THESIS

TRANSITIONS OF SEMI-ARID FORESTS AND WOODLANDS IN THE FACE OF SEVERE WILDFIRE AND CLIMATE CHANGE

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ABSTRACT

TRANSITIONS OF SEMI-ARID FORESTS AND WOODLANDS IN THE FACE OF SEVERE WILDFIRE AND CLIMATE CHANGE

Increased wildfire activity and climate change are altering semi-arid forests and woodlands in the southwestern U.S. Large, severe wildfires, driven by increased fuel density from centuries of fire suppression and spread of invasive species, combined with increasing drought conditions and temperatures, raise concern for the ability of forests to regenerate within their historical ranges. We studied piñon-juniper woodlands (PJ) and ponderosa pine forests (ponderosa), which exist at the hot and dry climatic limit of forested ecosystems in North America, and are at risk of conversion to non-forested ecosystems or shifts to more suitable climates. PJ woodlands often border ponderosa pine forests at the ecotone boundary, providing an indicator for potential range shifts. We utilized data from 201 sites across 24 high-severity burns in southern and western Colorado and northern New Mexico on a gradient of PJ woodland, PJ-ponderosa ecotone, and ponderosa pine forest to observe tree regeneration 17+ years post-fire. We examined seedling regeneration against changes in 30-year means of climate variables from pre-fire to post-fire, vegetation cover, geographic variables, and surface fuel load. We found that seedling densities of juniper, piñon pine, and ponderosa pine significantly decreased from their pre-fire densities. Piñon pine and juniper seedling regeneration were highest in sites with less increase in vapor pressure deficit (VPD) and longer time since fire (TSF); ponderosa pine seedling regeneration was highest in sites with less decrease in winter precipitation; and seedling regeneration of each species was highest closer to seed sources and when associated with a nurse object. Substantial proportions of PJ woodland (41%), ecotone (37%), and ponderosa pine forest (20%) sites transitioned to grassland or shrubland communities, while mean elevations of PJ woodlands and ponderosa pine forests trended upwards post-fire. In sites that regenerated as PJ woodland or ecotone, piñon pine seedlings were either non-existent or found at much lower densities than juniper. Transitions of woodlands and forests to non-forested communities and higher elevations are expected to be exacerbated under an increase 2°C in the future climate, however, natural shifts to suitable climates are unlikely given the rate of climate change and increased large, homogenous severe wildfires. Our findings suggest that PJ woodlands and ponderosa pine forests are contracting in the southwestern US, and management will likely be required to assist regeneration in suitable climates if persistence of these ecosystems is desired.

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CHAPTER 1

Introduction

In recent decades, forests in the western United States have faced an increase in wildfire size and severity (Singleton et al. 2019; Parks and Abatzoglou 2020, Parks et al. 2025). Increased frequency of large, severe fires is often attributed to interactions of human disturbances, including fire suppression, climate change, invasive species, and grazing practices (Allen et al. 2002; Westerling 2016). As large, severe fires burn more frequently, there is concern that increasing climate change impacts, such as drought and heat, alter conditions required for forest regeneration, facilitating transitions to higher elevations and latitudes or rapid state shifts to non-forested ecosystems (Davis et al. 2019; Davis et al. 2020; Coop et al. 2020, Guiterman et al. 2022). This is especially prevalent in arid regions, such as southwestern United States, where forests are already approaching the edge of their climatic niche and temperatures have already increased approximately 1.5°C (2020-2025 mean anomaly compared to 1901-2000 mean; Climate at a Glance, NOAA, last accessed February 2026).

Piñon-juniper woodlands (PJ), dominated by piñon pine (*Pinus quadrifolia, P. edulis and P. monophyla*) and juniper (*Juniperus osteosperma and J. monosperma*) occur at the hottest and driest climatic limit of forests and woodlands in North America and occupy approximately 23.5 million hectares. Ponderosa pine (*Pinus ponderosa*) forests occupy approximately 5.8 million hectares in the southwestern US and often border PJ woodlands at higher elevations. The area where these ecosystems overlap, referred to here as the ecotone, exhibits vegetation from both communities and can serve as an important indicator of range shifts or vegetation conversion (League and Veblen 2006). As drought and increased temperatures threaten these ecosystems, both are perhaps most vulnerable to regeneration failures or a reduction in density following increased frequency of large, severe wildfires (Stevens-Rumann and Morgan 2019; Rodman, et al. 2019; Minott and Kolb 2020; Coop et al. 2020; Davis et al. 2023; Noel et al. 2023; Redmond et al. 2023; Phillips et al. 2024; Nigro et al. 2025).

Given the prevalence of PJ woodlands and ponderosa pine forests in the southwest, occupying over one quarter of the land cover, the critical ecosystem services they provide could be at risk. Both ecosystems improve water quality, sequester carbon in the soil and biomass, control erosion, regulate nutrient cycling, carry vital cultural significance to indigenous communities, and provide recreational opportunities (Swetnam 1984; Graham and Jain 2005; Neff et al. 2009; Breshears et al. 2011; Hurteau and Brooks 2011; Dore et al. 2012; Hurteau et al. 2014; Whitehair et al. 2024). PJ woodlands specifically provide habitat to obligate wildlife, such as the Pinyon Jay (*Gymnorhinus cyanocephalus*), and provide resources such as pine nuts and firewood (Breshears et al. 2011; Boone et al. 2018). Ponderosa pine forests additionally are used for timber and provide habitat to wildlife such as the Mexican spotted owl (*Strix occidentalis lucida*) and northern goshawk (*Astur atricapillus*; Bagdon et al. 2016). With increasing concern over losses of ecosystem services provided by forests and woodlands, understanding how climate change and changing fire regimes influence recovery of PJ woodlands and ponderosa pine forests is critical.

While there is growing concern over modern fire behavior, fire has long been an important driver of ecosystem processes of both communities, albeit with very different regimes. Historically, fires that burned in PJ woodlands were high-severity (Romme et al. 2009); however, such fires were infrequent due to low-density stands and little fuel continuity, with some estimates suggesting fire return intervals (FRI) ranging from 200 to 600 years (Floyd et al. 2004, Huffman et al. 2008). Wildfires corresponded with high wind events, or increased fuel loads, and were stand-replacing, which also increased the difficulty in accurately determining the FRI (Floyd et al. 2008; Board et al. 2018). In contrast to PJ woodlands, ponderosa pine forests historically experienced low-severity surface fires as frequently as every 5-25 years (Haffey et al. 2018; McKinney 2019). Ponderosa pine trees are well adapted to these surface fires due to their thick bark and self-pruning of lower branches (Korb et al. 2019). Thus historically, ponderosa pine forests were low-density stands with a heterogeneous structure, reinforcing low to moderate severity fire and limiting high-severity fire (Larson and Churchill 2012; Battaglia et al. 2018; Hessburg et al. 2019).

In recent decades PJ woodlands and ponderosa pine forests both experienced drastic changes in their fire regimes. Increased drought and temperatures, along with increased duration of hot and dry seasons contribute to lower fuel moisture and longer fire seasons (Westerling 2006; Singleton et al. 2019; Woolman et al. 2022). In ponderosa pine forests, a long history of fire suppression policies in the US has altered stand composition and increased fuel load and continuity, which, in addition to hotter and drier conditions, has increased the frequency of large, homogenous, high-severity fires (Singleton et al. 2019; Mueller et al. 2020; Hood et al. 2021; Fulé et al. 2021). In PJ woodlands, the spread of invasive grasses often increases fuel continuity (Harris et al. 2003; Romme et al. 2009). Cheatgrass (*Bromus tectorum*), for example, is a widespread invasive grass within the region, known for invading independently of fire, and quickly establishing after fires promoting more frequent fire return (Brooks et al. 2004; Condon et al. 2011; Balch et al. 2013; Bradley et al. 2017). PJ woodlands have also exhibited increased densities or “infilling” in some of the Great Basin region, further increasing fuel continuity within portions of woodlands (Fillipelli et al. 2020).

Post-fire tree establishment is becoming increasingly difficult due to changing fire regimes and resulting high-severity patches, in addition to hotter and drier climates in both ecosystems (Westerling 2016; Abatzoglou and Williams 2016). Ponderosa pine trees have a short seed-dispersal range, generally limited to two times the height of the tree and occasionally up to 180m, which limits tree regeneration after large, severe homogenous fires (Chambers et al. 2022; Kemp et al. 2016). Contrarily, birds and small mammals distribute piñon pine and juniper seeds longer distances (Vander Wall and Balda, 1981; Chambers, et al. 1999). While juniper seeds have a long lifespan of up to 50 years and are continuously produced (Johnsen 1959; Chambers et al. 1999; Koepke et al. 2010), piñon pine seeds exhibit episodic seed production and only 1-2 years of seed viability in the soil (Tueller and Clark 1975; Redmond et al. 2019). Ponderosa pine, like piñon pine, is an episodic seed producer, which limits the number of seed production events that could lead to successful forest establishment in early post-fire years (Krannitz and Duralia 2004; Rother et al. 2015; Petrie et al. 2016; Rodman et al. 2020). These limitations give rise to concerns over losses in regeneration, range shifts, and range contractions following large, high-severity disturbances.

Recent studies have documented little to no PJ woodland regeneration after drought (Flake 2016; Redmond et al. 2018; Minott and Kolb 2020) and wildfire (Floyd et al. 2021; Woolet et al. 2023, Phillips et al. 2024). Where regeneration of PJ woodlands does occur, higher concentrations of juniper than piñon are likely given that juniper is more drought tolerant (Breshears, et al. 2009). Researchers have also documented a lack of regeneration in ponderosa pine forests after disturbance (Savage et al. 2013; Haffey et al. 2018; Rodman et al. 2020; Minott and Kolb 2020), and even in the absence of stand-replacing disturbance (Petrie et al. 2023). Climatic variables such as climate water deficit (CWD) and vapor pressure deficit (VPD) are often associated with regeneration declines, whereas successful regeneration often occurs with greater moisture availability during growing seasons (Hankin et al. 2019; Mueller et al. 2020). Tree establishment in both communities is expected to decline as moisture availability continues to decrease and temperatures continue to increase, especially when catalyzed by large, homogenous severe wildfires (Stevens-Rumann et al. 2018; Kemp et al. 2019, Davis et al. 2024, Noel et al. 2025a). Two studies conducted at the ecotone suggest drought-induced upward elevations shifts of the ecotone (Allen and Breshears 1998) and transitions of ponderosa pine forest to PJ woodland at the ecotone (Minott and Kolb 2020), however severe wildfire was not present in either study.

Thus, here we examined the regeneration dynamics of piñon-juniper woodlands, ponderosa pine forests, and the ecotone after high-severity fire. We expand upon, and incorporate data from, two recent studies that were conducted in the Southern Rockies and Colorado Plateau, which focused on regeneration patterns of PJ woodlands (Woolet et al. in review) and ponderosa pine forests (Vicini et al. 2025) independently. To our knowledge, no studies have attempted to determine how interactions between climate change and changes to fire regimes might impact tree regeneration along a PJ-ecotone-ponderosa gradient. To help determine regeneration dynamics across our ecosystem gradient, we answered the questions: (1) How are ponderosa pine forests and piñon-juniper woodlands regenerating from wildfires in the Southwestern US? (2) How do climate variables explain seedling presence across the ecosystem gradient and what other factors influence regeneration patterns? And (3) which regions are climatically suitable for seedlings where natural regeneration is not occurring, indicating an opportunity for management to facilitate forest and woodland transitions?

Methods

Site Selection

We examined 24 fires in southern and western Colorado and northern New Mexico (*Figure 1*). Site elevation ranges from 1724m to 2661m. Fires were selected using environmental site potential (ESP) raster data from LANDFIRE (landfire.gov last accessed May 2024), which included all expected primary vegetation within the study area. We obtained fire boundary polygons and fire severity raster data from Monitoring Trends in Burn Severity (MTBS; mtbs.gov last accessed May 2024) of fires that occurred between 17-36 years prior to observation and included only boundaries containing both PJ woodland and ponderosa pine forest vegetation types. The climate for these fires was largely semi-arid with the dominance of PJ woodlands and ponderosa pine forests.

To determine sites suitable for data collection we created a buffer region that included the following parameters: within moderate and high severity pixels from MTBS to only account for regions that experienced total mortality; within 250m of touching PJ woodland and ponderosa pine forest ESP pixels to capture the region focused around the ecotone; within 150m of an unburned pixel or the fire perimeter given negative relationships between long seed source distances and seedling regeneration; and beyond 50m from the nearest road to mitigate unintended impacts from high-travel areas. Using the spatially generated site suitability as a guide, we prioritized field-based assessments in establishing sites that burned at high-severity with no living mature trees, were within visibility of living mature piñon pine, juniper, or ponderosa pine trees, were at least 50m from vehicle accessible roads and established trails, and were greater than 100m from other sites.

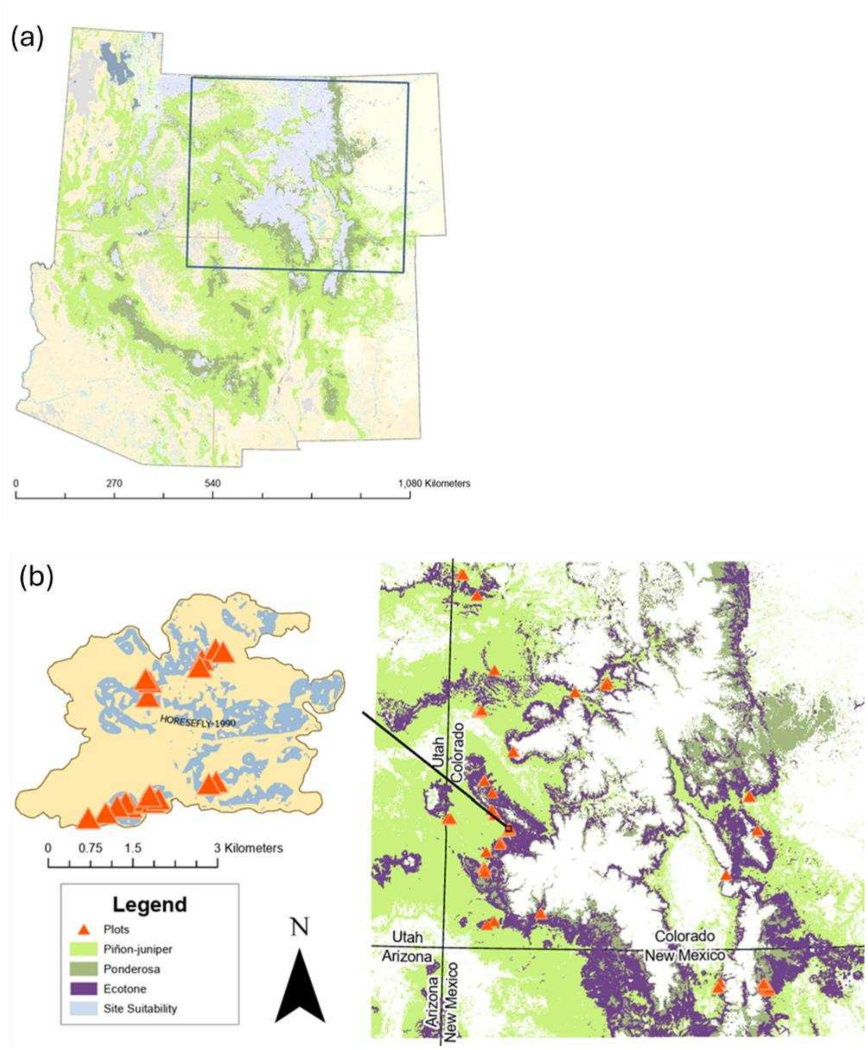
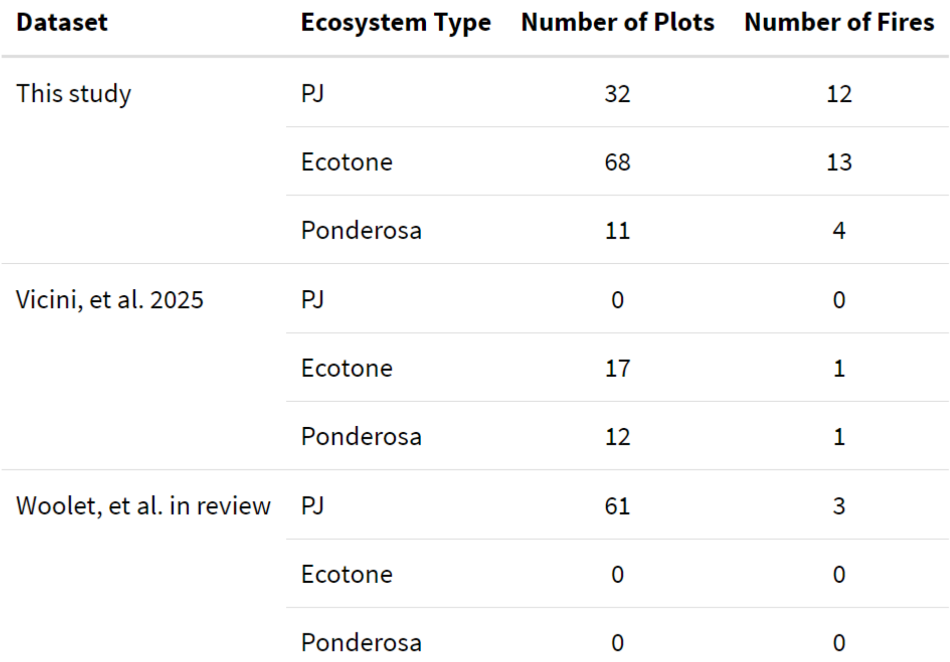


Figure 1. (a) Piñon-juniper woodland and ponderosa pine forest cover, which occupy over 25% land area the southwestern states of Colorado, New Mexico, Utah, and Arizona. Our study region is outlined by the blue square. (b) Site distribution across our study area including expected vegetation. The inset map highlights the boundary for the Horsefly Fire (1990), including suitability for research sites (light blue) based on fire severity, proximity to PJ woodland and ponderosa pine forest, proximity to unburned regions, and proximity to road access.

Sites were added to this dataset from two previous studies: Vicini et al. (2025) and Woolet et al. (in review). Site selection and field methods were largely similar with the exception that Vicini et al. (2025) selected for ponderosa pine forest dominated sites and Woolet et al. (*in review*) selected for PJ woodland dominated sites (*Table 1*). Both studies measured low, moderate, and high-severity fires, however, we only included data from sites that were categorized as high-severity (N=90).

Table 1. Breakdown of datasets used for analysis, including the number of sites collected in each ecosystem and the number of fires in which we collected data per ecosystem type. Some fires, such as the Horsefly Fire (1990) contain multiple, or all, ecosystem types within the scope of the study and are represented in each ecosystem type category. We collected data from 111 sites for this study mostly in the ecotone, utilized and additional 29 sites from Vicini et al. (2025) which occurred in ponderosa pine forests and upper elevation ecotone, and utilized an additional 61 sites from Woolet, et al. (in review) which all occurred in PJ woodlands.



Dataset	Ecosystem Type	Number of Plots	Number of Fires
This study	PJ	32	12
	Ecotone	68	13
	Ponderosa	11	4
Vicini, et al. 2025	PJ	0	0
	Ecotone	17	1
	Ponderosa	12	1
Woolet, et al. in review	PJ	61	3
	Ecotone	0	0
	Ponderosa	0	0

Field Methods

In our study, we utilized data from a total of 201 sites (0.04ha sites), including 90 leveraged from Vicini et al. (2025) and Woolet et al. (in review). All data was collected between 2023-2025 during the growing season. We collected geographic characteristics such as coordinates (latitude/longitude), elevation (m), slope (%), aspect (degrees), and distance (m) to the 5 nearest seed-producing living trees of each species from site center. We identified the species of every standing dead tree within the site and measured mortality level (level of canopy consumption including fully consumed, partially consumed, no consumption, and missing top), diameter, and height. We also identified and tallied stumps present within the site, which, in combination with standing dead tree tallies, provided an estimate of pre-fire mature tree density.

We tallied regeneration by species within the entire site and measured seedling height, diameter (if over 1.4m tall; measured at breast height for ponderosa pine; measured at root collar for piñon pine and juniper), and the presence/aspect of a nurse object, such as a rock, shrub, downed log, etc. that can alter microsite conditions and assist with the germination and growth of seedlings. We classified a seedling as nursed if it were directly beneath an object, or if it were within a horizontal distance equal to the height of an object up to 1m. We utilized a line-point intercept method (LPI) every 1m along a 25m north-south and east-west transect (n=48; no LPI taken at 0m and 25m) to estimate grass, forb, shrub, and tree presence at each site. We also estimated the 3 most abundant vegetation functional groups (of a possible 4: grass, shrub, forb, or tree) by percent within the site.

Climate Data

We obtained climate data at 4km resolution from TerraClimate (Abatzoglou et al., 2018; http://www.climatologylab.org/terraclimate.html last accessed August 2025). The data we used included monthly means of climate variables including VPD, CWD, precipitation, and max temperature (Tmax) from 1954 to 2024, each of which are commonly used as measures of aridity in regeneration studies (Rodman et al. 2019; Hankin et al. 2019; Mueller et al. 2020; Petrie et al. 2023, Davis et al. 2023). We established 30-year climate normals, which is a mean monthly climate over a 30-year interval, for the 30-year-mean preceding the fire ignition and the 30-year-mean following fire ignition for each measured burn scar. In addition, we established 30-year-mean seasonal normals pre-fire and post-fire for the winter (November-April) and summer (May-October). For fires that occurred within 30 years of data collection, we included as many years as available for post-fire normals (date collected – fire ignition date). In ArcGIS Pro (Esri, 2025; version 3.5), we overlayed sites on our climate pixels and extracted climate normal means per site for easier analysis.

Analysis

All analysis was conducted using R (R Core Team 2021) and ArcGIS Pro. To answer our first question about general recovery trends, we made comparisons of seedling densities pre-fire to post-fire and tested for relationships between seedling density and other variables. We first compared pre-fire stand density to post-fire seedling density and used linear mixed effects models to determine significant differences between each species density pre-fire and post-fire. We included the fire name as a random effect given the possibility that seedling densities from different plots within the same fire are not independent of one another. We created a proportion plot to visualize the proportion in which sites that contained a species pre-fire exhibited regeneration of the same species post-fire. We used a chi-square test to examine if proportions of sites with and without regeneration varied by species, which is used to compare categorical independent observations. We then fit generalized linear models (GLM) to test for relationships between seedling regeneration and other variables including: distance to seed source, time-since-fire (TSF), vegetation cover (grass, shrub, forb), fuel load (1hr, 10hr, 100hr, and 1000hr volume), substrate cover (bare ground, litter, woody debris, and rock), geographic variables (slope, aspect, elevation, and latitude), and canopy cover. We also fit a GLM to test for relationships between seedling regeneration and heat load index, which is a factor of slope, aspect, and latitude (McCune and Keon 2002). GLM's were appropriate as potential relationships between these variables and seedling response are assumed to be linear and used a quasi-Poisson family to help account for overdispersion and zero-inflated data, which is expected when analyzing seedling counts. We used an ANOVA to test for significant differences in mean seedling density per site between seedlings that did or did not have nurse objects. We used chi-square tests to examine differences in the proportion of seedlings that did or did not have a nurse object for each species. We used pairwise chi-square tests (Bonferroni method) to determine differences in the proportion of nurse object types (rock, log, shrub, live tree, or dead tree) utilized by each species. Chi-square tests are appropriate when comparing non-continuous categorical variables and pairwise chi-square tests allow for individual comparisons of each category to isolate nurse object types that were most used.

To answer our second question about the influence of climate change on regeneration patterns, we examined pre-fire and post-fire 30-year means of annual and seasonal VPD, CWD, precipitation, and Tmax. For each plot, we quantified climate change as the difference between post-fire and pre-fire 30-year means (post-fire – pre-fire). We then created scatterplots to visualize relationships between seedling density per plot and changes in climate variables and fit GLM's to test for significant relationships. Additionally, we created histograms to visualize the distribution of mean

VPD, CWD, precipitation, and Tmax change across sites and calculated overall mean change across all sites.

To answer our third question about where regeneration is not occuring in climatically suitable regions, we first classified the pre-fire community of each of our sites as PJ woodland, ecotone, and ponderosa pine forest based on the distances to nearest seed sources. We considered viable seed sources based on proximity from site center to living mature trees. We prioritized classifying plots based on viable seed sources to account for sites where trees were fully consumed in fires or decayed in the years after the fire providing an imprecise measure of pre-fire presence. A site within range of viable seed sources suggests potential to contain these species in a pre-fire climate. If viable juniper and piñon seed sources were present with no viable ponderosa pine seed source present, we classified the site as PJ woodland. If viable seed sources were present for each species, we classified the site as ecotone. If viable ponderosa pine seed sources were present with no viable juniper or piñon seed sources present, we classified the site as ponderosa pine forest. Where seed sources were not present, we classified the site based on identified stumps and dead trees within the site. We classified the post-fire community of our sites based on the presence of piñon, juniper, and ponderosa pine seedlings: sites containing all three species were classified as ecotone; those containing piñon, juniper, or both as PJ woodland; and those containing only ponderosa pine were classified as ponderosa pine forest. Where we did not observe tree regeneration, we classified the site based on the dominant recovering vegetation: grass, forb, or shrub.

To better visualize forest and woodland transitions, we utilized a tool called Vegetation Futures (vegetationfutures.org; hereafter: VF), developed by Hoecker et al. (2026) which estimates primary vegetation potential in current and 2°C future (a potential scenario where the global mean temperature has increased by 2° Celsius above pre-industrial values) climate scenarios among other capabilities. The authors present vegetation suitability under different climate scenarios based on climate analog impact models (AIMs), which provides a valuable tool for aiding land management decisions in the face of increasing disturbance. The vegetation data used is based on LANDFIRE Biophysical Settings (BpS). Four climate variables are considered including annual actual evapotranspiration (AET), annual CWD, mean daily Tmax in July, and mean daily minimum temperature (Tmin) in January. VF estimates vegetation potential in a 2°C climate scenario based on climate conditions that represent current vegetation communities. Here, we use this tool to compare the potential vegetation under a 2°C climate future with our observations of natural recovery after high-severity fire within our study area.

First, we masked VF raster data to our fire boundaries. We created an alluvial diagram to show estimated current and 2°C future vegetation transitions from VF across all studied fires and created a boxplot to compare elevation change by community between climate scenarios. We used a two-way ANOVA to test significant differences in elevations from current to future climate, differences in elevations across vegetation types, and combined effects of climate period and vegetation type on elevation. We similarly created an alluvial diagram to show vegetation transitions of our sites pre-fire to post-fire along with a boxplot to compare elevation change by community pre-fire to post-fire. We ran a two-way ANOVA to test for significant differences in elevation across community type and pre-fire to post-fire period. We calculated the percentage of each vegetation transition pathway for both our sites and VF estimates. In this analysis, we equate our pre-fire vegetation to VF current climate vegetation estimates. We evaluate post-fire outcomes to determine whether severe fire in today's climate (~1.1°C above global pre-industrial values; IPCC, 2022) has a comparable or greater impact on vegetation recovery than a 2°C warming scenario that does not include severe fire.

Results

General Regeneration Trends

Across sites where juniper was present prior to the fire, the mean pre-fire mature tree stand density was 224 trees/ha and the mean post-fire density was 46 trees/ha. Across sites where piñon pine was present prior to the fire, the mean pre-fire stand density was 135 piñon trees/ha and the mean post-fire stand density was 41 piñon trees/ha. Across sites where ponderosa pine was present prior to the fire, the mean pre-fire stand density was 221 ponderosa pine trees/ha and the mean post-fire stand density was 102 ponderosa pine trees/ha. Based on results of a linear mixed effects model with fire name as a random effect to compare pre-fire mature tree density and post-fire seedling density, we found significantly less regeneration of juniper (P<0.001), piñon pine (P<0.001), and ponderosa pine (P=0.003; Figure 2a). Approximately half of all sites that contained a species pre-fire exhibited regeneration of the same species post-fire and a chi-square test indicated no significant difference in proportions across species (Figure 2b). Approximately 64% of sites contained seedlings of at least one conifer species post-fire.

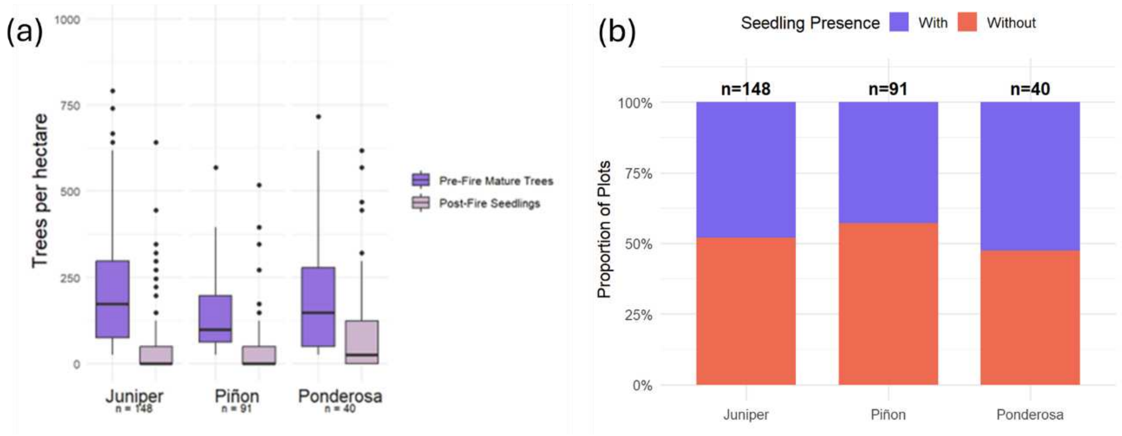


Figure 2. (a) Density of pre-fire mature trees compared to post-fire seedlings per hectare. Sites were measured 17-36 years post-fire (mean=25.9 years). Each species exhibited significantly less regeneration after severe fires than the presence of mature trees before fires. All sites were included where at least one mature tree was measured for a given species and excludes sites where a seed source was not visible for a given species. (b) Proportion of sites by species with and without seedling regeneration of the same species. Nearly half of sites with trees present pre-fire did not have seedling regeneration of the same species.

Where seedlings were present, a GLM revealed a significant relationship between greater distances to seed sources and decreased seedling abundance of piñon pine (P=0.015) and ponderosa pine (P=0.038). Juniper seedlings exhibited a similar trend; however, results of the GLM were not statistically significant (P=0.696). Given the decay function of regeneration at longer distances to living trees, we excluded sites from regeneration analysis where living mature piñon and ponderosa pine were greater than 152m from site center. These values were based on our findings of drastic drop-offs in seedling presence beyond these distances (*Figure 3*). The results of a GLM revealed longer TSF intervals also had a significant positive correlation with juniper

(P=0.013) and piñon pine (P<0.001) regeneration but did not have a relationship with ponderosa pine regeneration (P=0.544).

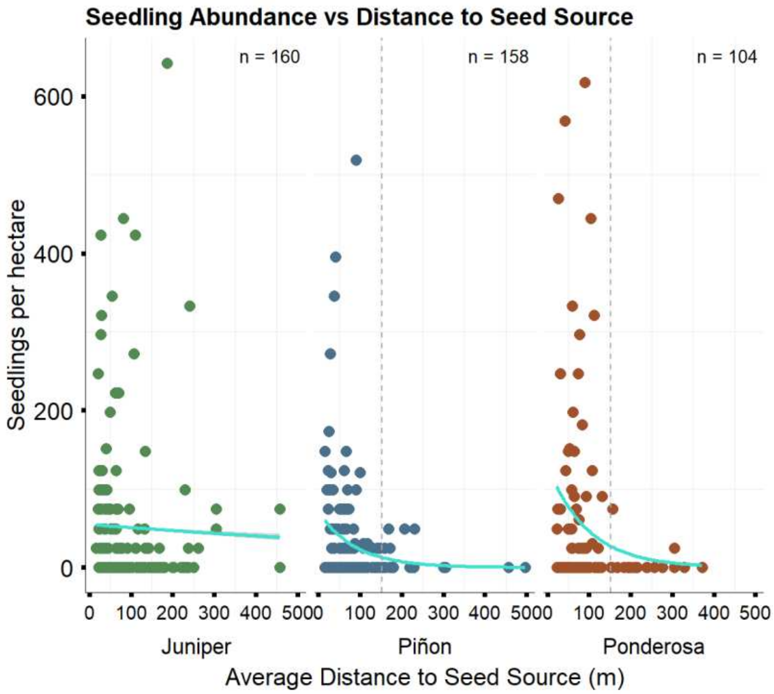


Figure 3. Shows relationship between distance to seed source and seedling densities of each species. Dashed gray lines indicate cutoffs where piñon and ponderosa seedling regeneration dropped off at 152m from living mature trees.

We did not observe a significant relationship between seedling density in any species and site vegetation cover (grass, shrub, or forb), fuel load (1hr, 10hr, 100hr, or 1000hr volume), substrate cover (bare ground, litter, woody debris, or rock), geographic variables (slope, aspect, latitude, or heat load index), or canopy cover. An ANOVA revealed that each species, when present, had a greater density of seedlings with a nurse object than without a nurse object per site (juniper: P=0.001; piñon pine: P<0.001; ponderosa pine: P=0.007; *Figure 4a*). A chi-square test determined that significantly more of each species of seedling had a nurse object (juniper=78%; piñon pine=89%;

ponderosa pine=74%) versus seedlings that did not have a nurse object (P<0.001 for all species). Shrubs were the most common nurse object types for each species, followed by logs (*Figure 4b*). A pairwise chi-square test (Bonferroni method) showed that piñon pine was associated with shrubs significantly more than any other nurse object type (P=0.018 when tested against logs; P<0.001 when tested against each other nurse type).

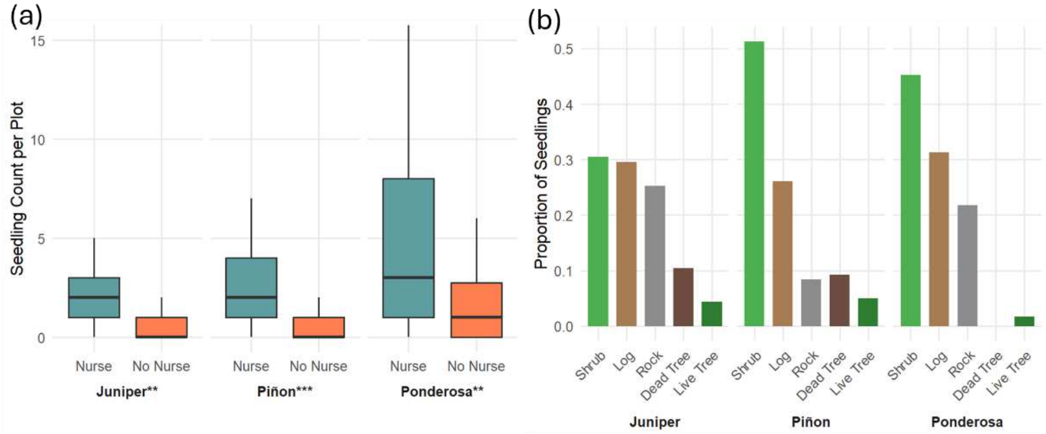


Figure 4. (a) Boxplot showing the mean number of seedlings per plot that had a nurse (blue) object and did not have a nurse object (orange), where seedlings were present. There were significantly more seedlings of each species that did have a nurse object versus species that did not have a nurse object, denoted by asterisks after species names. (b) Proportion plot showing the proportion of nurse object types associated with each species. Shrubs were the most common nurse object for each species and piñon pine significantly favored shrubs over each nurse object type.

Climate Impacts on Regeneration

Post-fire CWD and VPD means both increased from 30-year pre-fire means within almost all sites (*Figure 5*). The mean CWD change was 4.88mm from pre-fire to post-fire (~9% increase) and the mean VPD change was 0.033kPa (~4% increase). Per the results of a GLM, piñon seedling density significantly decreased with increasing CWD (P=0.007), while both juniper (P=0.001) and piñon (P<0.001) density significantly decreased with increasing VPD (Figure 6). There was no significant relationship with ponderosa pine density and both CWD (P=0.186) and VPD (P=0.758), however winter precipitation, which typically falls as snow in ponderosa pine forests in this region, was positively correlated with ponderosa pine density (P=0.004; *Figure 6c*). Juniper and piñon pine density were not significantly correlated with winter precipitation (juniper: P= 0.862; piñon pine: P= 0.159). Juniper seedling density significantly decreased with increasing Tmax (P=0.036), but piñon pine (P=0.252) and ponderosa pine (P=0.543) densities did not exhibit a significant trend.

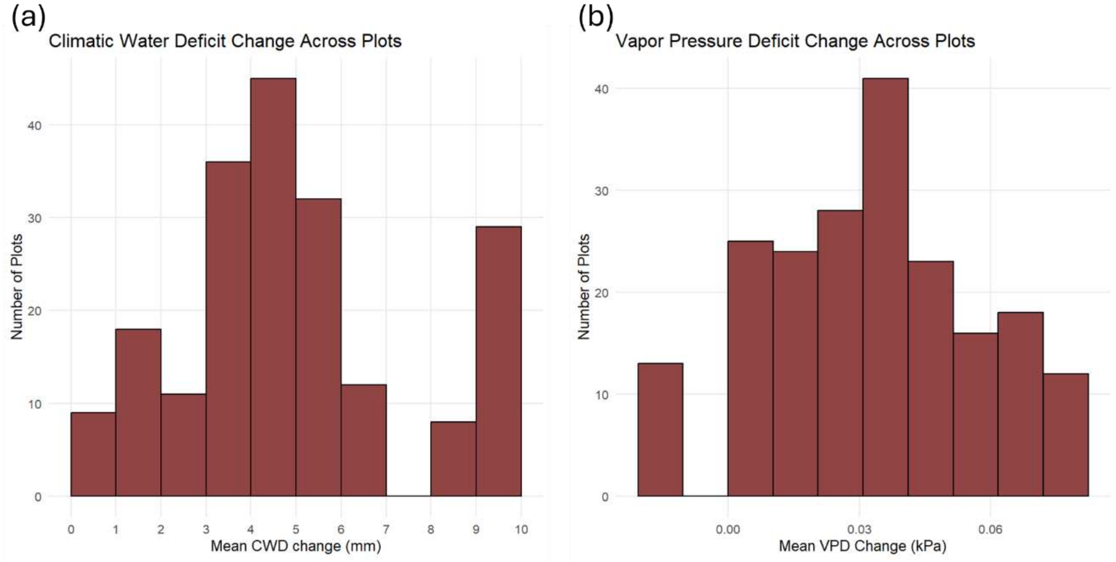


Figure 5. (a) Mean climatic water deficit change of 30-year mean pre-fire to approximately 30-year mean post-fire across sites. CWD increase was observed in all sites with a mean CWD change of 4.88mm. (b) Mean vapor pressure deficit change pre-fire to post-fire across sites. VPD increased across sites with a mean VPD change of 0.033kPa.

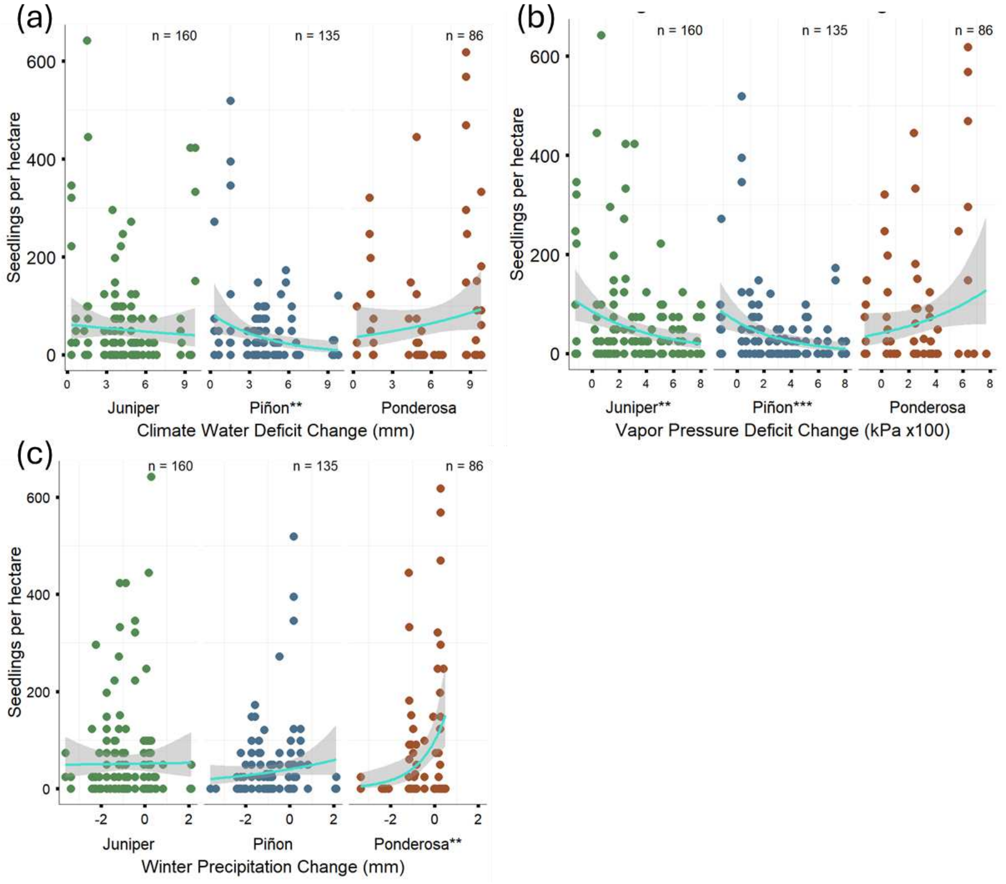
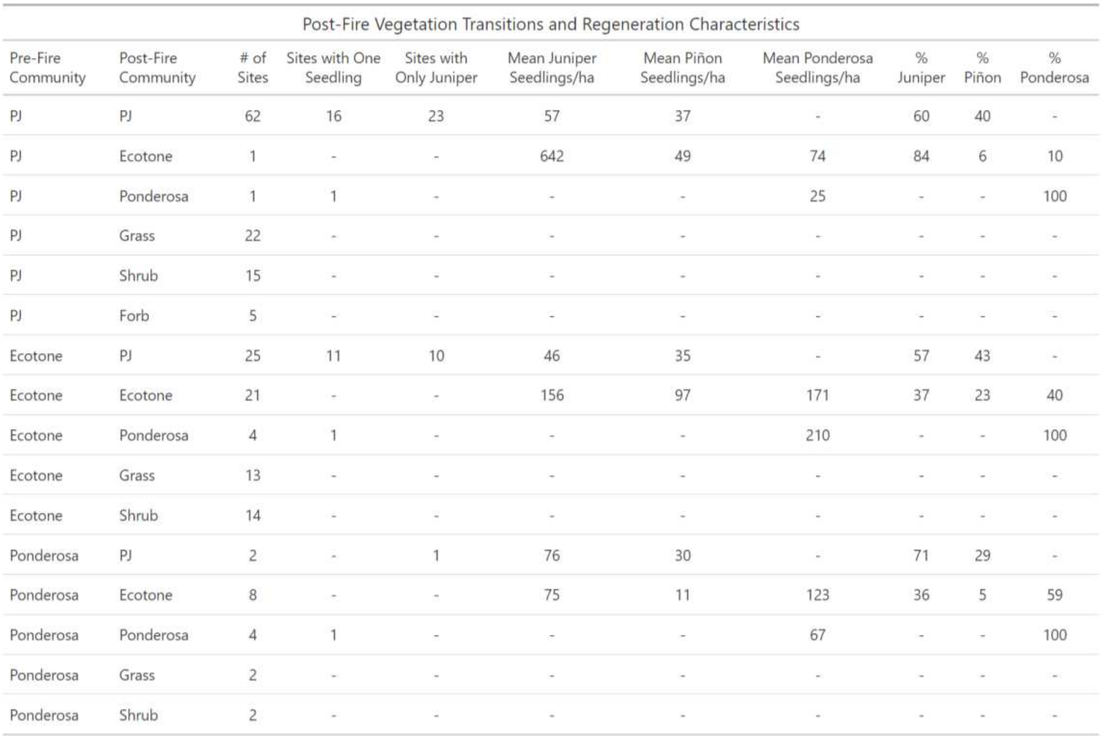


Figure 6. Seedling density response to change in different climate variables pre-fire to post-fire. Asterisks denote statistical significance. (a) Piñon pine exhibited significantly lower density with increasing CWD, but juniper and ponderosa pine regeneration was not significant with CWD. (b) Juniper and piñon pine exhibited significantly lower density with increasing VPD, but ponderosa pine density was not significant with VPD. (c) Ponderosa pine exhibited less density in sites with decreasing winter precipitation, but juniper and piñon pine density was not significant with winter precipitation. Sites beyond the previously defined distance to seed source limits are excluded.

Vegetation Trajectories and Transitions

Within our studied fires, PJ woodland sites regenerated as PJ woodland in 58% of sites and transitioned into grass dominant non-forested communities in 41% of sites (*Figure 7; Table* 2). Ecotone sites transitioned to PJ woodland in 32% of sites, while 34% of sites transitioned to non-forested communities, and 27% regenerated as ecotone, which was categorized by a combination of juniper or piñon pine seedlings and ponderosa pine seedlings. Ponderosa pine forest sites transitioned to ecotone in 44% of sites, transitioned to non-forested communities in 21% of sites, remained ponderosa pine forest in 21% of sites, and transitioned to PJ woodland in 11% of sites. The mean elevation (*Figure 8*) of PJ woodland shifted across sites from 2192m pre-fire to 2234m post-fire (+42m), of ecotone from 2294m-2271m (-23m), and of ponderosa pine forest from 2340m-2347m (+7m). An ANOVA for pre-fire to post-fire elevation by community type yielded insignificant results for PJ woodland (P=0.093), ecotone (P=0.517), and ponderosa pine forest (P=0.917).

Table 2. Shows how pre-fire communities (PJ woodland, ecotone, and ponderosa pine forest) transitioned into post-fire communities and mean seedling distributions across post-fire sites. Percent juniper, piñon pine, and ponderosa pine represent individual species seedlings per total seedlings in the plot.



Post-Fire Vegetation Transitions and Regeneration Characteristics

Pre-Fire Community	Post-Fire Community	# of Sites	Sites with One Seedling	Sites with Only Juniper	Mean Juniper Seedlings/ha	Mean Piñon Seedlings/ha	Mean Ponderosa Seedlings/ha	% Juniper	% Piñon	% Ponderosa
PJ	PJ	62	16	23	57	37	-	60	40	-
PJ	Ecotone	1	-	-	642	49	74	84	6	10
PJ	Ponderosa	1	1	-	-	-	25	-	-	100
PJ	Grass	22	-	-	-	-	-	-	-	-
PJ	Shrub	15	-	-	-	-	-	-	-	-
PJ	Forb	5	-	-	-	-	-	-	-	-
Ecotone	PJ	25	11	10	46	35	-	57	43	-
Ecotone	Ecotone	21	-	-	156	97	171	37	23	40
Ecotone	Ponderosa	4	1	-	-	-	210	-	-	100
Ecotone	Grass	13	-	-	-	-	-	-	-	-
Ecotone	Shrub	14	-	-	-	-	-	-	-	-
Ponderosa	PJ	2	-	1	76	30	-	71	29	-
Ponderosa	Ecotone	8	-	-	75	11	123	36	5	59
Ponderosa	Ponderosa	4	1	-	-	-	67	-	-	100
Ponderosa	Grass	2	-	-	-	-	-	-	-	-
Ponderosa	Shrub	2	-	-	-	-	-	-	-	-

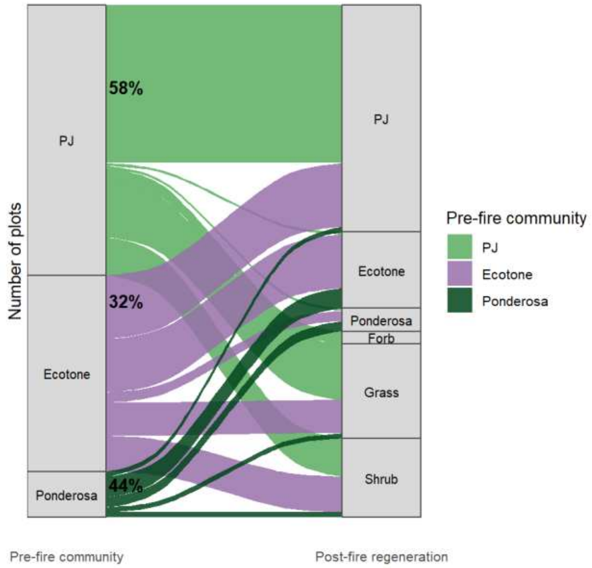


Figure 7. Alluvial plot showing our site vegetation transitions pre-fire to post-fire. Amongst sites studied, PJ woodland sites most often remained PJ woodland, closely followed by non-forested communities (shrub and grass). Ecotone sites most often regenerated as PJ woodland, closely followed by non-forested communities. Ponderosa pine forest sites most often transitioned to ecotone, followed by non-forested communities and regeneration of ponderosa pine.

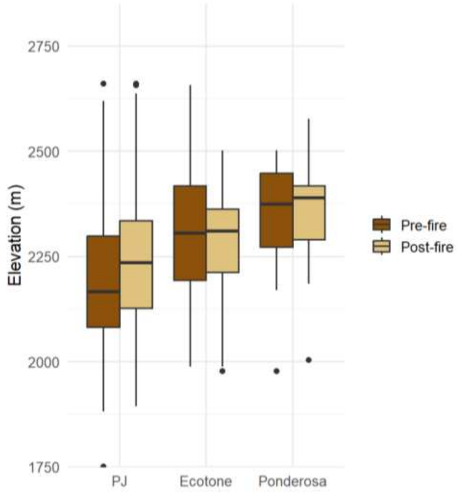


Figure 8. Boxplots showing the elevation of PJ woodland, ecotone, and ponderosa pine forest pre-fire (dark brown) to post-fire (light brown) within our study fires. Mean elevation of PJ woodland and ponderosa pine forest slightly increased across sites pre-fire to post-fire. The mean elevation of the ecotone decreased slightly pre-fire to post-fire. The results of ANOVA's comparing the difference in means of each species elevation pre-fire to post-fire were not significant.

Using the Vegetation Futures model, a large majority of PJ woodland within our studied fire boundaries were expected to transition to non-forested ecosystems, split approximately equally between grassland and shrubland, with 28% estimated to regenerate as PJ woodland (*Figure 7*). Over half of ecotone was estimated to transition to grassland dominated ecosystems, with less than half estimated to transition to PJ woodland. More than half of ponderosa pine forest was estimated to transition to ecotone and PJ woodland, 22% of our sites were predicted to transition to shrubland dominated, and 22% were predicted to remain as ponderosa pine forest. The mean elevation of each community within our fire boundaries was estimated to increase between the current climate and the 2°C future (*Figure 10*): PJ woodland increased from a mean of approximately 2158m-2333m (+175m); ecotone from 2280m-2487m (+207m); and ponderosa pine forest from 2457m-2552m (+95m). The results of a two-way ANOVA were significant between community type and elevation ($P<0.001$) as well as climate period and elevation ($P<0.001$)

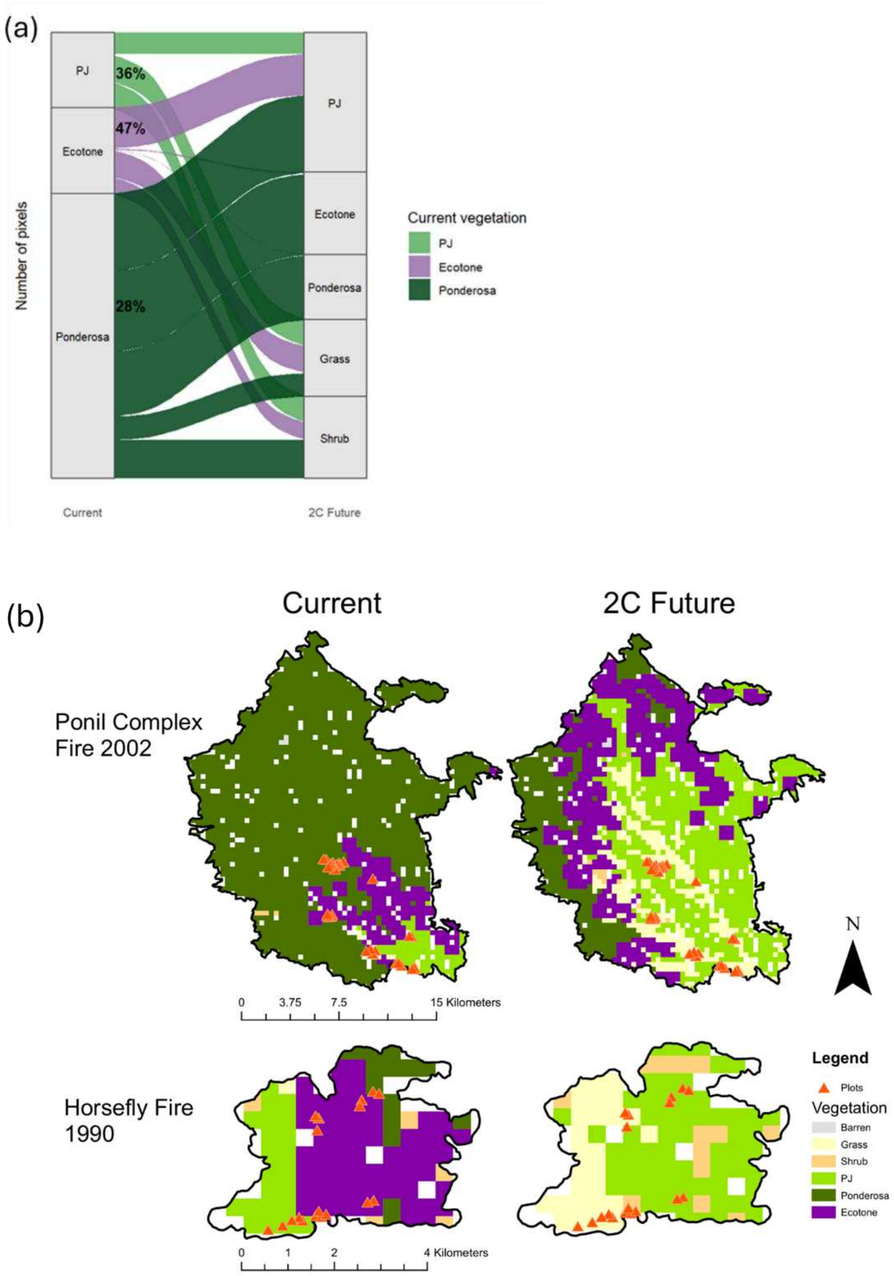


Figure 9. (a) Alluvial plot showing transitions from Vegetation Futures current vegetation to vegetation in a 2°C future within all 24 fire boundaries studied. Current vegetation represents potential vegetation in a current climate, and do not represent vegetation after the high-severity fires that have already occurred. (b) Expected vegetation transition within two fire boundaries studied. The Ponil Complex Fire (2002) in northern New Mexico transitioned from ponderosa pine forest dominated in the current climate to PJ woodland and ecotone dominated in a 2°C future. The Horsefly Fire (1990) in southwestern Colorado transitioned from ecotone dominated in the current climate to PJ woodland and shrub/grass dominated in a 2°C future.

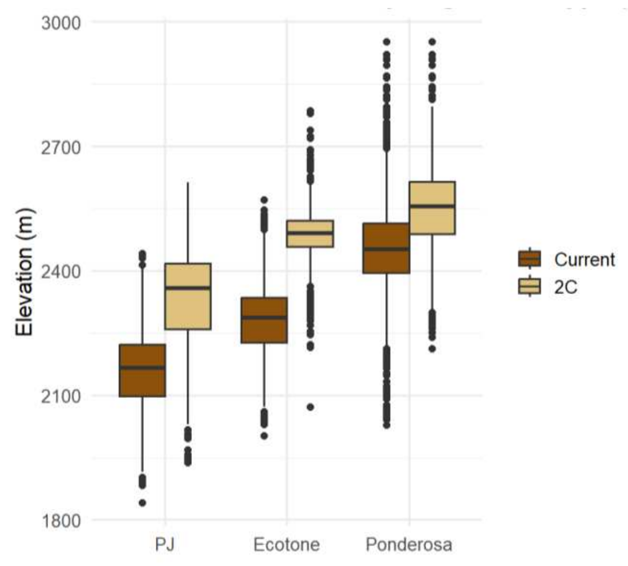


Figure 10. Boxplots showing the elevation of PJ woodland, ecotone, and ponderosa pine forests in a current (dark brown) to 2°C future (light brown) based on Vegetation Futures cover within the boundaries of our study fires. Mean elevation of PJ woodland, ecotone, and ponderosa pine forest increased under the VF model from the current climate to the 2°C future.

Discussion

Increasing large, severe wildfires are limiting tree regeneration in the southwestern US. Piñon pine and ponderosa pine, especially, are seeing very little regeneration farther from living mature trees, which will likely be exacerbated by larger and more frequent severe fires. Even within a suitable distance to seed sources, increasing water stress is further limiting seedling regeneration in all species within our study area. CWD and VPD increased in almost all sites from 30-year pre-fire means to 30-year post-fire means and juniper and piñon pine regeneration was significantly lower at sites with greater increases in VPD, while we observed fewer ponderosa pine seedlings with decreasing winter precipitation. We found that portions of PJ woodland and ponderosa pine forest are not recovering post-fire and are instead converting to non-forested communities, such as grasslands and shrublands. However, nearly two-thirds of sites did have at least one conifer seedling present. While these sites were often at very low densities and largely consisted of drought-tolerant juniper, which could indicate systems that will not recover to maturity with increasing aridity, they may also support woodland and forest regeneration with longer TSF. It is likely that suitability for both ecosystems will shift to higher elevations, especially under climate warming scenarios. However, it is unlikely that range shifts representing pre-fire densities will occur naturally given the rate of climate change and the associated increase in severe disturbances.

General Regeneration Trends

Our data shows that juniper, piñon pine, and ponderosa pine regeneration densities are much lower than pre-fire densities (*Figure 2*). While we did find at least one conifer seedling in almost two thirds of sites, many only contained one seedling or only contained drought-tolerant junipers. Although, piñon pine regeneration was scarce, it is possible that as juniper trees continue to mature, they may facilitate regeneration of piñon pine as nurse objects (Redmond and Barger 2013). Additionally, decreasing densities of PJ woodlands may be partially explained by historically long regeneration times, often requiring decades to centuries to return to a dominant woodland (Floyd, et al. 2004). Our study sites represented a mean TSF of 25.9 years and both juniper and piñon pine seedling abundance exhibited a significant positive relationship with greater TSF. With favorable future climate our sites may eventually see tree establishment that represents the structure of pre-fire woodlands, but as the climate continues to rapidly change, future tree establishment windows continue to narrow (Davis et al. 2023, Noel et al. 2024). We did not observe a relationship between ponderosa pine and TSF, perhaps due to episodic seedling establishment, which is associated with above average growing season water availability (Rother and Veblen 2017; Rodman et al. 2020).

We also found that seedling recruitment significantly declined farther from living mature trees, as documented in previous tree regeneration studies of ponderosa pine forests (Chambers et al. 2016; Haffey et al. 2018). PJ woodlands are highly dependent upon mammals and birds as dispersal agents (Chambers et al. 1999), thus a decline in seed dispersing birds or a lack of use of these landscapes by these species, such as the obligate Pinyon Jay (Boone et al. 2018; Woolet et al. 2023), may partially explain the lack of seedling recruitment in piñon pine at farther distances from living trees. Though other bird usage of post-fire landscapes may explain the non-significant relationship between juniper regeneration and distance to seed source (Woolet et al. 2023).

Although our study did not observe a significant relationship between densities of juniper, piñon pine, or ponderosa pine and the percent cover of non-forested vegetation, we did observe positive relationships between regeneration of all species and the presence of nurse objects (*Figure 3*). Even in otherwise dry climates, shrubs, which were the most common nurse object for each tree species, can alter microsite conditions to be more suitable for juniper and piñon pine regeneration (Floyd et al. 2015; Redmond et al. 2018) as well as ponderosa pine regeneration (Crockett and Hurteau 2022; Marsh et al. 2023). While shrub presence post-fire can support regeneration, dense Gambel oak shrublands, which were often present in study sites, and grass dominance, especially cheatgrass, decades after fire may indicate systems that will not return to their pre-fire state by prohibiting recruitment of other vegetation, altering successional pathways, and increasing fire frequency (Abella and Fulé 2008; Balch et al. 2013; Fusco et al. 2019; Floyd et al. 2021; Phillips et al. 2024).

Climate Impacts on Regeneration

Increasing water stress is further limiting juniper, piñon pine, and ponderosa pine regeneration. Across our studied wildfires, we observed increases in CWD and VPD from pre-fire to post-fire means (*Figure 5*), similar to region wide trends of increasing CWD (Stevens-Rumann et al. 2018; Rodman et al. 2019) and VPD (Williams et al. 2014; Davis et al. 2018; Mueller et al. 2020) in recent decades. Seedling regeneration of both juniper and piñon pine was lower with increasing CWD and especially increasing VPD (*Figure 6*), consistent with other studies of PJ woodland recovery after severe drought (Redmond et al. 2018) and fire (Phillips et al. 2024). Ponderosa pine seedling regeneration did not have a significant relationship with CWD or VPD change, however, declines in water availability have been documented as a limiting factor to ponderosa pine regeneration (Haffey et al. 2018; Davis et al. 2020; Puhlick et al. 2021; Petrie et al. 2023). We found that ponderosa pine regeneration was lower at sites with significantly lower winter precipitation (*Figure 6c*), which is a dominant source of water use for ponderosa pine forests in this region (Kerhoulas et al. 2013). Our findings, however, included a small sample size of pre-fire ponderosa pine forests (n=19), which were measured in regions where winter precipitation often remained relatively unchanged and seedling regeneration was often abundant, such as the Mason Fire (2005) in southwest Colorado. Further research is warranted to fully understand the impacts of seasonal water availability on ponderosa pine regeneration, as it may provide insight into suitable regions for ponderosa pine forest recovery.

Vegetation Trajectories and Transitions

Our study suggests that severe fire may be a catalyst for transitions of PJ woodlands and ponderosa pine forests to grasslands and shrublands. PJ woodland most often remained PJ woodland, however, nearly half of sites converted to grass dominated non-forested communities (*Figure 7*). While we did not differentiate between native and invasive grass in our data collection, cheatgrass recruitment has been observed in response to fire in semi-arid forests and woodlands (Huffman et al. 2012; Fornwalt et al. 2010; Birch et al. 2026) and was present at many of our sites. In addition, 37% of PJ woodland sites that remained PJ woodland only had juniper regeneration, which is supported in previous studies that have observed greater juniper regeneration than piñon pine regeneration post-fire (Huffman et al. 2013). Approximately 26% of PJ woodland sites that remained PJ woodland only had one seedling (<25 trees per ha), our cutoff to classify the post-fire community as PJ woodland. Thus, there is potential concern that these post-fire communities will lack recruitment necessary to reestablish woodlands and ultimately convert to non-forested communities, or a very low-density woodland. Analysis using Vegetation Futures (VF) predicted similar trends for PJ woodlands, albeit with a much greater transition to non-forested communities in a 2°C climate future (*Figure 9*). Substantial conversion of PJ woodlands to non-forested ecosystems is especially likely given recent large-scale drought-induced mortality coupled with increasing fire activity in the region even in established PJ woodland communities (Floyd et al. 2009; Gaylord et al. 2013; Redmond and Barger 2013; Floyd et al. 2015; Shriver et al. 2022; Rodman et al. 2025).

The most common regeneration pathway in pre-fire ecotone sites was conversion to non-forested, followed by conversion to PJ woodland. Pre-fire ecotone sites transitioned into more shrub-dominant post-fire communities, suggesting a potential pathway for future PJ woodland recovery (*Figure 7*; *Table 2*). However, despite exhibiting substantial shrub presence, ecotone sites that converted to PJ woodland had lesser piñon pine recruitment and a greater proportion of single-seedling sites than pre-fire PJ woodlands that remained PJ woodland, again bringing into question the viability of these ecosystems long-term. Ecotone sites only remained ecotone in about one quarter of sites, suggesting that regeneration of ponderosa pine seedlings is not occurring regularly at the ecotone. Our VF estimates, again, follow a similar but more substantial trend, with over half of ecotone sites expected to transition to non-forests communities in a 2°C future as well as almost no ponderosa pine presence, and, therefore, almost no ecotone regenerating in its current range. As ponderosa pine trees at the ecotone are at the trailing edge of ponderosa pine forests, range contraction at these sites is likely already becoming more common (Parks et al. 2019; Nigro et al. 2025), especially in a 2°C future (Hoecker et al. 2023).

Ponderosa pine forests most often transitioned into ponderosa dominated ecotone sites post-fire, followed by regeneration as ponderosa sites, and further followed by conversion to non-forest. Our VF estimates were similar to these findings, but with a greater proportion of transitions from ponderosa pine forest to PJ woodland and a lesser proportion of transitions to ecotone. Ponderosa pine forest transitions to ecotone are likely due to greater site suitability for PJ woodlands at higher elevations, although piñon pine still only represented approximately 5% of seedlings (3 seedlings observed over 8 sites) compared to 36% juniper and 59% ponderosa pine. A study in Arizona and New Mexico suggested that regeneration of at least 125 seedlings per hectare would be required for ponderosa pine stands to resemble their historical range of variability (HRV) at maturity (Ouzts et al. 2015). Across our sites where ponderosa pine was present pre-fire only 22% of sites met the HRV threshold of 125 seedlings per ha, which is supported by studies that have observed range contractions in ponderosa pine forests in response to climate change (Parks et al. 2019; Minott and Kolb 2020; Davis et al. 2020). However, the mean seedling density of post-fire ponderosa pine forests was approximately 126 seedlings per hectare, and the mean density of ponderosa pine seedlings in post-fire ecotone sites was approximately 155 seedlings per hectare. Thus, in most study sites, ponderosa pine was either not present or present at low density post-fire. In remaining sites, ponderosa pine seedlings were found at high densities, which is not always desirable given positive relationships between fire severity and ponderosa pine densities (Petrie et al. 2025). These findings, in addition to positive relationships between ponderosa pine seedling densities and with winter water availability, provide insight into conditions and regions that harbor suitability for regeneration and optimism that some sites may recover naturally.

Additionally, within our study sites PJ woodlands and ponderosa pine forests exhibited slight upward elevation trends pre-fire to post-fire, reflecting nearby regeneration patterns, and suggesting shifts in suitability to higher elevations (Korb et al. 2019; Chambers et al. 2016; *Figure 8*). Our results were perhaps insignificant because elevation is not a perfect proxy for site conditions with aspect and topographic variability leading to lower elevation establishment in some areas (Kemp et al. 2016). Using the VF model, however, we estimated a significant shift in suitability to higher elevations in all communities between the current climate and a 2°C future (*Figure 10*).

Our analysis based on the VF model predicted more widespread transitions and greater increases in elevation of woodlands and forests in a 2°C future than our site observations after severe fire in our current climate, however we expect that the effects will compound, leading to large-scale transitions of forests and woodlands to non-forested communities. Despite their estimates of more widespread woodland and forest transitions, VF provides a potentially conservative estimate, as it is based on climate analog models and not compounding impacts of climate change such as increased wildfire frequency and severity.

Limitations

While our study contributes to growing knowledge in forest and woodland regeneration patterns in the face of wildfire and climate change, we acknowledge several limitations. First, there is a lack of detailed fire data prior to 1984, the earliest year of fire records provided by MTBS, limiting our ability to study longer TSF periods that could have provided information on long post-fire periods in PJ woodlands and ponderosa pine forests. Further research of PJ woodland regeneration trends long after fire will be critical to our understanding of climate impacts on regeneration given the multi-decadal length required for regeneration to mature woodland. However, the rate of climate change must be considered, as conditions for regeneration today will likely be different in the coming decades (Petrie et al. 2017; Davis et al. 2023). Second, we sampled a small number of ponderosa pine forest sites (N=19) compared to PJ woodland (N=105) and ecotone (N=71) sites leading to difficulties in interpreting some results for ponderosa pine forests. Despite small sample sizes, we did find statistically significant trends with ponderosa regeneration and winter water availability, thus providing an opportunity for further research into viable climates for ponderosa pine forest persistence under climate change. Third, we did not collect data on specific grass and shrub species, which may have limited observations of species-specific relationships between vegetation and tree seedlings. For example, we could not quantify if cheatgrass cover was associated with declines in tree regeneration, nor could we statistically highlight potential regional trends of cheatgrass recruitment as observed in nearby regions (Floyd et al. 2021). Fourth, the climate data acquired from TerraClimate was likely too coarse (4km) to capture potential site-specific climate conditions. Long-term studies that measure site-specific climatic conditions pre-fire and post-fire alongside regeneration patterns could yield more precise results.

Management Implications

Forest management in the face of changing fire regimes has often focused on treatments that attempt to maintain heterogeneous stand structure, reduce the risk of stand-replacing fire, and return forests to their historical fire regimes (Allen et al. 2002; Churchill et al. 2013; Davis et al. 2024). In ponderosa pine forests, fuel reduction treatments have been successful in mitigating stand replacing fire, often achieved via thinning (Waltz et al. 2014), and prescribed fire (Shive et al. 2013; Hettema et al. 2025; Huffman et al. 2026). Such treatments may be effective at reducing the size and severity of wildfire (Davis et al. 2024); however, they rarely address a lack of seedling regeneration even where stand-replacing disturbances have not occurred (Petrie et al. 2025). Perhaps due to the historic fire regime of severe fires in PJ woodlands, prescribed fires, thinning, and mastication in PJ woodlands do not reduce fire severity (Phillips et al. 2024) and often promote greater recruitment of cheatgrass, which can further limit tree and shrub recovery (Huffman et al. 2013; Havrilla et al. 2017; Urza et al. 2017, Coop et al. 2017, Bradley et al. 2018).

Replanting efforts may be necessary if persistence of these forest types is desired. In many cases where sites no longer have a suitable climate for tree regeneration, assisted migration provides a potential pathway for successful PJ woodland and ponderosa pine forest persistence (Bower et al. 2024). Sites with higher moisture availability should be prioritized, which may require shifts to higher elevations and latitudes than the pre-fire range (Stevens-Rumann and Morgan 2019; Marshall et al. 2023). Another consideration may be planting seedlings sourced from drought-adapted trees in more arid regions for both piñon pine (Gehring et al. 2017; Noel et al. 2025b) and ponderosa pine (Rehfeldt et al. 2014; Kolb et al. 2016). Planting under nurse shrubs will likely lead to greater recruitment success given their correlation with higher seedling recruitment (Urza et al. 2019; Redmond et al. 2023).

A framework such as RAD (resist-accept-direct) could be employed by managers to determine desired management outcomes and pathways to achieve those outcomes (Schuurman et al. 2020, 2022). In this framework, resisting includes preservation of existing woodlands and forests, accepting includes adaptation to increased fire behavior and potential woodland and forest contraction, and directing includes assisted regeneration of woodlands and forests in regions where the climate is suitable for future persistence of these communities (Noel et al. 2023).

Conclusions

It is increasingly evident that changing climate and fire regimes are leading to declines and shifts in suitability to upper elevations in PJ woodlands and ponderosa pine forests across the southwest. Trees are unable to disperse seeds across the large homogenous burn scars that are increasingly common in modern post-fire landscapes. Decreasing moisture availability reduces the likelihood of seedling establishment even where seeds are distributed. Transitions to persistent grassland and shrubland are common outcomes of large, severe fires with little to suggest that they will return to woodlands and forests, which will be exacerbated by a potential future global climate of 2°C warming. Management aimed at restoring woodlands and forests to their historical fire regimes or facilitating recovery and range shifts will likely be required to maintain the critical ecosystem services that these forest types provide. However, it is important to note that we did find natural regeneration of trees occurring in some regions and gained insights into the conditions that promoted this regeneration. We highlighted relationships between seedling recovery and greater water availability as well as presence of nurse objects. Considering these variables, in addition to other variables that may influence regeneration of PJ woodlands and ponderosa pine forests, a management directive that encourages adaptation and flexibility is necessary to mitigate the decline of these ecosystems in the face of climate change and increasing wildfire risk.

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