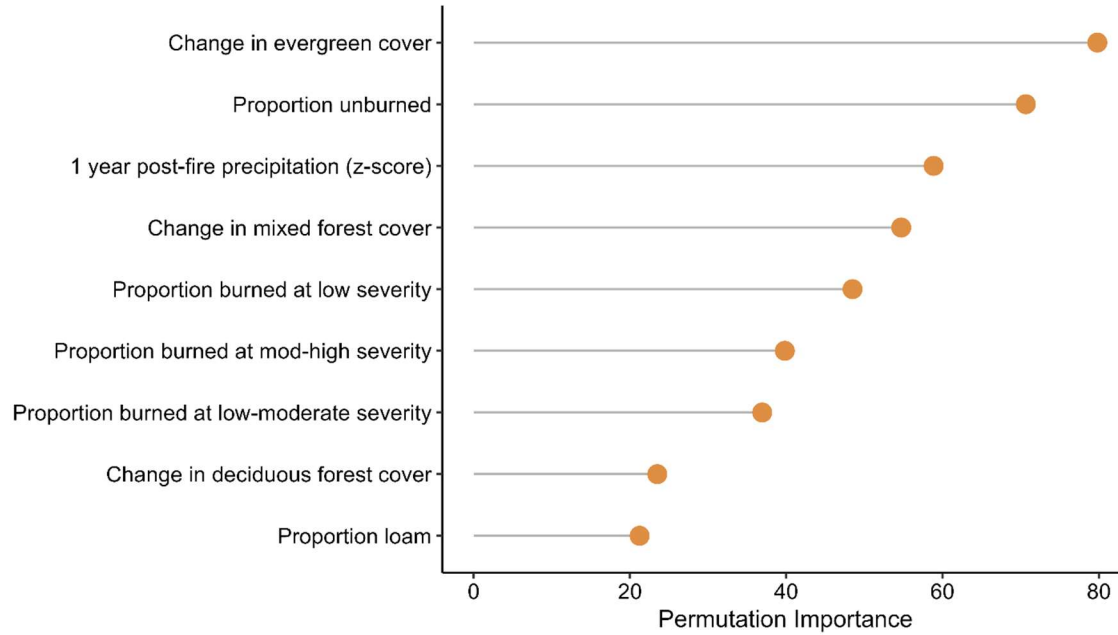
The random forest model predicting ET departure (mean annual pre-fire ET – mean annual post-fire ET) at 1-year post-fire explained substantial variance (R^2 of 0.81 and RMSE of

57.11), using 1000 trees, mtry of 3, and a minimum node size of 20 (Figure 11). Vegetation loss was a primary driver of ET reductions, with decrease in evergreen forest (PI = 79.81), mixed forest (PI = 54.71), and deciduous forest (PI = 23.49) associated with greater declines in ET relative to pre-fire conditions. In contrast, fire severity and climate variables were associated with increased ET relative to pre-fire levels. Higher proportions of unburned area (dNBR class 0; PI = 70.65) and areas that burned at low severity (dNBR class 1; PI = 48.45), moderate-high severity (dNBR class 3; PI = 39.82), and low-moderate severity (dNBR class 2; PI = 36.92) were associated with increases in ET post-fire compared to pre-fire. Similarly, greater post-fire precipitation (1-year post-fire z-score, PI = 58.86) were associated with increases in ET compared to pre-fire. Proportion loam (PI = 21.24) was associated with decreases in ET compared to pre-fire, although this effect was relatively weak.

The random forest model predicting ET departure (mean annual pre-fire ET – mean annual post-fire ET) at 20-year post-fire explained moderate variance (R^2 of 0.65 and RMSE of 60.46), using 1000 trees, mtry of 3, and minimum node size of 20 (Figure 12). Evergreen forest loss remained the dominant predictor associated with long-term decreases in ET relative to pre-fire rates (PI = 77.73). Climate variables corresponded with increased ET, including long-term VPDmax (24-year average, PI = 42.72), post-fire VPDmax (20-years post-fire z-score, PI = 40.84), and proportion summer precipitation (PI = 33.196). Fire severity variables also remained important, with proportion of pixel unburned (dNBR class 0; PI = 41.87) and proportion of area burned at low severity (dNBR class 1; PI = 38.41), low-moderate severity (dNBR class 2; PI = 29.58), and moderate-high severity (dNBR class 3; PI = 30.71) influencing increases in ET relative to pre-fire. Topographic effects were also prevalent, where flatter slopes (PI = 26.87) were associated with greater ET declines, while steeper slopes corresponded to relative increases

or no changes in ET, and proportion loam ($PI = 24.65$) was associated with increases or no change in ET.

A. ET departure Variable Importance, 1-year post-fire



B. ET departure ALE Plots, 1-year post-fire

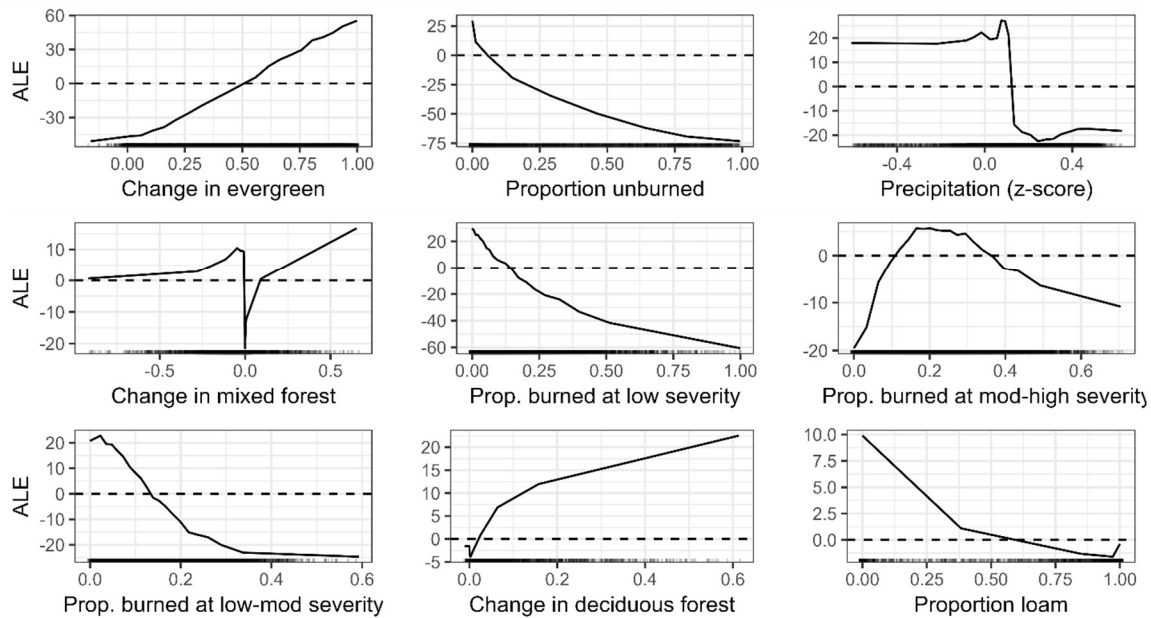
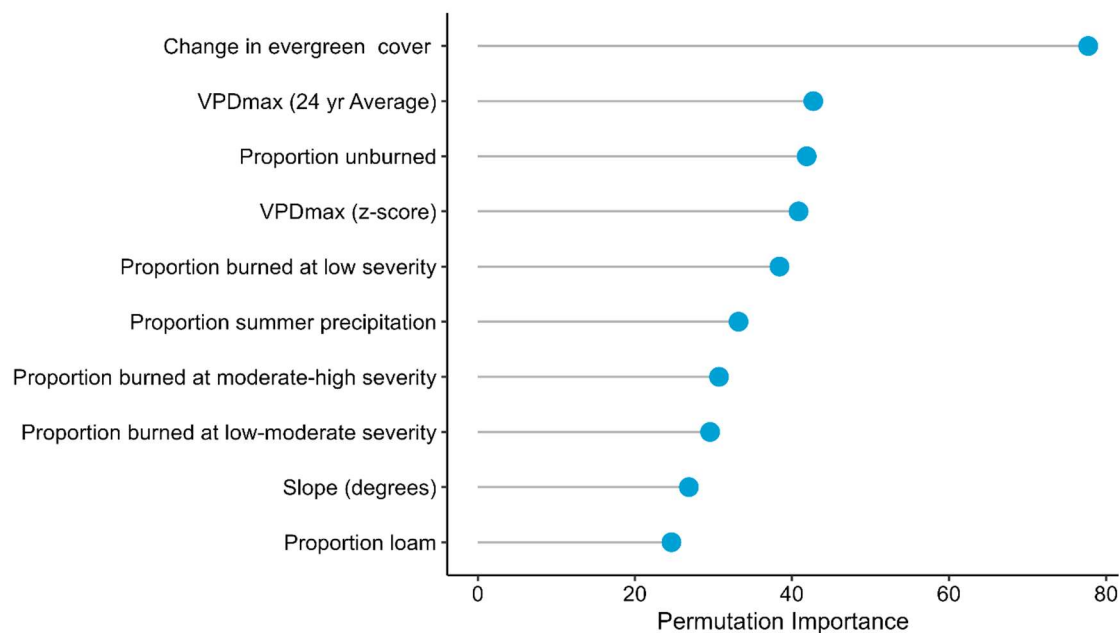


Figure 11. Variable importance (A.) and accumulated local effects (ALE) plots (B) depicting the average marginal effect of each predictor on evapotranspiration departure from pre-fire to 1-year post-fire. The horizontal dotted line at $y = 0$ indicates no effect. Positive y -values correspond to decreases in ET from pre-fire levels, while negative y -values indicate ET increases. Rug marks denote the distribution of observed predictor values, with sparsely populated regions indicating higher uncertainty in model estimates. Also note the differences in y -scale for the variables. For variables depicting change in vegetation cover, negative x -values indicate gains in cover, while positive x -values indicate losses in cover.

A. ET departure Variable Importance, 20-years post-fire



B. ET departure ALE Plots, 20-years post-fire

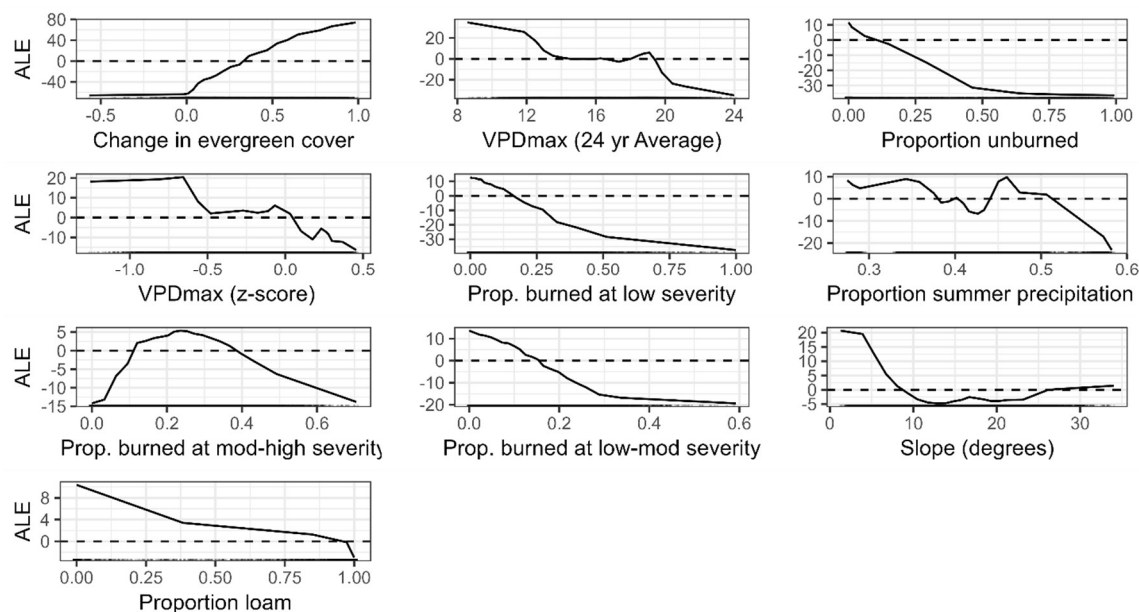


Figure 12. Variable importance (A.) and accumulated local effects (ALE) plots (B) depicting the average marginal effect of each predictor on evapotranspiration departure from pre-fire to 20-year post-fire. The horizontal dotted line at $y = 0$ indicates no effect. Positive y -values correspond to decreases in ET from pre-fire levels, while negative y -values indicate ET increases. Rug marks denote the distribution of observed predictor values, with sparsely populated regions indicating higher uncertainty in model estimates. Also note the differences in y -scale for the variables. For variables depicting change in vegetation cover, negative x -values indicate gains in cover, while positive x -values indicate losses in cover.

Discussion

Here, we analyzed six fires that burned in 2002 to investigate the short- and long-term influences wildfire has on ET, ET:P, and ET departure, with a particular interest in the influence of vegetation trajectories. We found that climate, vegetation, fire-severity, and topography all influence post-fire ET trends, but in different ways. Our findings indicate that temperature, precipitation, and evergreen forest cover have the most influence on post-fire ET. Higher temperature and greater precipitation cause higher ET, while fire-caused evergreen forest loss leads to ET reductions. While climate variables set the baseline for ET, as indicated in pre-fire models, vegetation cover dictates how much ET changes post-fire, aligning with past research showing the importance of post-fire vegetation structure as key drivers of ET change (Poulos et al. 2021, Collar et al. 2023).

Fire causes long-term shifts from evergreen to shrub cover

The year 2002 was particularly dry, contributing to dry fuels that led to the large fires that burned throughout the western US (Weiss et al. 2009). Due to the extent and the proportion of land burned at high-severity, many researchers have used them as study sites to understand vegetation recovery pathways under fire regime change. Specifically, the Hayman Fire, Ponil Complex, and Rodeo-Chediski fires all exhibited large swaths of land that burned at high-severity and still have limited conifer recruitment based on field surveys. Lack of conifer establishment is largely attributed to the size of burned patches and increased distances to seed sources (Chambers et al. 2016, Owen et al. 2017, Walker et al. 2019, Coop 2022), as well as hotter and drier climate (Rodman et al. 2020, Petrie et al. 2023). Indeed, prior to wildfires, most of our study regions were evergreen dominated. After one year, remotely sensed images indicate a nearly-even split between evergreen, grass, and shrub. By 20 years post-fire, only about half of

the burn footprints showed recovery to evergreen-dominated, with the remaining half persisting as shrubs. These vegetation pathways show that the 1-year post-fire grassland existed as a transient vegetation pathway, aligning with typical post-fire succession, while shrub dominance may persist as an alternative stable state (Guiterman et al. 2022).

ET losses occur within all fires and linked to evergreen forest loss

Annual ET and annual ET:P in all fires were significantly reduced 1-year post-fire and in all but one fire after 20-years. Within each fire, ET was reduced by 167.36 – 338.64 mm/year, and by 20 years ET was reduced by 7.27 – 116.03 mm/year, with greater reductions in fires that had more evergreen forest loss. This is consistent with other work in dry forest types, showing fire-induced reductions in ET with gradual recovery over time as forests recovered (Poon and Kinoshita 2018, Collar et al. 2023).

Before 2002, ET exceeded precipitation in all fires; while this is typical of southwestern dry forests, the rate may have been exacerbated by the early 2000s drought (Weiss et al. 2009). One year after the fires, precipitation exceeded ET in all fires, potentially allowing for short-term increases in water yield (Wine and Cadol 2016, Blount et al. 2019), but this outcome is dependent on downstream vegetation characteristics, interannual climate variability (i.e. wet vs dry years, Collar et al. 2023), and post-fire hydrological responses such as erosion and overland flow (Goeking and Tarboton 2020). By 20 years, annual ET again exceeded precipitation in all fires but still remained lower than pre-fire levels.

Importantly, the recovery of ET:P 20-years post-fire, relative to pre-fire rates, occurred despite substantial long-term vegetation change, including the conversion of about half of the pre-fire evergreen forests to shrubland. While shrub cover and abundance were not quantified, dense shrub communities, like Gambel oak (*Quercus gambelii*) that are prevalent in many SW

post-fire ecosystems, would contribute to high ET rates (Poulos et al. 2021). Alternatively, increased soil evaporation from canopy gaps in areas lacking tree cover may further elevate ET, especially in years that are dry. Greater soil evaporation can alter post-fire recovery patterns by reducing soil moisture available for conifer regeneration (Wooten et al. 2022, Foster et al. 2020), although this dynamic is also dictated by precipitation patterns (Koehn et al. 2022) and soil texture (Puhlick et al. 2021).

Changes in post-fire annual ET across the southwest is driven by forest loss

Evergreen forests are substantial contributors to ET, therefore losses of evergreen forest will cause reduction in landscape ET (Goeking and Tarboton 2020). Our results show that vegetation change leads to significant departures in both short- and long-term ET. One-year post-fire, vegetation change caused 137.57 mm decrease in ET, and 103.36 mm decrease in ET 20-years post-fire. Departures were also observed when accounting for precipitation (ET:P). What is interesting about the ET departure and ET:P departure models, is that the baseline condition (no vegetation change) in the 1-year post-fire period already shows significant departure from pre-fire rates. In contrast, in the 20-year post-fire models, pixels that had no vegetation change were not significantly different from pre-fire. This suggests that ET and ET:P were substantially altered immediately following fire, even in the absence of vegetation change, and that vegetation change further amplified these departures. Thus, we can surmise that short-term post-fire changes in ET and ET:P are driven by a combination of fire-related effects and vegetation change, while long-term departures are largely influenced by whether there was a shift in vegetation.

Exploring the other mechanisms for ET change, we employed random forest which indicated that fire severity metrics and climate variables also contributed to ET departures.

Together, these results indicate that while evergreen forest cover plays a critical role across time scales, fire severity and climate, particularly VPD, are key drivers of variability in post-fire ET response. Perhaps differences in VPD rates pre-fire and 1-year post-fire drive the high departure observed under baseline vegetation conditions, while VPD pre-fire and 20-years post-fire are more comparable.

Climate dictates ET potential, and vegetation change influences realized ET

The models indicate the high importance of top-down drivers (climate and soil/topography) as influential of ET, where greater precipitation, higher average temperature, and higher vapor pressure deficit are related to greater ET rates, as expected. The interaction of these variables (climate and vegetation) show competing and complimentary effects on ET, with climate dictating the ET capacity and vegetation dictating the realized ET rates (Figure 12).

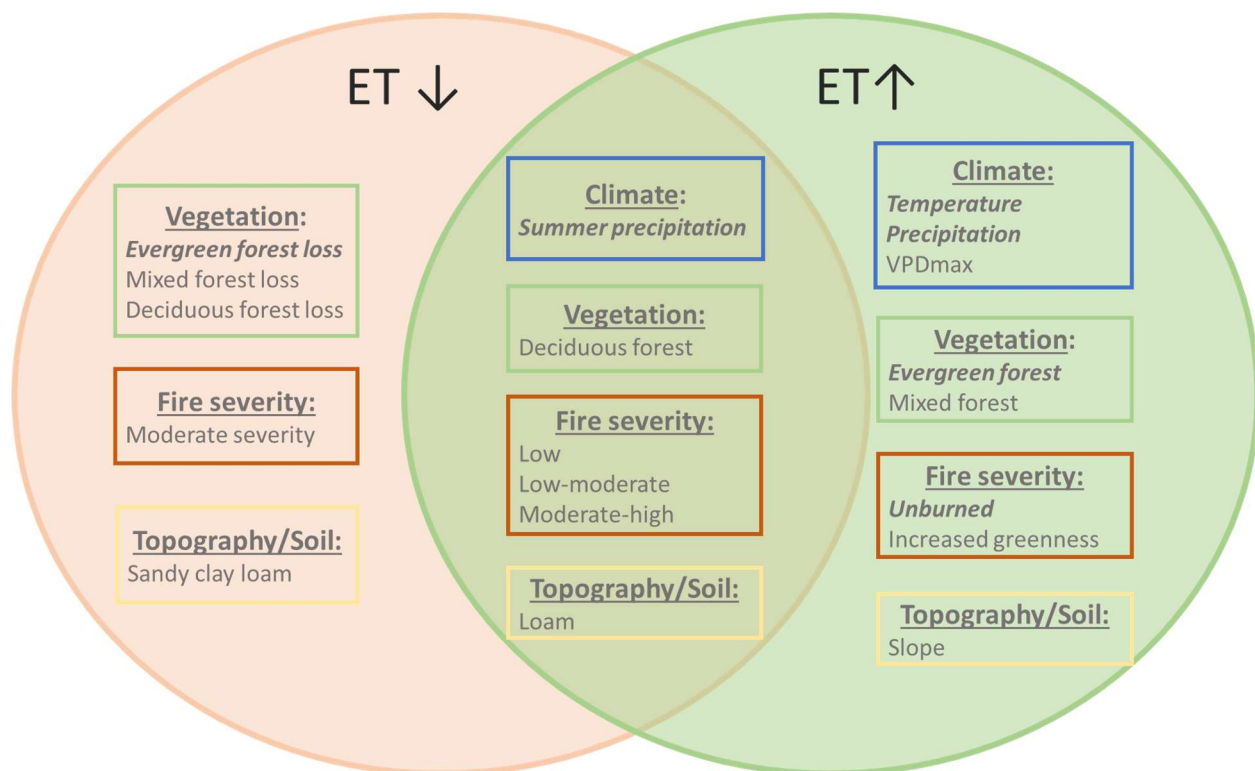


Figure 12. Conceptual diagram summarizing random forest model results for variable contributions to evapotranspiration (ET). Variables are grouped and colored by categories, including climate (blue), soil/topography (yellow), fire severity (dark orange), and vegetation (green). Bold and italicized variables indicate those which appeared consistently in models and were associated with strong effects on model predictions.

Fire severity was weakly influential on ET and ET departure both short-term and long-term. Different fire severities directly affect ET by altering vegetation and soil characteristics, although high-severity fire typically has more of an effect than low-severity fire due to the high mortality of canopy trees (Poon and Kinoshita 2018, Poulos et al. 2021). Because our model structure aims to reduce multicollinearity, we can assume that the fire severity characteristics that were removed as model predictors (such as high-severity fire, which was absent from all models) were correlated with vegetation cover. This distinction is important: our results suggest that it may not fire severity itself that directly drives ET response, but rather the specific ecological and biophysical effects that fire has on the landscape, especially those that alter vegetation structure, surface properties, and hydrological characteristics. Perhaps this is why low and moderate severities had such low importance and accumulated local effects. Incorporating more direct representations of fire effects, such as albedo (Poon and Kinoshita 2018), soil ash content (Thomaz 2018), soil hydrophobicity (Hubbert et al. 2006), infiltration capacity (Moody et al. 2009, Inbar et al. 2020), proportion bareground exposed (Poon and Kinoshita 2018), and plant functional group composition (Montes-Helu et al. 2009, Poulos et al. 2021) would likely improve explanatory power and also provide more mechanistic insights into how fire alters ET.

Non-stand replacing fire causes ET to increase due to increased transpiration from boosted productivity of remaining trees and understory plants, increasing sublimation of snowpack, and increasing evaporation from greater soil exposure (Goeking and Tarboton 2020 and works cited therein). In our models, low and moderate severity fire was associated with both

decreased and increased ET. It is possible that some pixels that had higher prevalence of low and moderate severity fire already had low ET rates relative to other areas (perhaps due to fewer trees or less herbaceous fuel structure (i.e. bare ground) and therefore had minimal changes to ET because ET was already low to begin with. This may be why when assessing ET departure (which would pick up low-to-no change), greater pixel proportions burned at low and moderate severities caused ET to *increase* relative to pre-fire rates, which tracks expectations. These contrasting patterns highlight the importance of baseline conditions when interpreting ET change, but also emphasizes our argument for using specific fire effects measurements to disentangle specific mechanisms and directionality of ET change.

Limitations and future directions

While the results of this work align with other research in the southwestern US, we have several limitations and areas for future considerations. Because the early 2000s were such hot and dry years, our pre-fire ET estimates may be particularly high and not truly representative as baseline conditions (Weiss et al. 2009). However, we were restricted by data availability, with SSEBop monthly data only available beginning at year 2000. With that said, it is possible that our departures are not as drastic as they are made out to seem. Additionally, a 1000 m resolution scale is quite large, especially when considering the influence of vegetation and burn patterns. While our processing and data analysis pipeline aimed to address some of this by calculating proportions of vegetation classes in each pixel, other nuances, like topography, slope, aspect, elevation, are averaged, leading to losses in topographic effects, as indicated by their low effect sizes in the random forest models and ALE plots.

More importantly, our representation of fire is limited to severity classifications, which may not adequately capture the mechanisms driving ET change. As discussed previously, fire

severity primarily acts as a proxy for other ecological and biophysical fire effects. However, our analysis does not account for these effects, such as changes in albedo, soil ash content, soil hydrophobicity, infiltration capacity, or shifts in plant functional groups. Similarly, NLCD cover types are represented by broad categories which do not separate by individual species, plant size, or water use strategies, and they do not incorporate canopy cover and tree density, which also play important roles in ET. Incorporating these more direct measures of post-fire conditions would likely improve model performance, predictability, and strengthen mechanistic interpretation.

Lastly, our analysis is conducted at the fire-perimeter scale, which may overlook broader hydrologic responses. Assessing at the watershed scale and including metrics such as proportion burned at different severities may provide more reliable insights into fire effects on ET. This work provides the baseline for additional research that could look more thoroughly into characteristics of fire on ET. For example, examining how fire patch size influences ET across time, such as differences between large, contiguous burn patches, or edge versus interior effects, could indicate important insights into how fire behavior and shifting regimes influence ET. Additionally, the key variables identified here as influencing long-term ET could be used to inform ET projections for contemporary fires. Although vegetation trajectories remain uncertain, ET responses could be bracketed based on potential recovery pathways (e.g., recovery to evergreen forest versus shrubland) and combined with projected temperature and precipitation. Such estimates could support timely water resource planning by improving predictions of post-fire water yield.

Conclusion

This study found long-term shifts in vegetation cover from large wildfires, which had lasting influence on ET for several decades. Before the fires, our study regions were comprised of ~90% evergreen forest, and after 20 years, only 50% of the landcover was evergreen. We found that pre-fire, ET was most influenced by top-down climate-related processes, like annual precipitation and annual mean temperature, which makes sense due to the overall dominance of evergreen trees. One-year post-fire, while precipitation and temperature remained important variables, the percent cover of evergreen forest also highly influenced the ET, with regions with more evergreen maintaining high ET, and regions with less evergreen cover having less ET. This finding, paired with research showing strong indication for conifer recruitment failure in the western US (e.g., Davis et al. 2023), highlight that persistent reductions in evergreen forest cover following high-severity wildfire influences ecosystem processes beyond vegetation dynamics, altering regional water balance for decades, and potentially feedbacking into persistent vegetation shifts.

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Author Contributions

Jamie Woollet: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization; **Camille Stevens-Rumann** Conceptualization, Writing-

editing draft, Funding acquisition; **Ryan Morrison** Conceptualization, Writing-editing draft, Funding acquisition; **Mike Battaglia** Conceptualization, Writing-editing draft

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CONCLUSION

PJ woodlands are a widespread, ecologically and culturally important ecosystem. Over the past several decades, large wildfires have become more prevalent and recovery conditions have become hotter and drier. Combined, these factors contribute to further losses of the already contracting ecosystem. In this dissertation, I used observational and experimental approaches to better understand biotic influences that can act as bottlenecks to post-fire piñon and juniper recovery. In Chapter 1, I assessed natural recruitment of piñon pine and juniper, and outlined variables associated with tree seedling recruitment in interior and edge burned patches. In Chapter 2, I aimed to understand how inoculation and different planting strategies, including planting under/adjacent to different nurse types and in different fire ages, influence outplanted piñon seedling success, with a keen interest in fungal community dynamics. Lastly, in Chapter 3, I aimed to understand implications of vegetation shifts by expanding my study area to the broader southwestern US, investigating how short- and long-term wildfire-induced vegetation change alters evapotranspiration in large 20-year old burned areas.

Recovery patterns of 25-27 year old burned PJ woodlands in western Colorado showed a stark relationship to seed availability and proximity to seed sources, contributing to one key bottleneck for woodland recovery. In the fires included in this study, tree recruitment was occurring, albeit at low rates, and was most prevalent at burned edges near seed sources. This was an interesting finding, as the recovery of this system is associated with avian seed dispersers who can disperse seeds far from the seed source. Another bottleneck to natural recovery was the developing vegetation, where piñon and juniper tree seedlings were less likely in plots that had a high colonization of non-native plants. Lastly, piñon and juniper seedlings in burned patches

were most associated with Gambel oak as a nurse plant, relative to other available nurse objects. In the context of post-fire management, managers working with limited resources can prioritize action to the interior of high-severity burned patches where natural tree recruitment is unlikely, and focus action on reducing non-native plant establishment which would help to facilitate natural recovery of trees and other native plants.

Experimental work with piñon seedlings further revealed importance of biotic influences on seedling survival. While I hypothesized that greenhouse-initiated soil inoculation with whole-soil inoculum would enhance outplanted seedling performance by providing supplemental ectomycorrhizal fungi (EMF) to burned soil, the local soil communities rapidly overcome the inoculation-effect. Instead, seedling survival was most strongly influenced by planting under Gambel oak and adjacent to standing dead trees, aligning with the vegetation bottleneck from Chapter 1. While inoculation itself did not influence seedling survival, seedling survival was linked to soil that had greater relative abundance of EMF present, most of which was already present in the field soil that seedlings were planted into, encapsulating the third bottleneck for tree recovery. The findings from this chapter showed that the nurse types piñon seedlings are planted under/near and the field soil that seedlings are planted into are more important than greenhouse-induced inoculation treatments.

Finally, by expanding to the broader southwest, this dissertation demonstrates that failure of trees to recover have long-term ecosystem consequences. Across the southwestern United States, wildfire-driven shifts from evergreen-dominated systems to non-forested states resulted in persistent reductions in evapotranspiration (ET) that lasted at least two decades. Climate, vegetation, fire-severity, and topography all influence post-fire ET trends in different ways, where higher temperature and greater precipitation cause ET increases, while fire-caused

evergreen forest loss leads to ET reductions. Such hydrological changes have important implications for water balance, carbon dynamics, and regional climate, showing that uncharacteristic high-severity fire has broad and long-term influences on both ecological and human communities.

From a management perspective, these results suggest that interventions should prioritize interior high-severity burn areas where natural regeneration is least likely. Here, managers may focus on reducing non-native plant establishment and utilizing nurse objects such as Gambel oak to enhance planting success. With that said, future work is needed to better understand the mechanisms for why, how, and where Gambel oak and local EMF taxa facilitate piñon seedling recruitment and survival in burned landscapes, as well as the extent to which they can assist piñon seedlings in a changing climate.

Broadly, this work demonstrates that decisions about post-fire restoration will influence not only vegetation recovery, but also long-term ecosystem processes such as evapotranspiration. As fire regimes continue to shift, understanding the mechanisms that constrain or facilitate recovery will be critical for maintaining the structure and function of piñon-juniper woodlands, as well as other forest communities. This dissertation provides evidence that while recovery is increasingly uncertain, it is not uniformly constrained and that strategic management that works with, rather than against, existing biotic relationships can meaningfully influence post-fire vegetation trajectories.

APPENDICES

APPENDIX 1

Table A1.1. Soil types and percent of the fire footprint for each fire. Map Unit is the taxonomic class, often the soil series, as defined by the Web Soil Survey. Map unit was looked up in the NRCS soil series look up (<https://soilseries.sc.egov.usda.gov/osdname.aspx>) to determine great group or subgroup, which was used to determine soil order as outlined in NRCS USDA (<https://www.nrcs.usda.gov/sites/default/files/2022-09/Keys-to-Soil-Taxonomy.pdf>)

Fire	Map Unit	Soil Order	Area of Fire Footprint (acres)	Area of Fire Footprint (hectare)	Percent of Fire Footprint
Hatchet	Torriorthents, cool-Rock outcrop complex	Entisol	2854.3	1155.1	50%
	Biedsaw-Sunup gravelly loams	Mollisol	1126.3	455.8	20%
	Wrayha-Rabbitex-Veatch complex, very stony	Entisol and Mollisol	859.5	347.8	15%
	Hesperus-Empedrado, moist-Pagoda complex	Mollisol	297.5	120.4	5%
	Tosca channery loam, MLRA 48A	Mollisol	222	89.8	4%
	Badland		170.8	69.1	3%
	Rock outcrop-Torriorthents complex	Entisol	102.2	41.4	2%
	Battlement loam	Entisol	35.8	14.5	1%
Disappointment	Zigzag-Rock outcrop complex	Entisol	1125.8	455.6	31%
	Narraguinnep clay loam	Mollisol	925.2	374.4	25%
	Narraguinnep-Gladlow complex	Mollisol and Inceptisol	749.7	303.4	21%
	Sili-Zigzag complex	Inceptisol and Entisol	565.2	228.7	16%
	Argiustolls-Haplustalfs complex	Mollisol and Alfisol	146.6	59.3	4%
	Sili clay loam	Inceptisol	70.5	28.5	2%
	Ormiston-Beje complex	Alfisol and Mollisol	22.1	8.9	1%
Wray	Wrayha stony clay loam	Mollisol	767.3	310.5	44%
	Gladel-Bond-Rock outcrop complex	Inceptisol and Aridisol	401.8	162.6	23%
	Rock outcrop-Orthents complex	Rock	261.8	105.9	15%
	Nortez-Fivepine loams	Mollisol	146.6	59.3	9%
	Gurley-Skein loams	Mollisol and Inceptisol	51.5	20.8	3%

Monticello-Witt loams	Mollisol and Aridisol	58.5	23.7	3%
Rock outcrop	Rock	37.8	15.3	2%

Table A1.2. Linear regression statistics for assessing differences in percent rock, soil, and litter cover across interior burned, edge burned, and unburned plots.

Variable	df	Adjusted R ²	f-statistic	p-value
% Rock	73	0.0098	1.37	0.260
% Soil	73	-0.0124	0.5405	0.585
% Litter	73	-0.027	0.014	0.986

Table A1.3. Mixed-effect model results for forest characteristics (stumps ha⁻¹, dead juniper trees ha⁻¹, dead piñon trees ha⁻¹, live juniper trees ha⁻¹, live piñon trees ha⁻¹, total trees ha⁻¹, average distance to live piñon (m), and average distance to live juniper(m)) in burned interior, burned edge, and unburned plots.

Response	Fixed Effect	Estimate	Std. Error	t-value	p-value	Random Effect	Variance (SD)
Stumps	Intercept (Unburned)	205.33	62.70	3.28	0.018*	fire (Intercept)	5753 (75.85)
	Treatment = Edge	186.13	54.66	3.41	0.001*	Residual	30199 (173.78)
	Treatment = Interior	178.67	54.95	3.25	0.002*		
Dead Juniper	Intercept (Unburned)	18.67	25.06	0.75	0.467	fire (Intercept)	328.7 (18.13)
	Treatment = Edge	63.05	27.74	2.27	0.026*	Residual	7779 (88.20)
	Treatment = Interior	83.33	27.89	2.99	0.004*		
	Intercept (Unburned)	41.33	10.90	3.79	0.011*	fire (Intercept)	183 (13.53)

Dead Piñon	Treatment = Edge	-34.65	9.26	-3.74	<0.001*	Residual	867 (29.44)
	Treatment = Interior	-31.33	9.31	-3.37	0.001*		
Live Juniper	Intercept (Unburned)	317.33	26.02	12.20	<0.001*	fire (Intercept)	0 (0)
	Treatment = Edge	-307.01	31.70	-9.69	<0.001*	Residual	10155 (100.80)
	Treatment = Interior	-316.00	31.87	-9.92	<0.001*		
Live Piñon	Intercept (Unburned)	236.00	15.45	15.28	<0.001*	fire (Intercept)	0 (0.00)
	Treatment = Edge	-235.35	18.82	-12.51	<0.001*	Residual	3580 (59.83)
	Treatment = Interior	-236.00	18.92	-12.51	<0.001*		
Total Tree	Intercept (Unburned)	18.67	25.06	0.75	0.467	fire (Intercept)	3289 (18.13)
	Treatment = Edge	63.05	27.74	2.27	0.026*	Residual	7779 (88.20)
	Treatment = Interior	83.33	27.89	2.99	0.004*		
Average Distance to Live Piñon	Intercept (Unburned)	20.03	11.56	1.73	0.095	fire (Intercept)	25 (4.99)
	Treatment = Edge	36.21	13.64	2.65	0.01*	Residual	1881 (43.37)

	Treatment = Interior	136.88	13.72	9.98	<0.001*		
Average Distance to Live Juniper	Intercept (Unburned)	8.22	9.46	0.87	0.388	fire (Intercept)	0 (0.00)
	Treatment = Edge	27.89	11.52	2.42	0.018*	Residual	1342 (36.63)
	Treatment = Interior	139.68	11.58	12.06	<0.001*		

Table A1.4. Kruskal-Wallis statistics for assessing differences in percent cover of bareground, grass, forb, shrub, other, non-native plants, piñon seedlings ha⁻¹, and juniper seedlings ha⁻¹ across interior burned, edge burned, and unburned plots.

Variable	χ^2	p-value
% Bareground	31.73	< 0.001
% Grass	22.63	< 0.001
% Forb	12.28	0.002
% Shrub	9.57	0.008
% Other	0.225	0.894
% non-native	18.83	<0.001
Piñon seedlings	40.14	<0.001
Juniper seedlings	35.19	<0.001

Table A1.5. ANOVA statistics for assessing differences in fuel loading across interior burned, edge burned, and unburned plots. Fuel loads are measured in Mg ha⁻¹

	df	Sum square	R ²	F-value	p-value
1 hr	2	0.02	0.44	29.1	< 0.001
10 hr	2	0.42	0.07	2.56	0.085
100 hr	2	4.68	0.06	2.29	0.109
1000 hr	2	50.3	0.03	1.28	0.285

Table A1.6. PERMANOVA statistics for assessing Bray-Curtis dissimilarity distances in plot structure across treatments (unburned, interior burn, edge burn), fires (Hatchet, Disappointment, Wray), and status (burned, unburned)

	df	R ²	F-value	p-value
Treatment	2	0.214	9.93	0.001
Fires	2	0.11	4.68	0.001
Status	2	0.21	19.53	0.001

Table A1.7. T-test statistics for assessing the proportion of piñon and juniper seedlings found under a nurse object versus proportion not under a nurse object in each plot.

	df	t-value	p-value
Piñon	76	9.32	< 0.001
Juniper	84	5.51	< 0.001

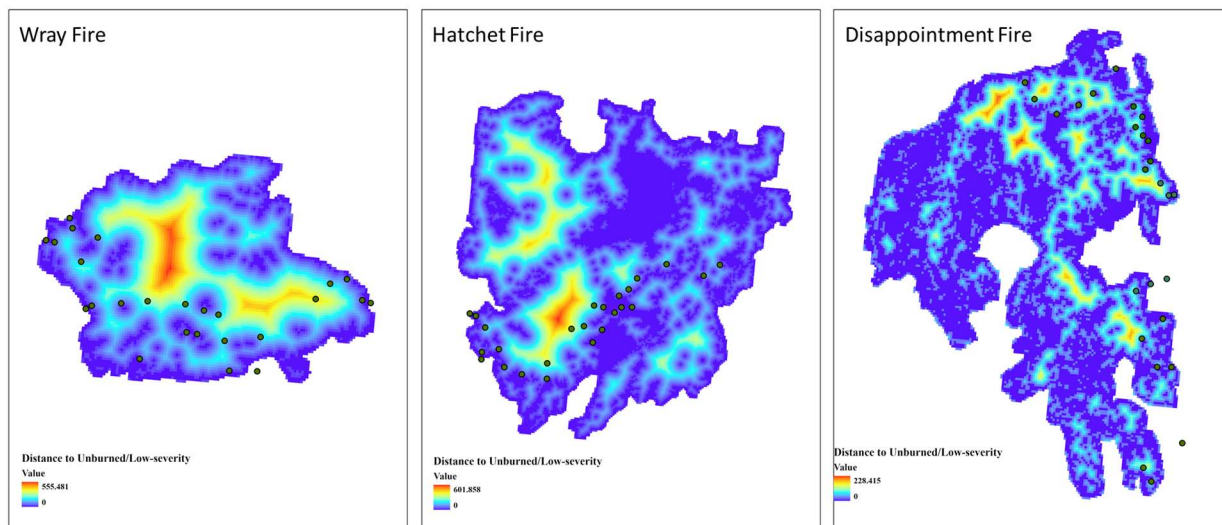


Figure A1.1. Figure of the mean Euclidean distances to unburned and low severity pixels, calculated from dnbr6 rasters from Monitoring Trends in Burn Severity (MTBS, Eidenshink et al. 2007 [<https://www.mtbs.gov>]). Maps were created in ArcGIS Pro (ESRI, 2025).

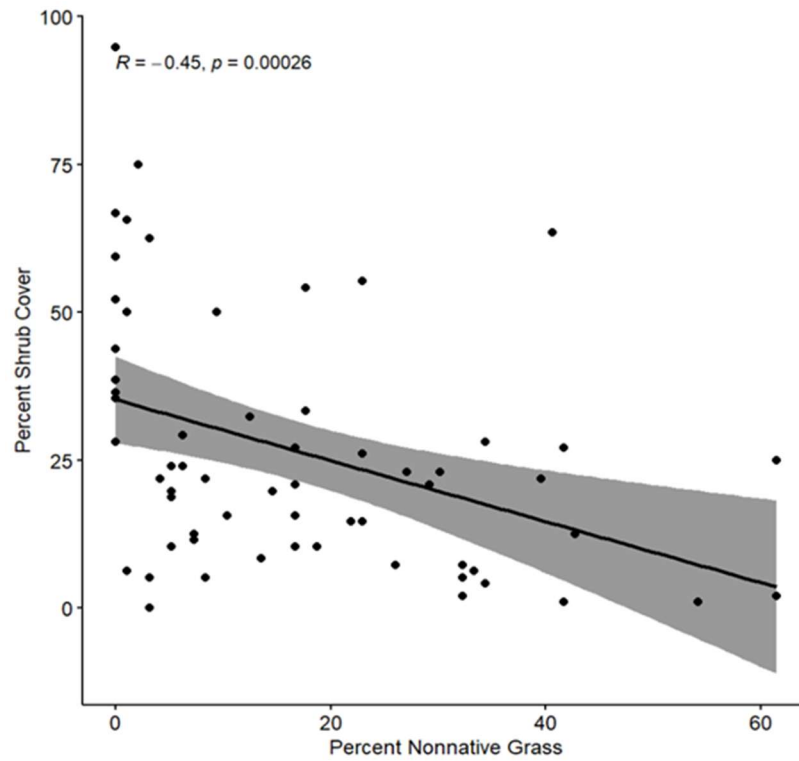


Figure A1.2. Spearman rank correlation test shows a significant inverse relationship ($\rho = -0.45$, $p\text{-value} = 0.00026$), indicating that plots with higher percent shrub cover had lower percent native grass cover, and *vice versa*.

APPENDIX 2

Table A2.1 Baseline soil chemistry values (mean (sd)) from soils collected prior to planting piñon seedlings in Fall 2023. Soil samples were collected from a representative of each treatment Fire x inoculation treatment x nurse object type with a 5 cm x 10 cm soil core, and were divided by top horizon (0 – 5 cm) and lower horizon (5 – 10 cm). Chemistry values are averaged by fire age and soil layer.

<i>Fire Age</i>	<i>Soil Layer</i>	<i>pH</i>	<i>EC mmho/cm</i>	<i>OM (%)</i>	<i>NO3- ppm</i>	<i>P ppm</i>	<i>S ppm</i>	<i>K ppm</i>	<i>N lb/ac</i>	<i>Total C (%)</i>	<i>Total N (%)</i>	<i>C:N</i>
<i>OldBurn</i>	Lower	7.99 (0.30)	0.28 (0.23)	3.54 (1.84)	3.00 (3.29)	7.40 (3.37)	2.80 (0.79)	391.10 (166.07)	3.00 (3.29)	2.00 (1.08)	0.13 (0.08)	15.97 (2.34)
<i>OldBurn</i>	Top	7.62 (0.58)	0.12 (0.05)	4.21 (2.13)	10.44 (7.92)	12.90 (4.65)	5.22 (2.82)	498.11 (226.16)	7.42 (5.46)	2.23 (1.21)	0.16 (0.09)	14.08 (1.73)
<i>RecentBurn</i>	Lower	7.77 (0.57)	0.23 (0.14)	4.42 (1.39)	6.40 (7.28)	18.60 (15.71)	5.70 (4.74)	609.11 (410.18)	5.67 (5.73)	2.72 (1.28)	0.17 (0.09)	17.58 (6.45)
<i>RecentBurn</i>	Top	7.09 (0.62)	0.20 (0.10)	4.40 (1.31)	8.50 (5.72)	25.00 (14.38)	7.00 (4.40)	522.30 (207.89)	5.67 (3.81)	2.72 (1.32)	0.18 (0.08)	15.43 (5.46)

Table A2.2 Read counts filtered at each dada2 processing step

Sample	SequencingRun	input	filtered	denoisedF	nonchim
PIED-I-OB-02-L-T0	1	50264	43305	42991	44282
PIED-I-OB-02-L-T1	1	107957	92419	91707	44287
PIED-I-OB-02-Seedling-T0	1	34742	26859	26475	30264
PIED-I-OB-02-T-T0	1	60648	54010	53490	39580
PIED-I-OB-02-T-T1	1	52699	42673	42172	40697
PIED-I-OB-06-L-T2	1	70356	57693	57109	33585
PIED-I-OB-06-T-T2	1	69698	60842	60374	32045
PIED-I-OB-07-L-T0	1	53208	46698	46384	26704
PIED-I-OB-07-L-T1	1	104683	87377	86762	22828
PIED-I-OB-07-Seedling-T0	1	45605	36342	35885	33585
PIED-I-OB-07-T-T0	1	45481	39229	38953	29614
PIED-I-OB-07-T-T1	1	50154	42036	41602	32294
PIED-I-OB-09-L-T0	1	46435	38284	37888	3037
PIED-I-OB-09-L-T1	1	109017	88065	87550	14308
PIED-I-OB-09-Seedling-T0	1	55018	44950	44508	25710
PIED-I-OB-09-T-T0	1	38470	30430	30029	40309
PIED-I-OB-09-T-T1	1	61279	51735	51385	31803
PIED-I-OB-17-L-T2	1	78520	68358	67799	38463
PIED-I-OB-17-T-T2	1	61942	54270	53784	35562
PIED-I-OB-52-L-T2	1	75337	63406	62856	40228
PIED-I-OB-52-T-T2	1	94866	82597	82047	30679
PIED-I-OB-57-L-T2	1	88350	73921	73373	28731
PIED-I-OB-57-T-T2	1	85030	72301	71709	19334
PIED-I-OB-61-L-T0	1	52899	48409	47919	29130
PIED-I-OB-61-L-T1	1	43875	37188	36771	44282
PIED-I-OB-61-Seedling-T0	1	64956	52460	52036	44287
PIED-I-OB-61-T-T0	1	69620	58304	57659	30264
PIED-I-OB-61-T-T1	1	66593	57633	57099	39580
PIED-I-OB-68-L-T0	1	75482	63791	63375	40697
PIED-I-OB-68-L-T1	1	62892	51911	51308	33585
PIED-I-OB-68-L-T2	1	95376	78968	78400	32045
PIED-I-OB-68-Seedling-T0	1	41927	30666	30185	26704
PIED-I-OB-68-T-T0	1	67686	58668	58310	22828
PIED-I-OB-68-T-T1	1	46233	39951	39276	33585
PIED-I-OB-68-T-T2	1	85150	73367	72681	29614

PIED-I-RB-12-L-T0	1	109000	89466	89214	32294
PIED-I-RB-12-L-T1	1	107210	88103	87799	3037
PIED-I-RB-12-Seedling-T0	1	60500	51204	50760	14308
PIED-I-RB-12-T-T0	1	79089	67635	67116	25710
PIED-I-RB-12-T-T1	1	105987	91270	90794	40309
PIED-I-RB-14-L-T2	1	69960	62756	62067	31803
PIED-I-RB-14-T-T2	1	93292	80426	79756	38463
PIED-I-RB-32-L-T0	1	45161	33241	33005	35562
PIED-I-RB-32-L-T1	1	95985	80884	80258	40228
PIED-I-RB-32-L-T2	1	61604	50642	50233	30679
PIED-I-RB-32-Seedling-T0	1	68786	53152	52587	28731
PIED-I-RB-32-T-T0	1	64407	54681	54113	19334
PIED-I-RB-32-T-T1	1	81178	74926	74381	29130
PIED-I-RB-32-T-T2	1	69558	61616	61124	44282
PIED-I-RB-39-L-T2	1	73122	59952	59320	44287
PIED-I-RB-39-T-T2	1	81514	69887	69218	30264
PIED-I-RB-46-L-T0	1	61032	53420	52924	39580
PIED-I-RB-46-L-T1	1	97078	83156	82582	40697
PIED-I-RB-46-Seedling-T0	1	70894	55613	54870	33585
PIED-I-RB-46-T-T0	1	48058	42211	41651	32045
PIED-I-RB-46-T-T1	1	79712	68537	67751	26704
PIED-I-RB-49-L-T1	1	86193	69823	69007	22828
PIED-I-RB-49-L-T2	1	109174	87429	86953	33585
PIED-I-RB-49-Seedling-T0	1	72990	56918	56415	29614
PIED-I-RB-49-T-T0	1	64099	54301	53873	32294
PIED-I-RB-49-T-T1	1	119907	103271	102441	3037
PIED-I-RB-49-T-T2	1	77651	69657	69218	14308
PIED-I-RB-60-L-T0	1	45488	39225	38904	25710
PIED-I-RB-60-L-T1	1	59720	52763	52296	40309
PIED-I-RB-60-Seedling-T0	1	72511	57772	57287	31803
PIED-I-RB-60-T-T0	1	50784	42578	42121	38463
PIED-I-RB-60-T-T1	1	83643	74540	73910	35562
PIED-S-OB-12-L-T0	1	48279	42729	42362	40228
PIED-S-OB-12-L-T1	1	53693	44923	44364	30679
PIED-S-OB-12-L-T2	1	62550	50606	50057	28731
PIED-S-OB-12-Seedling-T0	1	73645	61358	60859	19334
PIED-S-OB-12-T-T0	1	57431	45946	45640	29130

PIED-S-OB-12-T-T1	1	53650	46395	45850	44282
PIED-S-OB-12-T-T2	1	44951	39893	39501	44287
PIED-S-OB-22-L-T2	1	33697	27348	26949	30264
PIED-S-OB-22-T-T2	1	48167	36850	36457	39580
PIED-S-OB-27-L-T2	1	72528	60754	60076	40697
PIED-S-OB-27-T-T2	1	50697	45095	44593	33585
PIED-S-OB-38-L-T0	1	34433	28092	27657	32045
PIED-S-OB-38-L-T1	1	82189	74663	74185	26704
PIED-S-OB-38-Seedling-T0	1	85152	72553	72185	22828
PIED-S-OB-38-T-T0	1	42563	36490	35830	33585
PIED-S-OB-52-L-T1	1	69477	57907	57315	29614
PIED-S-OB-52-Seedling-T0	1	63494	47834	47539	32294
PIED-S-OB-52-T-T1	1	39995	34936	34529	3037
PIED-S-OB-55-L-T0	1	48640	42994	42631	14308
PIED-S-OB-55-L-T1	1	66923	58766	58341	25710
PIED-S-OB-55-L-T2	1	74350	65065	64727	40309
PIED-S-OB-55-Seedling-T0	1	38749	32806	32512	31803
PIED-S-OB-55-T-T0	1	53841	45005	44483	38463
PIED-S-OB-55-T-T1	1	49820	45213	44785	35562
PIED-S-OB-55-T-T2	1	84354	72400	71892	40228
PIED-S-OB-56-L-T0	1	36559	31678	31288	30679
PIED-S-OB-56-L-T1	1	83050	68775	68161	28731
PIED-S-OB-56-Seedling-T0	1	47323	36649	36263	19334
PIED-S-OB-56-T-T0	1	45232	37671	37289	29130
PIED-S-OB-56-T-T1	1	73613	59295	58701	44282
PIED-S-OB-74-L-T2	1	56208	45827	45398	44287
PIED-S-OB-74-T-T2	1	52678	42416	41909	30264
PIED-S-RB-09-L-T0	1	72416	55953	55482	39580
PIED-S-RB-09-L-T1	1	55467	48680	48207	40697
PIED-S-RB-09-Seedling-T0	1	84531	71779	71526	33585
PIED-S-RB-09-T-T0	1	43195	36846	36410	32045
PIED-S-RB-09-T-T1	1	45649	37545	37056	26704
PIED-S-RB-11-L-T0	1	66271	53557	53162	22828
PIED-S-RB-11-L-T1	1	64689	54865	54491	33585
PIED-S-RB-11-Seedling-T0	1	59793	44604	44129	29614
PIED-S-RB-11-T-T0	1	66345	56324	55798	32294
PIED-S-RB-11-T-T1	1	58916	50419	49959	3037

PIED-S-RB-12-L-T2	1	65149	55824	55395	14308
PIED-S-RB-12-T-T2	1	89308	73223	72685	25710
PIED-S-RB-14-L-T2	1	33316	28586	28247	40309
PIED-S-RB-14-T-T2	1	43386	36372	35936	31803
PIED-S-RB-26-L-T0	1	79967	61790	61223	38463
PIED-S-RB-26-L-T1	1	67879	58773	58275	35562
PIED-S-RB-26-Seedling-T0	1	124132	102793	102430	40228
PIED-S-RB-26-T-T0	1	76057	64251	63632	30679
PIED-S-RB-26-T-T1	1	71900	62510	61872	28731
PIED-S-RB-44-L-T0	1	83263	74579	74019	19334
PIED-S-RB-44-L-T1	1	100486	79401	78777	29130
PIED-S-RB-44-L-T2	1	67712	49942	49409	44282
PIED-S-RB-44-Seedling-T0	1	49423	36963	36623	44287
PIED-S-RB-44-T-T0	1	88436	72681	72238	30264
PIED-S-RB-44-T-T1	1	48794	39619	39166	39580
PIED-S-RB-44-T-T2	1	69021	61105	60584	40697
PIED-S-RB-56-L-T0	1	56420	47173	46735	33585
PIED-S-RB-56-L-T1	1	82702	68740	68208	32045
PIED-S-RB-56-Seedling-T0	1	106519	87755	87400	26704
PIED-S-RB-56-T-T0	1	65363	55756	55127	22828
PIED-S-RB-56-T-T1	1	83958	73175	72563	33585
PIED-S-RB-72-L-T2	1	88258	67969	67524	29614
PIED-S-RB-72-T-T2	1	76572	60677	60251	32294
I-OB-03-L-T3	2	338965	277435	276394	275642
I-OB-03-T-T3	2	469218	383837	382416	373546
I-OB-27-L-T3	2	290116	259410	258775	257853
I-OB-27-T-T3	2	306726	271368	270471	267098
I-OB-37-L-T3	2	259765	230508	229820	229724
I-OB-37-T-T3	2	377846	311165	310200	308574
I-OB-68-L-T3	2	368067	306789	305717	304113
I-OB-68-T-T3	2	374354	320331	319032	315750
I-OB-70-L-T3	2	291157	241831	240794	238254
I-OB-70-T-T3	2	266578	228310	227390	225267
I-RB-15-L-T3	2	333485	278144	277348	273046
I-RB-15-T-T3	2	391088	311285	309949	304473
I-RB-17-L-T3	2	251214	212613	211780	208960
I-RB-17-T-T3	2	234961	203107	202400	195929
I-RB-28-L-T3	2	325946	269513	268363	263490
I-RB-28-T-T3	2	349880	297743	296564	293042

I-RB-32-L-T3	2	342813	295900	294995	290958
I-RB-32-T-T3	2	286561	245068	244144	242422
S-OB-12-L-T3	2	377652	312322	311011	307964
S-OB-12-T-T3	2	352832	290967	289977	284982
S-OB-22-L-T3	2	269274	215901	214939	214661
S-OB-22-T-T3	2	229282	182288	181680	181465
S-OB-27-L-T3	2	366859	319960	318816	315344
S-OB-27-T-T3	2	325195	285042	283722	279955
S-OB-38-L-T1	2	372987	311266	310173	307536
S-OB-52-L-T0	2	345518	288820	287602	284976
S-OB-52-T-T0	2	371196	318924	317562	315164
S-OB-55-L-T3	2	336391	284540	283437	279890
S-OB-55-T-T3	2	342221	298457	297413	293555
S-OB-74-L-T3	2	253821	208631	207791	207024
S-OB-74-T-T3	2	367098	319753	318591	316226
S-RB-12-L-T3	2	341368	274162	272777	265343
S-RB-12-T-T3	2	380644	327001	325987	317114
S-RB-22-L-T3	2	358778	288425	287306	281938
S-RB-22-T-T3	2	314459	272731	271966	269293
S-RB-26-T-T0	2	406697	335101	333729	326963
S-RB-44-L-T3	2	334530	274489	273559	270088
S-RB-44-T-T3	2	309658	262536	261271	256237
S-RB-72-L-T3	2	319928	271804	270540	250286
S-RB-72-T-T3	2	311465	254792	253691	248362
PIED-I-OB-37-L-T4	3	50047	44429	44282	44282
PIED-I-OB-37-T-T4	3	50226	44576	44287	44287
PIED-I-OB-49-L-T4	3	34878	30471	30264	30264
PIED-I-OB-49-T-T4	3	45588	39859	39580	39580
PIED-I-OB-68-L-T4	3	47294	40969	40709	40697
PIED-I-OB-68-T-T4	3	38147	33832	33585	33585
PIED-I-RB-15-L-T4	3	38186	32362	32048	32045
PIED-I-RB-15-T-T4	3	31375	26981	26707	26704
PIED-I-RB-41-L-T4	3	26112	23001	22828	22828
PIED-I-RB-41-T-T4	3	38823	33756	33585	33585
PIED-I-RB-52-L-T4	3	33280	29992	29742	29614
PIED-I-RB-52-T-T4	3	36618	32593	32294	32294
PIED-S-OB-08-L-T4	3	3438	3130	3037	3037
PIED-S-OB-08-T-T4	3	16225	14516	14308	14308
PIED-S-OB-16-L-T4	3	29365	26083	25710	25710
PIED-S-OB-16-T-T4	3	45968	40885	40439	40309
PIED-S-OB-55-L-T4	3	35748	32055	31806	31803

PIED-S-OB-55-T-T4	3	41923	38754	38478	38463
PIED-S-RB-12-L-T4	3	39675	35982	35672	35562
PIED-S-RB-12-T-T4	3	47249	40618	40260	40228
PIED-S-RB-29-L-T4	3	34934	30859	30681	30679
PIED-S-RB-29-T-T4	3	32702	28989	28735	28731
PIED-S-RB-70-L-T4	3	21664	19682	19493	19334
PIED-S-RB-70-T-T4	3	32738	29425	29130	29130

Table A2.3 Seasonal percent survival and mean height (sd) in cm for each treatment (fire age x soil treatment x nurse object). Percent survival does not include seedlings that were missing or lack confirmed survival outcome. USB is Utah Serviceberry.

Fire Age	Soil Treatment	Nurse Object	Height T0	Survival T1	Height T1	Survival T2	Height T2	Survival T3	Height T3	Survival T4	Height T4
Old Fire	Inoculated	Gambel Oak	7.57 (1.21)	100	7.55 (1.85)	87	9.57 (2.94)	86	9.81 (2.23)	71.4	14.6 (2.50)
		USB	6.47 (1.85)	100	6.85 (1.73)	42	10.97 (0.94)	38	10.52 (1.66)	15.4	14.4 (4.17)
		Log	6.18 (1.75)	81	6.10 (1.88)	31	6.60 (2.34)	31	6.68 (1.89)	6.25	16.4
		Rock	6.94 (1.68)	93	5.98 (2.12)	21	7.37 (1.70)	21	6.47 (2.24)	0	-
		Interspace	6.74 (1.22)	93	6.29 (1.50)	29	10.06 (2.43)	21	8.13 (1.22)	6.67	[not measured]
	Non-inoculated	Gambel Oak	5.62 (1.08)	100	5.87 (1.83)	79	8.82 (2.75)	80	7.68 (2.32)	53.3	13.4 (3.40)
		USB	6.54 (1.91)	93	5.98 (1.86)	36	7.63 (2.86)	31	7.30 (2.14)	14.3	10.3 (1.84)
		Log	7.08 (1.28)	100	6.50 (1.56)	42	8.68 (1.75)	36	8.60 (3.62)	7.69	14.8
		Rock	7.44 (1.66)	100	7.11 (1.86)	7	10.20 (0.00)	7	9.10 (0.00)	0	-
		Interspace	6.26 (1.85)	100	5.49 (2.27)	7	10.40 (0.00)	7	11.00 (0.00)	0	-
Recent Fire	Inoculated	Gambel Oak	7.10 (1.82)	93	7.14 (2.23)	80	8.38 (2.34)	67	9.14 (1.63)	35.7	12.5 (0.92)
		USB	7.57 (1.59)	100	6.17 (1.93)	42	8.74 (1.13)	38	8.96 (1.08)	8.3	21.2
		Log	7.73 (1.56)	93	7.29 (1.87)	71	9.07 (1.57)	73	9.31 (1.49)	57.1	16.3 (6.28)
		Grass	8.22 (1.78)	100	6.77 (1.89)	0	-	0	-	0	-
		Interspace	7.75 (2.08)	100	6.41 (2.55)	40	9.82 (2.84)	33	9.92 (3.61)	0	-

Non-inoculated	Gambel	7.19	87	7.27	54	8.20	57	7.79	21.4	15.3
	Oak	(2.42)		(1.99)		(2.10)		(2.15)		(3.20)
	USB	7.17	93	7.61	64	7.77	46	7.18	15.4	12.3
		(1.45)		(2.05)		(2.57)		(2.35)		(1.13)
	Log	6.23	93	7.01	86	7.78	79	7.07	42.9	11.1
		(1.23)		(1.45)		(1.44)		(2.20)		(2.72)
	Grass	7.39	87	7.59	0	-	0	-	0	-
		(1.98)		(1.45)						
	Interspace	6.44	100	6.46	33	6.66	21	8.47	0	-
		(1.76)		(1.96)		(1.87)		(1.32)		

Table A2.4 Mann-Whitney U test of the differences in alpha-diversity measures at each time point, comparing fire age (Time 0 - Time 4) and inoculation treatment (Time 1 - Time 4), and separated by soil layer.

Timepoint	Soil Layer	Recent Burn vs Old Burn				Inoculated vs Non-inoculated			
		Chao	Shannon	Simpson	Pielou	Chao	Shannon	Simpson	Pielou
Timepoint 0	Top	0.579	0.353	0.218	0.315				
	Lower	0.549	0.400	0.356	0.497				
Timepoint 1	Top	0.400	0.315	0.400	0.243	0.661	0.447	0.315	0.356
	Lower	0.349	0.809	0.654	0.223	0.809	1.000	0.918	0.605
Timepoint 2	Top	0.887	0.813	0.887	0.669	0.093	0.093	0.074	0.167
	Lower	0.669	0.161	0.055	0.133	0.114	0.963	0.963	0.888
Timepoint 3	Top	0.360	1.000	0.897	0.697	0.796	0.667	0.436	1.000
	Lower	0.515	0.633	0.573	0.515	0.162	0.222	0.546	0.387
Timepoint 4	Top	0.180	1.000	0.485	0.589	0.937	0.937	0.937	0.699
	Lower	0.394	0.310	0.093	0.310	0.589	0.589	0.937	0.700

Table A3.5. Mean relative abundance (and standard deviation) of ectomycorrhizal (EMF), pathogenic and parasitic, and saprotrophic guilds by fire age and treatment. Time 0 is the baseline pre-planting soil, therefore compares old burn and recent burn. Mann-Whitney U tests were performed for the two soil horizons at Time 0, stars indicate significant differences ($p < 0.05$). Kruskal-Wallis non-parametric tests were used to test for differences in relative abundances at Time 1 – 4; if there were significant differences ($p < 0.05$), Dunn's test with Bonferroni adjustment were used to conduct pairwise comparisons, indicated by letters.

Guild	Soil Layer	Fire Age	Treatment	Time 0	Time 1	Time 2	Time 3	Time 4
Ectomycorrhizal	Seedling Soil	---	Inoculated	0.16 (0.23)*				
		---	Non-inoculated	0.001 (0.00)*				
	Top (0 - 5 cm)	Old Burn	Inoculated		0.011 (0.02)	0.075 (0.12)	0.07 (0.07)	0.184 (0.20)
		Old Burn	Non-inoculated	0.067 (0.09)	0.041 (0.07)	0.061 (0.13)	0.066 (0.07)	0.047 (0.05)
		Recent Burn	Inoculated		0.002 (0.00)	0.001 (0.00)	0.054 (0.10)	0.005 (0.00)
		Recent Burn	Non-inoculated	0.003 (0.00)	0.005 (0.00)	0.004 (0.00)	0.03 (0.06)	0.007 (0.01)
	Lower (5 - 10 cm)	Old Burn	Inoculated		0.037 (0.05)	0.152 (0.21)	0.188 (0.21)	0.259 (0.27)
		Old Burn	Non-inoculated	0.155 (0.22)	0.01 (0.01)	0.233 (0.22)	0.179 (0.18)	0.244 (0.25)

Pathogenic and parasitic		Recent Burn	Inoculated		0.033 (0.07)	0.006 (0.01)	0.072 (0.08)	0.065 (0.11)
		Recent Burn	Non-inoculated	0.045 (0.10)	0.101 (0.18)	0.045 (0.05)	0.085 (0.13)	0.058 (0.07)
	<i>Seedling Soil</i>	---	Inoculated	0.002 (0.00)*				
		---	Non-inoculated	0.0003 (0.00)*				
	<i>Top (0 - 5 cm)</i>	Old Burn	Inoculated		0.061 (0.06) ^a	0.009 (0.01)	0.012 (0.01)	0.007 (0.00)
		Old Burn	Non-inoculated	0.026 (0.03)*	0.165 (0.18) ^a	0.024 (0.03)	0.03 (0.02)	0.023 (0.01)
		Recent Burn	Inoculated		0.011 (0.01) ^{ab}	0.008 (0.00)	0.01 (0.01)	0.011 (0.02)
		Recent Burn	Non-inoculated	0.006 (0.01)*	0.006 (0.00) ^b	0.005 (0.01)	0.005 (0.00)	0.005 (0.00)
	<i>Lower (5 - 10 cm)</i>	Old Burn	Inoculated		0.036 (0.04)	0.004 (0.00)	0.015 (0.03)	0.003 (0.00)
		Old Burn	Non-inoculated	0.013 (0.01)*	0.034 (0.03)	0.018 (0.03)	0.02 (0.02)	0.016 (0.01)
		Recent Burn	Inoculated		0.008 (0.01)	0.005 (0.01)	0.007 (0.00)	0.004 (0.00)
		Recent Burn	Non-inoculated	0.014 (0.03)*	0.004 (0.00)	0.008 (0.02)	0.004 (0.00)	0.005 (0.00)
Saprotrophic	<i>Seedling Soil</i>	---	Inoculated	0.023 (0.01)*				
		---	Non-inoculated	0.409 (0.41)*				
	<i>Top (0 - 5 cm)</i>	Old Burn	Inoculated		0.171 (0.07) ^a	0.286 (0.13)	0.156 (0.11)	0.147 (0.08)
		Old Burn	Non-inoculated	0.215 (0.15)*	0.151 (0.08) ^a	0.174 (0.09)	0.204 (0.07)	0.226 (0.09)
		Recent Burn	Inoculated		0.348 (0.16) ^a	0.308 (0.13)	0.223 (0.11)	0.398 (0.29)
		Recent Burn	Non-inoculated	0.436 (0.14)*	0.352 (0.1) ^a	0.262 (0.18)	0.342 (0.11)	0.198 (0.04)
	<i>Lower (5 - 10 cm)</i>	Old Burn	Inoculated		0.232 (0.23)	0.173 (0.09) ^{ab}	0.147 (0.14)	0.072 (0.06)
		Old Burn	Non-inoculated	0.207 (0.13)	0.388 (0.2)	0.089 (0.04) ^a	0.121 (0.05)	0.231 (0.16)
		Recent Burn	Inoculated		0.248 (0.19)	0.239 (0.12) ^{ab}	0.129 (0.05)	0.17 (0.04)
		Recent Burn	Non-inoculated	0.340 (0.25)	0.246 (0.09)	0.297 (0.16) ^b	0.262 (0.13)	0.185 (0.15)



Figure A2.1. Photographs of a) mature green cone, unopened, at time of piñon cone collection, b) dried and opened piñon cone where seeds could be extracted c) piñon seedling emergence ~1 weeks after sowing germinated seeds in containers. Most seedlings emerged around the same date within three days.

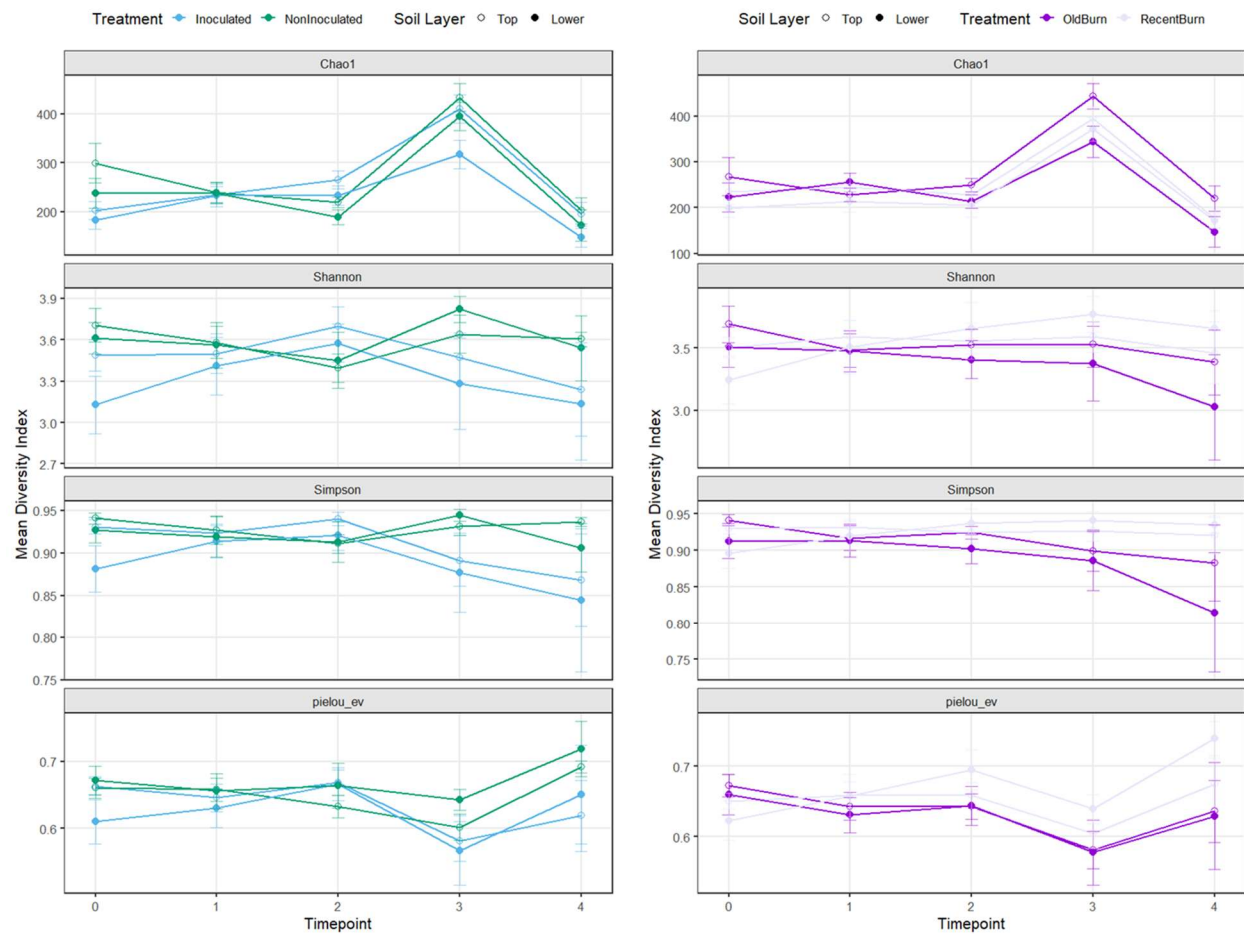


Figure A2.2. Mean diversity index for inoculated (blue) and non-inoculated (green) samples, and samples from the recent fire (lavender) and old fire (purple) at each timepoint.

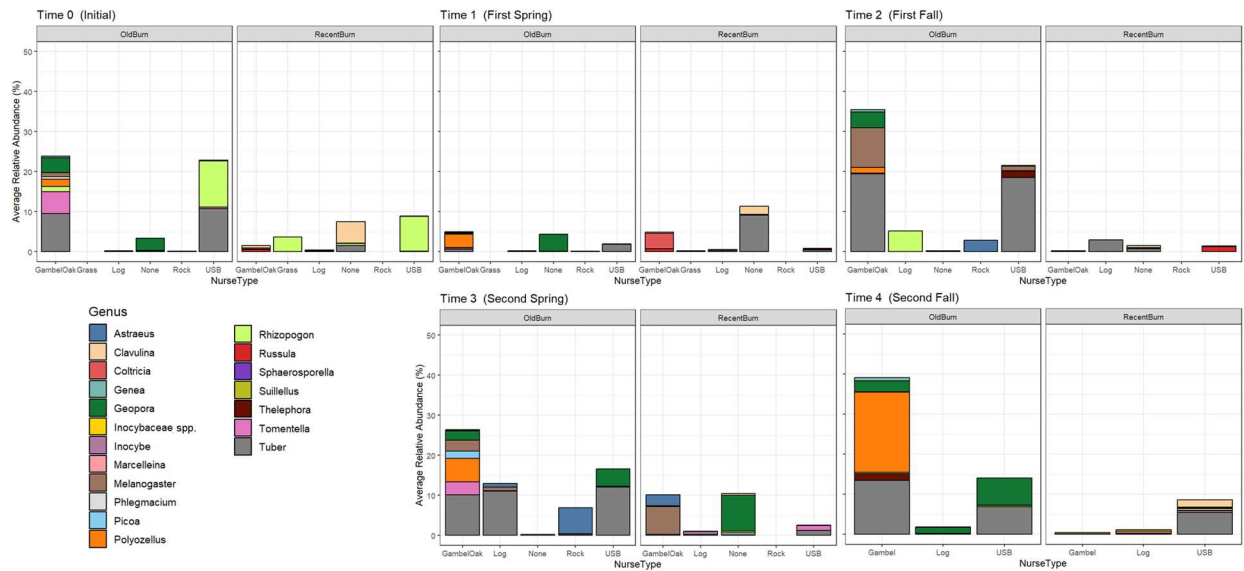


Figure A2.3 Ectomycorrhizal genera found under the different nurse objects at each time point. This figure is exploratory and should be interpreted with caution as our sampling design was not designed to thoroughly disentangle the EMF community differences between nurse objects. In this figure, community is assessed from two samples per nurse object per time point, and does not separate inoculated and non-inoculated samples.

APPENDIX 3

Table A3.1. Percent cover of National Land Cover Database (NLCD) classified vegetation before fires (2001), 1 year after the fire (2003), and 22 years after the fire (2023).

Fire	Vegetation Class	Percent Cover Pre-fire	Percent Cover 1-year Post- fire	Percent Cover 20-year Post- fire
Hayman	Evergreen Forest	82%	21%	26%
	Shrub/Scrub	14%	8%	60%
	Developed, Open Space	1%	1%	1%
	Grassland/Herbaceous	1%	69%	11%
	Woody Wetland	1%	1%	1%
Missionary Ridge	Evergreen Forest	45%	23%	30%
	Deciduous Forest	24%	10%	30%
	Mixed Forest	22%	7%	8%
	Shrub/Scrub	3%	3%	22%
	Developed, Open Space	1%	1%	1%
	Developed, Low Intensity	1%	1%	1%
	Grassland/Herbaceous	1%	51%	5%
	Pasture/Hay	1%	1%	1%
Ponil	Evergreen Forest	72%	34%	44%
	Shrub/Scrub	25%	17%	47%
	Grassland/Herbaceous	2%	48%	8%
Rattle	Evergreen Forest	67%	25%	28%
	Shrub/Scrub	24%	36%	67%
	Deciduous Forest	8%	1%	1%
	Woody Wetland	1%	0%	0%
	Grassland/Herbaceous	0%	37%	3%
Rodeo- Chediski	Evergreen Forest	91%	36%	58%
	Shrub/Scrub	6%	13%	40%
	Developed, Open Space	2%	2%	2%
	Grassland/Herbaceous	0%	48%	0%
Sanford	Evergreen Forest	69%	29%	35%
	Shrub/Scrub	27%	36%	63%
	Deciduous Forest	3%	1%	1%
	Mixed Forest	1%	0%	0%
	Grassland/Herbaceous	0%	33%	0%

Table A3.2 Predictor variables considered during random forest model optimization, variables retained after forward variable selection for the final model, and their corresponding permutation importance values for estimating evapotranspiration (ET) across three time periods: pre-fire (2000–2001), one year post-fire (2003–2004), and twenty years post-fire (2022–2024). The table also reports model hyperparameters (mtry, number of trees, minnode size) and performance metrics (R2 and RSME) derived from cross-validation on the testing dataset.

	Initial Variables	Final Variables	Importance	Model parameters	Model Accuracy
Pre-fire ET	PreFire_annualmean_ppt	PreFire_annualmean_ppt	145.368	mtry = 4	R2 = 0.55
	PreFire_mean_tmean	PreFire_mean_tmean	113.688	trees = 1000	RSME = 114.92
	PreFire_mean_vpdmax	pre_Prop_SummerPPT	109.044	minnode = 20	
	PreFire_Deciduous_Forest	PreFire_Evergreen_Forest	80.301		
	PreFire_Evergreen_Forest	Loam	65.575		
	PreFire_Mixed_Forest	PreFire_Mixed_Forest	64.776		
	PreFire_Shrub_Scrub	Slope	59.018		
	PreFire_Grassland_Herbaceous				
	ClayLoam				
	SandyClayLoam				
	Loam				
	SandyLoam				
	SiltLoam				
	Elevation				
	HLI				
	slope				
	pre_Prop_SummerPPT				
1-year Post-Fire ET	PostFire1_annualmean_ppt	PostFire1_annualmean_ppt	111.85	mtry = 3	R2 = 0.62
	PostFire1_mean_tmean	PostFire1_Evergreen_Forest	108.96	trees = 1000	RMSE = 94.39
	PostFire1_mean_vpdmax	Post1_Prop_SummerPPT	86.21	min node = 20	
	PostFire1_Deciduous_Forest	Loam	58.56		
	PostFire1_Evergreen_Forest	Slope	47.29		
	PostFire1_Mixed_Forest	dNBR_class_5	44.84		
	PostFire1_Shrub_Scrub	dNBR_class_1	34.78		

PostFire1_Grassland_Herbaceous

dNBR_class_0

dNBR_class_1

dNBR_class_2

dNBR_class_3

dNBR_class_4

dNBR_class_5

ClayLoam

SandyClayLoam

Loam

SandyLoam

SiltLoam

Elevation

HLI

slope

Post1_Prop_SummerPPT

	PostFire20_annualmean_ppt	PostFire20_mean_tmean	166.35	mtry = 5	R2 = 0.65
					RMSE =
	PostFire20_mean_tmean	PostFire20_annualmean_ppt	117.478	trees = 1000	112.90
	PostFire20_mean_vpdmax	PostFire20_Evergreen_Forest	102.909	min node size = 20	
20-years post-fire ET	PostFire20_Deciduous_Forest	post20_Prop_SummerPPT	93.746		
	PostFire20_Evergreen_Forest	Loam	81.685		
	PostFire20_Mixed_Forest	Slope	52.996		
	PostFire20_Shrub_Scrub	PostFire20_Deciduous_Forest	46.039		
	PostFire20_Grassland_Herbaceous	PostFire20_Mixed_Forest	41.461		
	dNBR_class_0	dNBR_class_5	37.329		
	dNBR_class_1	dNBR_class_1	35.136		
	dNBR_class_2	dNBR_class_3	33.215		
	dNBR_class_3	SandyClayLoam	14.321		
	dNBR_class_4				
	dNBR_class_5				

ClayLoam
SandyClayLoam
Loam
SandyLoam
SiltLoam
Elevation
HLI
slope
post20 Prop SummerPPT

Table A3.3 Predictor variables considered during random forest model optimization, variables retained after forward variable selection for the final model, and their corresponding permutation importance values for estimating evapotranspiration: precipitation (ET:P) across three time periods: pre-fire (2000–2001), one year post-fire (2003–2004), and twenty years post-fire (2022–2024). The table also reports model hyperparameters (mtry, number of trees, minnode size) and performance metrics (R2 and RSME) derived from cross-validation on the testing dataset.

	Initial Variables	Variable	Importance	Model parameters	Model Accuracy
Pre-fire ET:P	PreFire_mean_tmean	PreFire_mean_tmean	0.248	mtry = 4	R2 = 0.56
	PreFire_mean_vpdmax	pre_Prop_SummerPPT	0.244	trees = 1000	RSME = 0.22
	PreFire_Deciduous_Forest	PreFire_Evergreen_Forest	0.163	minnode = 20	
	PreFire_Evergreen_Forest	Slope	0.12		
	PreFire_Mixed_Forest	Loam	0.117		
	PreFire_Shrub_Scrub	PreFire_Deciduous_Forest	0.101		
	PreFire_Grassland_Herbaceous	PreFire_Mixed_Forest	0.091		
	ClayLoam	SandyClayLoam	0.032		
	SandyClayLoam				
	Loam				
	SandyLoam				
	SiltLoam				
	Elevation				
	HLI				
	slope				

1-year Post-fire ET:P	pre Prop SummerPPT				
	PostFire1_mean_tmean	Proportion evergreen forest	0.215	mtry = 4	R2 = 0.35
	PostFire1_mean_vpdmax	Annual mean temperature	0.142	trees = 100	RMSE = 0.22
	PostFire1_Deciduous_Forest	Annual mean VPDmax	0.128	minimum node size = 60	
	PostFire1_Evergreen_Forest	Proportion silt loam	0		
	PostFire1_Mixed_Forest				
	PostFire1_Shrub_Scrub				
	PostFire1_Grassland_Herbaceous				
	dNBR_class_0				
	dNBR_class_1				
	dNBR_class_2				
	dNBR_class_3				
	dNBR_class_4				
	dNBR_class_5				
	ClayLoam				
	SandyClayLoam				
	Loam				
	SandyLoam				
	SiltLoam				
	Elevation				
	HLI				
	slope				
20-years Post-fire ET:P	post1 Prop SummerPPT				
	PostFire20_mean_tmean	Annual mean temperature	0.427	mtry = 3	R2 = 0.77
		Proportion summer			
	PostFire20_mean_vpdmax	precipitation	0.227	trees = 1000	RMSE = 0.19
	PostFire20_Deciduous_Forest	Proportion evergreen forest	0.213	min node size = 20	
	PostFire20_Evergreen_Forest	Proportion deciduous forest	0.131		
	PostFire20_Mixed_Forest	Slope	0.114		
		Proportion increasing			
PostFire20_Shrub_Scrub	greenness	0.07			
PostFire20_Grassland_Herbaceous					

dNBR_class_0
dNBR_class_1
dNBR_class_2
dNBR_class_3
dNBR_class_4
dNBR_class_5
ClayLoam
SandyClayLoam
Loam
SandyLoam
SiltLoam
Elevation
HLI
slope
post20 Prop SummerPPT

Table A3.4 Predictor variables considered during random forest model optimization, variables retained after forward variable selection for the final model, and their corresponding permutation importance values for estimating evapotranspiration departure (ETdepart) one year post-fire (2003–2004), and twenty years post-fire (2022–2024). The table also reports model hyperparameters (mtry, number of trees, minnode size) and performance metrics (R2 and RSME) derived from cross-validation on the testing dataset.

	Initial Variables	Variable	Importance	Model parameters	Model Accuracy
1-year Post-fire ET departure	ppt_zscore_post1	ChangeEvergreen1	79.807	mtry = 3	R2 = 0.81
	ppt_24yrAvg	dNBR_class_0	70.652	trees = 100	RMSE = 57.11
	vpdmax_zscore_post1	ppt_zscore_post1	58.855	minimum node size = 20	
	vpdmax_24yrAvg	ChangeMixed1	54.711		
	tmean_zscore_post1	dNBR_class_1	48.477		
	tmean_24yrAvg	dNBR_class_3	39.82		
	ChangeDeciduous1	dNBR_class_2	36.922		
	ChangeEvergreen1	ChangeDeciduous1	23.495		
	ChangeMixed1	Loam	21.238		
	ChangeShrub1				

ChangeGrassland1					
dNBR_class_0					
dNBR_class_1					
dNBR_class_2					
dNBR_class_3					
dNBR_class_4					
dNBR_class_5					
ClayLoam					
SandyClayLoam					
Loam					
SandyLoam					
SiltLoam					
Elevation					
HLI					
slope					
post1_Prop_SummerPPT					
20-years post-fire ET departure	ppt_zscore_post20	ChangeEvergreen20	77.729	mtry = 3	R2 = 0.65
	ppt_24yrAvg	vpdmax_24yrAvg	42.715	trees = 1000	RMSE = 60.46
	vpdmax_zscore_post20	dNBR_class_0	41.873	min node size = 20	
	vpdmax_24yrAvg	vpdmax_zscore_post20	40.841		
	tmean_zscore_post20	dNBR_class_1	38.413		
	tmean_24yrAvg	post20_Prop_SummerPPT	33.196		
	ChangeDeciduous20	dNBR_class_3	30.705		
	ChangeEvergreen20	dNBR_class_2	29.575		
	ChangeMixed20	Slope	26.87		
	ChangeShrub20	Loam	24.654		
	ChangeGrassland20				
	dNBR_class_0				
	dNBR_class_1				
	dNBR_class_2				
	dNBR_class_3				

dNBR_class_4
dNBR_class_5
ClayLoam
SandyClayLoam
Loam
SandyLoam
SiltLoam
Elevation
HLI
slope
post20 Prop SummerPPT

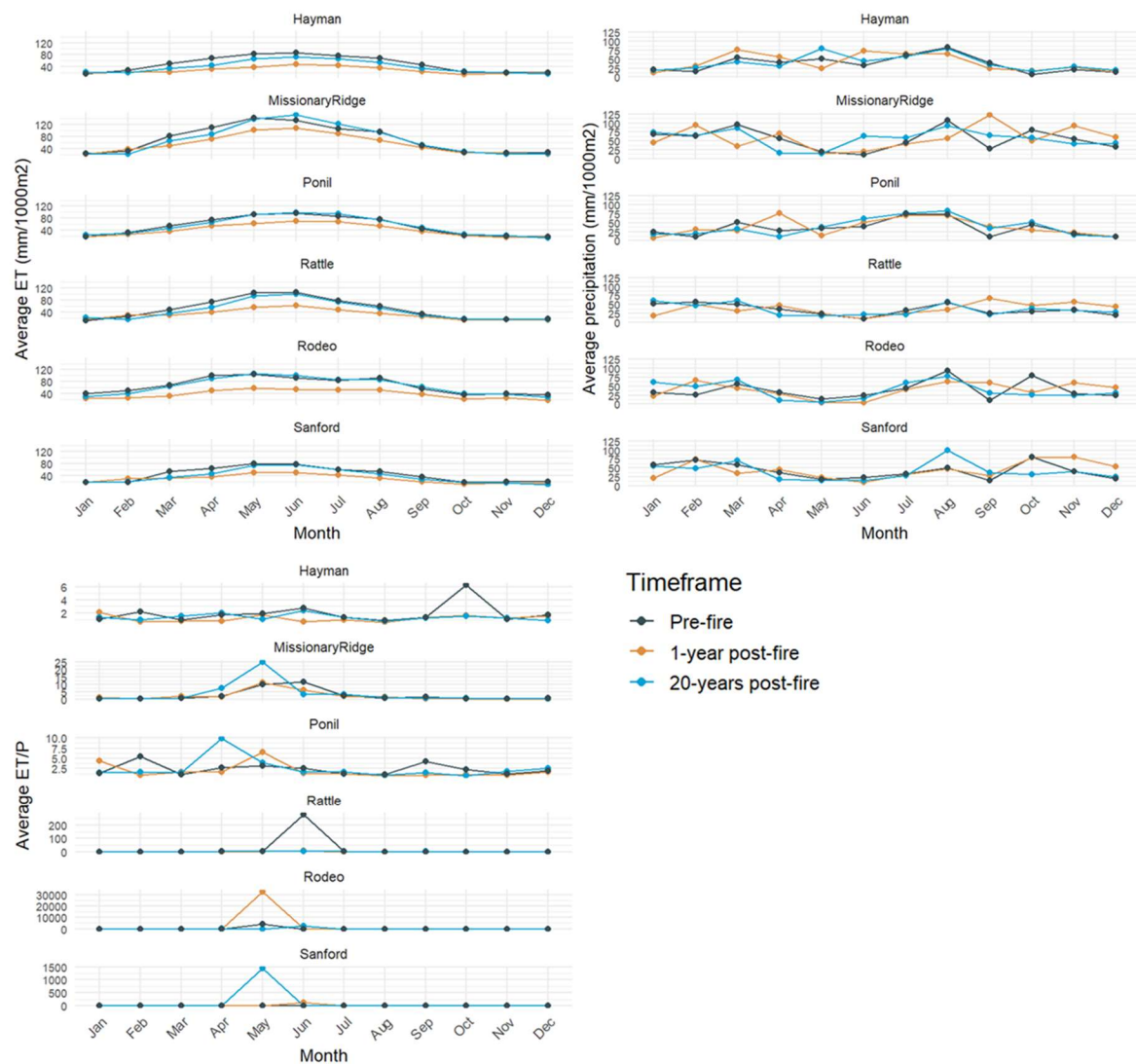


Figure A3.1. Average monthly ET (mm), precipitation (mm), and ET:P per pixel in each fire. Lines are colored by timeframe (pre-fire (2000 - 2001) = black, 1-year post-fire (2003 - 2004) = orange, and 20-years post-fire (2022 - 2024) = light blue. Notice the difference in ET:P y-scale in each fire.