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ORIGINAL ARTICLE

Management and Natural Regeneration in Multiple Ponderosa Pine Forests of the Southwestern United States

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Abstract
Management treatments in ponderosa pine forests of the southwestern United States (SWUS) are largely done for wildfire mitigation and restoration to lower tree densities. However, lack of natural ponderosa pine regeneration in undisturbed forests (i.e., no occurrence of stand-replacing events) may require management treatments to promote regeneration. We conducted a field and modeling study in 77 ponderosa pine forests across 7 SWUS locations, with the goal of evaluating management impacts on recent natural regeneration (∼20 y). We categorized management into 3 broad categories: unmanaged, thinned from above and/or below (thinning), and thinned + understory burned (burning). Although climate suitability declined from 1981-2020, management treatments – especially burning – promoted natural regeneration. High density regeneration, an undesirable outcome, occurred in 21% of managed sites. In addition to effects on near-surface temperature and soil moisture, management conducive to natural regeneration was associated with the density of competing tree species, understory litter and debris cover, and adult tree cone production. Natural regeneration occurred ∼5-10 y following management, underscoring sustained effects of management treatments on tree reproduction success. Our results show that forest management treatments have the potential to promote natural ponderosa pine regeneration in the SWUS, sometimes at undesirable high densities.
Study Implications: Natural ponderosa pine regeneration is declining in forests of the southwestern United States (SWUS), and may increasingly be incorporated as a goal of forest management treatments. Across a diverse set of managed and unmanaged SWUS forest sites, we found that contemporary management treatments – especially thinning + prescribed understory burning – supported natural ponderosa pine regeneration over the past two decades, which were climatically unfavorable in much of the region. Our results show that existing forest management treatments have the potential to promote natural ponderosa pine regeneration in the SWUS, but will require assessment and modification through time to remain effective.

Keywords Thinning · Burning · Seedling · Conifer

Extended author information available on the last page of the article

Introduction

Forest management is tasked with promoting forest resilience in the face of multiple – often interactive – agents of forest decline (Trumbore et al. 2015). Recognizing that forest densification, compositional change, and fuel loading in the southwestern United States (SWUS) resulted from complex interactions between logging, livestock grazing, and fire suppression in the 19th and 20th centuries (Moore et al. 2004), forest managers have sought to restore historical forest stand structures and low-severity fire regimes (Stoddard et al. 2021; Sakulich et al. 2022). Simultaneously over the past two decades, episodic multiyear droughts and increasing temperatures in forests of the SWUS have prompted research seeking to link restoration of historical forest structures, compositions, and fire regimes to climate adaptation and forest resilience (Park Williams et al. 2010). Management treatments creating lower forest densities and/or uneven-aged stand structures in some cases have considerable benefits for adult tree growth and reproductive output, soil water availability, and resistance to drought and biotic stress agents (Flathers et al. 2016; Andrews et al. 2020; Bradford et al. 2022; McCauley et al. 2022). Prescribed understory burning has been found to maintain desirable forest stand densities, limit the incidence of destructive wildfire, improve soil nutrient availability, and promote natural tree regeneration (Thomas and Waring 2015; Stoddard et al. 2021; Wasserman et al. 2022). Yet, recent predictions suggest that the effectiveness of both thinning and burning treatments in maintaining forests may begin to decline in the late 21st century as a result of warming temperatures and more severe drought (Stoddard et al. 2021). It is not yet clear if historical forest stand characteristics targeted by contemporary forest management treatments will retain their ability to support forest resilience in a changing climate (Loehman et al. 2018).

Although it has been clear for some time that ponderosa pine forests often fail to regenerate naturally following large stand-replacing wildfires (Rother and Veblen 2016; Donovan et al. 2019; Korb et al. 2019; Chambers et al. 2022), the paucity of natural regeneration in less disturbed forests has only recently been identified and confirmed with observations (Petrie et al. 2017, 2023b). Petrie et al. (2023b) found that short-term natural regeneration failure over a recent two-decade period across the SWUS was primarily climate-driven, but that natural regeneration failure could potentially be mitigated by forest management treatments. Conversely, management treatments can also promote high density natural regeneration that exceeds desired stocking levels, and may require follow-up treatments to reduce tree densities and mitigate wildfire risk imparted by high understory fuels (Battaglia et al. 2009; Westlind and Kerns 2017; Wasserman et al. 2022). A small body of research has linked management treatments to different components of natural regeneration, including masting events, recruitment, and seedling survival (see Flathers et al. 2016; Francis et al. 2018, and Crockett and Hurteau 2022 for recent examples), although it is unclear to what degree location-specific regeneration research can be applied to a broader region. In a future where managers may be tasked with incorporating natural regeneration as a goal of their activities, it is useful to determine the impacts of management treatments such as stand thinning and prescribed understory burning on natural regeneration in ponderosa pine forests across multiple locations, and to develop insight on how these treatments may lead to both natural regeneration failure and high density regeneration.

Management treatments altering stand density and forest understory characteristics are often maintained over multiple decades, potentially resulting in sustained changes to the conditions influencing natural regeneration (Thomas and Waring 2015; Young et al. 2020). It is unclear, however, why management treatments have differing natural regeneration outcomes in some forests, and similar outcomes in others (Wolk and Rocca 2009; Puhlick et al. 2013; Stevens et al. 2014; Francis et al. 2018; Wasserman et al. 2022). In this study we used forest treatment information (year of treatment, treatment type), field observations, meteorological estimates, and water balance modeling to contrast the contributions of climate conditions versus management treatments in shaping natural regeneration over the past 20 years across 77 ponderosa pine forest sites in 7 locations of the SWUS. We focused on categories of natural regeneration density as the primary response variables in our study, developed using guidance from the USDA Forest Service (Forest Service), Southwestern Region: no regeneration/short-term regeneration failure [R0: 0 seedling trees per acre (TPA); 0.0 trees m^{-2}], low seedling densities [R75: $>$ 0 to 75 TPA; $>$ 0.0 to 0.019 m^{-2}], moderate to higher seedling densities [R300: $>$ 75 to 450 TPA; $>$ 0.019 to 0.111 m^{-2}], and high density regeneration [R450: $>$ 450 TPA; $>$ 0.111 m^{-2}]. Due to variation in management treatments conducted across the SWUS, we broadly defined sites as unmanaged over the past 40-50+ years (unmanaged), those experiencing thinning from above and/or thinning from below (thinning), and those experiencing any form of a prescribed or natural, low-severity understory burn (burning). Our specific goals were to: (1) Quantify the over- and understory characteristics of unmanaged, thinned, and burned forest sites; (2) Contrast regeneration densities in unmanaged, thinned, and burned forest sites, and relate estimated timescales of natural regeneration at thinned and burned forest sites to treatment year; (3) Determine if management treatments were associated with short-term natural regeneration failure (R0) and high density regeneration (R450); and (4) Explore to what degree short-term natural regeneration failure (R0) and high density regeneration (R450) could be attributed to meteorological and water balance explanatory variables between unmanaged and managed forest sites. Although our analyses were limited to the most recent 20 years of natural regeneration due to uncertainty in the age of juvenile conifers at larger sizes (see Pirtel et al. 2021), we sought to provide a broadly focused perspective on associations between natural ponderosa pine regeneration, forest environments, and forest management treatments across the SWUS.

Site description

Our research focused on ponderosa pine-dominated forests in 7 regional locations in the SWUS: northern Arizona (NAZ), central Arizona (CAZ), southern New Mexico (SNM), northern New Mexico (NNM), southern Colorado (SCO), Front Range Colorado (FCO), and southern Nevada (SNV; Fig. 1a, Table 1). At each location we communicated with local forest managers, and selected forest stands for sampling that: a) were majority ponderosa pine, located on shallow slopes ($< 10°$ when possible),

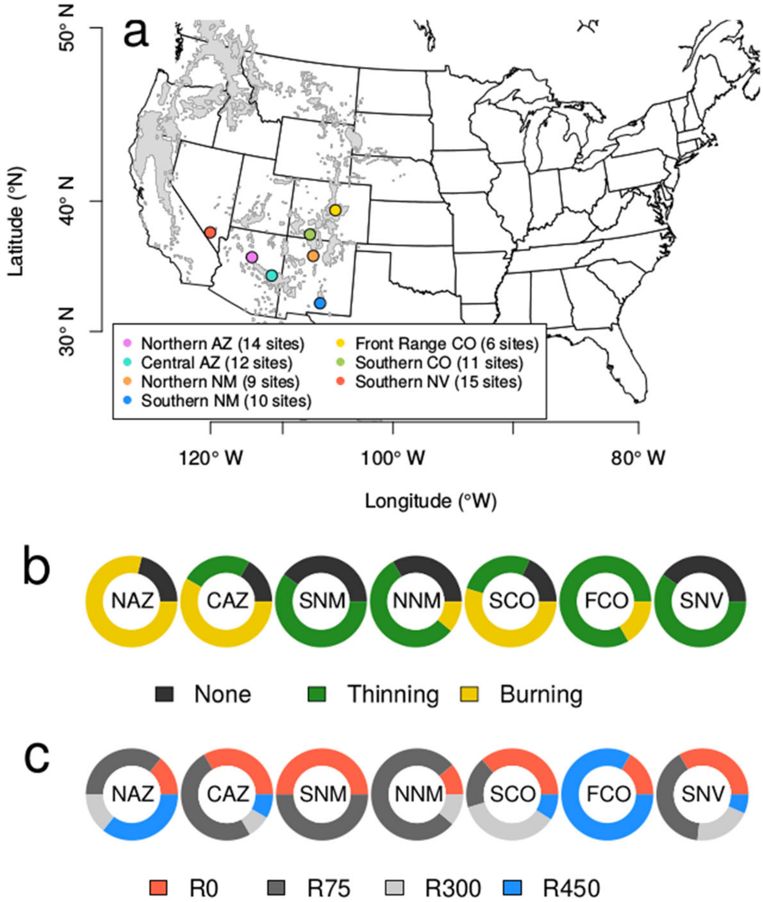

Fig. 1 Map of research locations and number of sites characterized at each location (Panel a), pie chart illustration of management treatments for sites at each location (Panel b), and pie chart illustration of ponderosa pine regeneration density for sites at each location (Panel c). In Panel b, management treatments include unmanaged sites (Unmanaged), overstory and/or understory thinning (Thinning), and any management including understory burning (Burning). In Panel c, regeneration densities include no regeneration/short-term regeneration failure [R0: 0 seedling trees per acre (TPA); 0.0 trees m^{-2}], low seedling densities [R75: $>$ 0 to 75 TPA; $>$ 0.0 to 0.019 m^{-2}], moderate to higher seedling densities [R300: $>$ 75 to 450 TPA; $>$ 0.019 to 0.111 m^{-2}], and high density regeneration [R450: $>$ 450 TPA; $>$ 0.111 m^{-2}]

and had sandy loam or loamy sand soils; b) that forest managers believed to represent the average condition of unmanaged, ponderosa pine-dominated forests (no disturbance or management treatment in the past 40-50+ years); c) that forest managers believed to represent the most common type or types of forest management treatments conducted at their location; and d) that forest managers believed to represent any unique treatments that they wished us to evaluate. Recognizing that we did not have the capacity to measure and resolve the influence of all variables and parameters influencing natural regeneration in managed and unmanaged forests of the SWUS, we sought to sample a narrower range of physiographic and edaphic conditions, and

Table 1 Study locations and management treatments

ID	Location	Average coordinates	Yr sampled	# sites	Management: # sites
Northern AZ	Coconino NF	35.271°N, 111.688°W	2021	3	B:3
	NAU Centennial Forest	35.170°N, 111.756°W	2019,2021	11	U:3,B:8
Central AZ	Apache-Sitgreaves NF	34.167°N, 109.869°W	2021	12	U:2,T:3,B:7
Southern NM	Lincoln NF	32.697°N, 105.616°W	2021	10	U:4,T:6
Northern NM	Santa Fe NF	35.848°N, 106.609°W	2021	7	U:2,T:5
	Valles Caldera NP	35.893°N, 106.606°W	2019	2	U:1,B:1
Southern CO	San Juan NF	37.285°N, 107.097°W	2021	11	U:2,T:3,B:6
Front Range CO	Manitou EF	39.111°N, 105.100°W	2019,2021	6	T:5,B:1
Southern NV	Humboldt-Toiyabe NF	36.327°N, 115.630°W	2019,2021	14	U:5,T:9
	Desert NWR	36.590°N, 115.214°W	2019	1	U:1
			total	77	U:20
					T:31
					B:26

The footnote defines detailed management treatments. In the analyses, management treatments were broadly categorized as Unmanaged (U), thinning from above and/or below thinning (T: Thinning), and any management including understory burning (B: Burning). 92% of sites categorized as Burning also experienced overstory thinning. Sampling locations included U.S. National Forests (NF), a National Preserve (NP), an Experimental Forest (EF), and a National Wildlife Refuge (NWR)

sample a broader range of forest stand conditions. As a result, our sampling and study results are best viewed as a broadly focused representation of natural regeneration in managed and unmanaged ponderosa pine forests across the SWUS.

We broadly categorized sites into 3 groups: those that were unmanaged or had no management for the past 40-50+ years (Unmanaged: 20 sites), those thinned from above and/or thinned from below (overstory reduction, and understory cutting/thinning with and without biomass removal; Thinning: 31 sites), and those with any management that included an understory burn (prescribed burn, broadcast burn, natural surface fire) that did not damage the forest overstory canopy (Burning: 26 sites; Fig. 1b; Table 1). The majority of burned sites (94%) were also thinned, so our burning category is better understood as thinned + burned. Differences between unmanaged forests and management treatments across the region (adult tree density reduction, understory treatment, time since treatment, etc.) resulted in wide variation in forest overstory and understory characteristics within each of these treatment categories (Supplementary material S1: Table S1). None of the forest sites had experienced a severe, stand replacing event in the past 60+ years.

The majority of sites that we sampled were managed (74%; Table 1), and of managed sites 44% were thinned, and 56% were burned. Thinning and burning were not evenly distributed among locations – management in southern New Mexico and southern Nevada only included thinning, thinning was the primary management in northern New Mexico and Front Range Colorado, and thinning + prescribed understory burning was the primary management in northern Arizona, central Arizona, and southern Colorado

(Fig. 1, Table 2). The proportion of managed sites was highest in northern Arizona, central Arizona, southern Colorado, and Front Range Colorado (> 78%), whereas the proportion of managed sites was lower in southern New Mexico, northern New Mexico, and southern Nevada (< 67%; Table 1). Front Range Colorado only included managed sites, but 3 of these sites had high stand densities that exceeded the average basal area and canopy cover of unmanaged sites in other SWUS locations. Managed sites in Front Range Colorado had basal areas ranging from 18–38 m^2 ha^{-1} (226–792 adult trees ha^{-1}), and canopy covers ranging from 54.1–82.1%, compared to an average basal area of 23.0 ± 8.3 m^2 ha^{-1} (366 ± 267 adult trees ha^{-1}), and an average canopy cover of 47.0 ± 14.4 % for all other managed sites.

Methods

Site selection and field sampling

In 2019 and 2021, we characterized overstory and understory forest stand characteristics, vegetation (herbaceous, shrub; adult and juvenile ponderosa pines (*Pinus ponderosa*), piñon pines (*Pinus edulis, Pinus monophylla*), junipers (*Juniperus monosperma, Juniperus osteosperma*), and higher elevation tree species (*Abies con-*

Table 2 Summary of management actions, estimated ponderosa pine regeneration year at managed sites, estimated or actual management year, and the difference in years between regeneration year and management year

Location, Category	Managed [%]	Thinning [%]	Burning [%]	Regeneration yr, managed sites	Management yr	Regeneration yr – management yr
Northern AZ	78.6	0.0	78.6	2015±4	2002±2	+12.1±5.2
Central AZ	83.3	25.0	58.3	2014±5	2011±6	+3.6±9.4
Southern NM	60.0	60.0	0.0	2005±1	2013±1	-8.5±0.7
Northern NM	66.7	55.6	11.1	2014±6	2012±6	+2.7±2.3
Southern CO	81.8	27.2	54.6	2014±4	2005±2	+8.7±5.1
Front Range CO	100.0	83.3	16.7	2014±5	2002±3	+11.0±2.1
Southern NV	60.0	60.0	0.0	2014±12	2007±8	+9.3±12.7
Unmanaged	-	-	-	-	-	-
Thinning	100.0	100.0	-	2013±7	2007±7	+4.8±8.8
Burning	100.0	-	100.0	2015±4	2005±4	+10.0±7.0
R0	63.6	40.9	22.7	-	2010±7	-
R75	64.5	38.7	25.8	2012±7	2009±7	+3.1±8.9
R300	90.9	36.3	54.6	2017±4	2004±3	+12.1±7.1
R450	92.3	46.2	46.2	2013±4	2004±3	+9.3±4.5

Values are presented for sampling locations, management treatments (Unmanaged, Thinning, Burning), and ponderosa pine regeneration density (R0, R75, R300, R450). Estimated ponderosa pine regeneration year and management year are the average ± 1 standard deviation *color, Pseudotsuga menziesii, and others*)), physiographic and edaphic properties, and natural ponderosa pine regeneration density of 77 ponderosa pine forest sites (Fig. 1, Table 1; Petrie et al. 2024). Recognizing the important influence of soil properties and soil parent material on natural regeneration (Puhlick et al. 2021), our 7 study locations had similar sandy loam and loamy sand soil texture to minimize edaphic influence (e.g., we avoided locations with widely differing soil parent materials; Supplementary material S1: Table S2). Thus, our results are constrained to these soil types, which are common in SWUS ponderosa pine forests but do not encompass the full range of soil types and parent materials where these forests are found in the SWUS. Some sites were located within the same forest management unit, but in areas with different tree stand densities and understory characteristics (i.e., management treatments were not evenly applied across the unit). Thus, we expect that pseudoreplication of forest stand attributes at the scale of our sampling ($\sim$0.1 ha^{-1}) in these units was minimal. In other instances, sites were located in nearby managed and unmanaged forest stands, such that meteorological estimates for these sites were identical.

Natural ponderosa pine regeneration has been documented as occurring with greater success in higher light, canopy interspaces (Bigelow et al. 2011; Puhlick et al. 2012), and also in lower light, under canopy environments (Gray et al. 2005; Keyes et al. 2007; Flathers et al. 2016; Kolb et al. 2020). It was therefore unclear which microsites would be more favorable for natural regeneration across multiple locations of the SWUS. Our sampling sought to capture more and less sheltered microsites in each forest site, recognizing that the characteristics of these microsites (canopy cover, understory biomass, etc.) would differ between sites and management treatments. We estimated that a large single plot was more likely to capture regeneration at low densities compared to a linear transect, and would not bias our sampling towards canopy interspaces in unevenly thinned forests with very low adult tree densities. Thus, our analyses explored how differences in sheltered and unsheltered microsites across managed and unmanaged forests were associated with natural ponderosa pine regeneration. This sampling is best viewed as a characterization of within-stand transitional areas that include sheltered and unsheltered microsites, and not as a contrast of management differences within thinning and burning categories.

We sampled each site using a circular plot with a maximum radius of 20.0 m, and reduced this radius to as low as 5.0 m in instances where: a) regeneration density was visually determined to be exceedingly high; or b) to exclude a topographic change in slope or a surface water flow path. As a result, the average plot area of sites with high regeneration densities (R450) was significantly smaller (220 m^2) than plots with R0, R75, and R300 regeneration densities ($\sim$700 m^2), but the average plot areas of sites with R0, R75, and R300 densities were not significantly different from each other (2-tailed t-tests with independent observations; $p < 0.05$). To include more and less sheltered forest microsites in each plot, we located the center of each plot at the boundary between a moderately sized forest canopy interspace and a higher canopy cover area, using a spherical densiometer to estimate this boundary for each site based on canopy cover. We did not pre-evaluate regeneration in the field prior to setting the center of each plot.

Site characterizations included landscape attributes, over- and understory forest conditions, vegetation cover, and soil properties (Supplementary material S1: Table

S3; Field data published at Petrie et al. 2024). Measurements across the entire circular plot (subdivided into 4 quadrants) included natural regeneration (number, height, and ground-level diameter of ponderosa pine and other species of seedlings, counted separately), adult tree number, adult tree diameter at breast height (cm), basal area of adult trees measured from plot center (m^2 ha^{-1}), canopy cover from 4 measurements in each plot quadrant (%), soil properties from 4 measurements in each plot quadrant (0-10 cm depth), slope (°), and aspect (°). Measurements in the 8 quadrats included litter attributes (cover (%), depth (mm), density (g cm^{-3} - determined in the lab from field samples)), coarse woody debris cover (%), ponderosa pine cone density (# m^{-2}), herbaceous vegetation cover (%), and woody vegetation cover (%; see Supplementary material S1: Fig. S1 for a diagram of the plot design). We note that our measurement of cone density (requiring a cone to be 50% intact to be counted) does not capture the timing of masting events, seed dispersal, or seed persistence, and provides only a summary estimate of historical cone production at each site. Seedlings were $<$ 500 mm in height, which for ponderosa pines corresponds to a tree $< \sim$20 years in age (post-2000 germination date; see Pirtel et al. 2021). Regeneration density was calculated from the number of ponderosa pine seedlings in each plot, and reported in m^2. We note that the exact date of regeneration can only roughly be estimated from seedling height measurements, and our estimates of the most common regeneration date at our study sites are therefore approximate.

Site categories

To ascertain different components of management and natural regeneration, we categorized sites in 3 different ways. First, we categorized sites by management (see Site Description). Second, we categorized sites by ponderosa pine seedling density, developed using guidance from the Forest Service, Southwestern Region. The Southwestern Region certifies for natural regeneration at 60 seedling trees per acre (TPA; i.e., certifies that a forest stand is regenerated), and the guideline for seedling planting densities in the region is 300 seedling TPA (Fuller, personal communication, 2024; Youtz, personal communication, 2024; Gonzalez, personal communication, 2024). Full stocking density is defined as 110-150 established trees of 10” diameter size class per acre (Fuller, personal communication, 2024). Thus, certified natural regeneration does not infer full stocking density, and seedling planting guidelines estimate reductions in TPA (Fuller, personal communication, 2024). Seedling density guidelines in the region are adjusted in some cases based on historical tree stand densities, fire suppression objectives, existing adult tree density, and management objectives (advance regeneration versus timber production, for example; Fuller, personal communication, 2024; Gonzalez, personal communication, 2024). The Southwestern Region expects that follow up treatments will be required to obtain desired stocking levels in all managed forests (Gonzalez, personal communication, 2024).

Our seedling density categories included no regeneration/short-term regeneration failure [R0: 0 seedling TPA; 0.0 trees m^{-2}], low seedling densities [R75: $>$ 0 to 75 TPA; $>$ 0.0 to 0.019 m^{-2}], moderate to higher seedling densities [R300: $>$ 75 to 450 TPA; $>$ 0.019 to 0.111 m^{-2}], and high density regeneration [R450: $>$ 450 TPA;

> 0.111 m^{-2}]. Our R0 category portends to regeneration densities more likely to require planting to meet full stocking density. Our R75 category portends to natural regeneration densities that are below or slightly above certification standards, and are associated with seedling densities that are less likely to meet full stocking density. Our R300 category is very broad, and includes lower seedling densities that may or may not require planting to meet full stocking density, densities meeting the 300 seedling TPA guideline, and higher seedling densities that may or may not require management intervention (such as a prescribed burn) to reduce seedling densities. Our R450 category portends to seedling densities more likely to require management intervention to reduce high seedling densities. Linking regeneration density categories to required management intervention is an approximation, and cannot account for variation in future regeneration or seedling mortality that may influence treatment needs. These management-focused regeneration density categories are similar in magnitude to those used in a previous evaluation of short-term natural regeneration failure at these same sites (Petrie et al. 2023b).

Finally, we categorized managed forest sites by their most recent treatment year. We obtained the exact treatment year from forest managers when available. When the treatment year was not available, we estimated it using historical imagery to visually assess when change to forest density occurred (Gorelick et al. 2017). We caution that this estimation is unlikely to capture the most recent treatment year for burned sites because the dates of thinning and burning treatments often differ. To reduce this uncertainty, we categorized forest sites into 5 groups: Unmanaged (20 total sites), management before the year 2000 (7), management from 2000–2008 (29), management from 2009–2016 (14), and management from 2017–2020 (7). We note that these categories have differing time intervals, and the number of sites within these intervals differs. However, they capture the 3 most common management periods that we determined: the early 2000s around 2003-2004, the mid-2000s around 2010-2014, and recent management from 2018–2020.

Analysis variables

Our analyses incorporated measurements of natural ponderosa pine regeneration density, measurements of site characteristics, measurements and estimates of soil properties (Chaney et al. 2019), meteorological estimates and anomalies (1980–2020 from Daymet at 1 km^2 resolution Thornton et al. 2022; 1915–2011 at 1/16° resolution from Livneh et al. 2013), and SOILWAT2 water balance modeling at the daily time step (hereafter referred to as water balance modeling and water balance variables; Schlaepfer and Andrews 2019; Schlaepfer and Murphy 2019). Regeneration density was the primary dependent variable in our study, and was evaluated across categorical explanatory variables (management treatments, management time periods), and separately across explanatory variables of site characteristics, meteorological estimates and meteorological anomalies, and water balance variables (see Supplementary material S1: Tables S3–S5 for lists of variables; model simulations described and published at Petrie et al. 2023a). We conducted all data manipulations, calculations, and statistical analyses using R-project statistical computing software (R Development Core Team 2023).

Analyses 1: variation in site characteristics, natural regeneration density, and meteorology

Our first set of analyses sought to characterize variation in site characteristics, natural regeneration, and meteorology across our sampling sites. We used ANOVA and Tukey's Honest Significant Differences to identify significant differences in explanatory site characteristics variables between categories of management treatments (unmanaged, thinning, burning), management time periods (before 2000, 2000-2008, 2009-2016, 2017-2020), and regeneration densities (R0, R75, R300, R450). We tested the distribution of each explanatory variable for homoscedasticity using residuals and standardized residuals. In the ANOVA analyses, we transformed variables with uneven variances using the natural log (to correct for high standardized residuals) or by squaring (to correct for low standardized residuals). We did not test for interactions between management treatments, management time periods, and regeneration densities in the ANOVA analyses. Although we focus on significant differences in site characteristics variables at $p < 0.05$, we also report differences at $p < 0.1$ as a reference for future studies.

To visualize regeneration density across locations, management treatments, and management time periods, we calculated the percentage of R0, R75, R300, and R450 sites within these categories. We used Gaussian generalized linear models (GLM) to evaluate significant differences in regeneration density (response variable) between management treatments and management time periods (categorical explanatory variables). Although the distribution of regeneration density data had a slight positive skew, we did not use a log link in our GLMs in order to preserve observations of no regeneration (zero values). We used likelihood ratio (LR) tests to evaluate GLMs against the null model, and evaluated coefficients of the main effect (ME) using the R *multcomp* package. We used the same GLM approach to evaluate differences in the density of other tree species between management treatment categories. We did not test interactions between categorical explanatory variables in our GLM analyses.

To visualize regional change to driving meteorological variables of warm-season and cool-season precipitation [PPT: mm] and growing degree days [GDD: °C] from 1980–2020, we calculated the anomaly of PPT and GDD (*anomaly = (observed - mean)/standard deviation*) in each site-year using Daymet values (observed; Thornton et al. 2022) compared to long-term (Livneh et al. 2013) estimates (mean, standard deviation).

Analyses 2: determination of explanatory variables for high density natural regeneration (R450) using random forest analysis

Our second set of analyses sought to determine the explanatory variables (site characteristics, meteorology, water balance) distinguishing sites with high density regeneration (R450). To do this, we used an analytical methodology developed by

Petrie et al. (2023b) (see Appendix A for a detailed description), which they applied to sites with short-term regeneration failure (R0). In short, we used ANOVAs to build sets of the most likely explanatory variables for sites with high density regeneration (R450), and implemented sets of non-correlated variables in separate random forest analyses seeking to identify R450 sites. We evaluated the performance of different sets of variables using the balanced model accuracy (BA; we also report model sensitivity and specificity) of the separate random forest analyses (R Development Core Team 2023; *randomForest* package; Liaw and Wiener 2002). We ranked variables in the top random forest model based on their Gini Importance (GI; Menze et al. 2009), and estimated the threshold value for each of these variables designating model determination of R450 sites and non-R450 sites using partial dependence plots (*rpart.plot* package; Milborrow 2022). We did not use categorical explanatory variables in the random forest analyses.

Analyses 3: scoring R0 and R450 regeneration potential

As a final set of analyses, we sought to develop a scoring method to evaluate the potential for a forest site to experience regeneration at R0 or R450 densities. One way to do this is – for each explanatory variable from the random forest analysis – to calculate the percentage of observations where the partial dependence threshold is exceeded. This analysis can provide an interpretable evaluation of the "promotion" and "inhibition" of R0 or R450 for a site over a relatively long time period (see Petrie et al. 2023b). Although visually intuitive, this exceedance-focused analysis requires complex interpretation across multiple measures informing R0 or R450, since explanatory variables are weighted differently (as GI) by the random forest model.

We designed a methodology to calculate a single R0 or R450 score using only the explanatory variables from the top random forest models. For each site in each water year from 1981–2020, we scored explanatory variables "promoting" R0 or R450 selection that exceeded the partial dependence threshold as +1, and scored explanatory variables "inhibiting" R0 or R450 selection that exceeded the partial dependence threshold as -1 (variables not exceeding the threshold were scored 0.0). We then proportionally weighted the score of each exceedance variable as its GI divided by the model's total GI (R0 GI total: 30.8; R450 GI total: 20.9). We then calculated a total score as the sum of all variables. Because GI varies across promotion and inhibition variables, the maximum score indicating greatest promotion of R0 or R450 was positive but not equal to 1.0, and the minimum score indicating greatest inhibition of R0 or R450 was negative but not equal to -1.0. To place R0 and R450 scores on a more intuitive -1.0 to +1.0 scale (indicating the highest possible inhibition and highest possible promotion, respectively), we scaled the total value for each site based on the highest (if the total was positive) or lowest (if the total was negative) observed score across all 77 sites (R0 min: -0.38; R0 max: 0.62; R450 min: -0.80; R450 max: 0.20).

This weighted scoring approach allowed us to evaluate scores for R0 and R450 at each site in each water year, and to explore the promotion and inhibition of R0 and R450 between locations and management treatments. To do this, we calculated change to R0 and R450 scores as a timeseries from 1981-2020, and compared R0 and R450 scores between unmanaged and managed sites in each location over 1981–2000 and 2001–2020 time periods using ANOVA and Tukey's Honest Significant Differences ($p < 0.05$). We note that these scores should be considered approximate due to uncertainty in meteorological estimates and water balance simulations, and due to change in forest stand characteristics over time. Site characteristics measured in 2019 and 2021 were applied to the entire timeseries, and our 40-year timeseries analysis should therefore be considered an approximation of the long-term pattern of R0 and R450 scores. We compared the density distributions of raw and scaled R0 and R450 scores across all 77 sites from 1981–2020, and assessed to what degree our scoring method captured a variety of support for and inhibition of R0 and R450 (indicated by a broader range of observed scores).

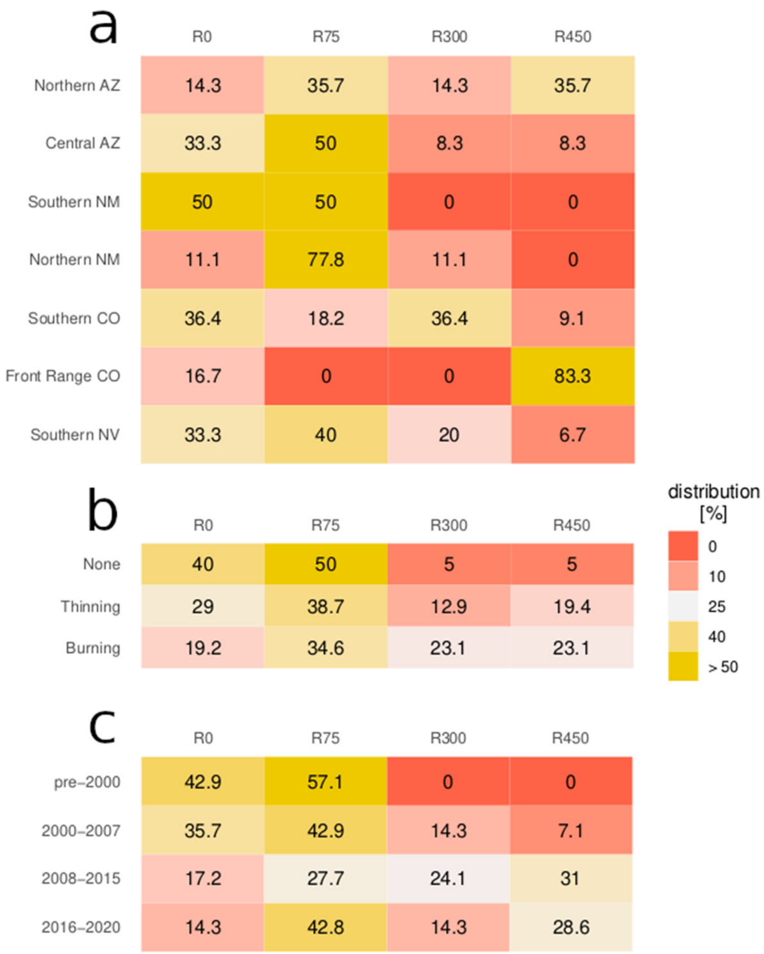

Fig. 2 Comparison of the observed distribution of sites as a percentage across ponderosa pine regeneration density (R0, R75, R300, R450) across locations (Panel a), management treatments (Unmanaged, Thinning, Burning; Panel b), and between management time periods (Unmanaged, before 2000, 2000-2008, 2009-2016, 2017-2020; Panel c)

Results

Management and natural regeneration

We did not find significant linear or nonlinear relationships between natural regeneration density and explanatory variables associated with site characteristics, meteorology, or water balance simulations across our 77 study sites. The majority of sites had natural regeneration at R0 (22 sites; 29% of all sites) or R75 levels (31; 40%), and fewer had regeneration at R300 (11; 14%) or R450 levels (13; 17%). The percentage of R0 sites was relatively higher in southern New Mexico (50% of sites), central Arizona (33%), southern Colorado (36%), and southern Nevada (33%; Figs. 1c and 2a), and the percentage of R450 sites was relatively higher in northern Arizona (35%) and Front Range Colorado (83%; Figs. 1c and 2a). Of the sites with natural regeneration, 78% were managed (43 sites), and of these 58% were burned (25 sites; Table 2). In contrast, ~64% of R0 sites were managed (14 sites), and of these ~36% were burned (5 sites; Table 2).

Our GLM for natural regeneration density (response variables) between management treatments (categorical explanatory variables) performed significantly better than the null model (LR: $p = 0.005$). Burning was the most significant predictor of regeneration density across our study sites (GLM: $p = 0.003$), and regeneration density was significantly different between burned sites and unmanaged sites (ME: $p = 0.047$), and between burned sites and thinned sites (ME: $p = 0.043$; Fig. 3a). Thinning was a weaker predictor of regeneration density (GLM: $p = 0.047$), and regeneration density was significantly different between thinned sites and unmanaged sites (Fig. 3a). Both burned and thinned sites had a lower percentage of R0 sites compared to unmanaged sites (Fig. 2b). We did not find significant differences in regeneration density that could be attributed to the time periods when management treatments were conducted (Fig. 3b), although sites that were more recently treated (2008-2015, 2016-2020) had

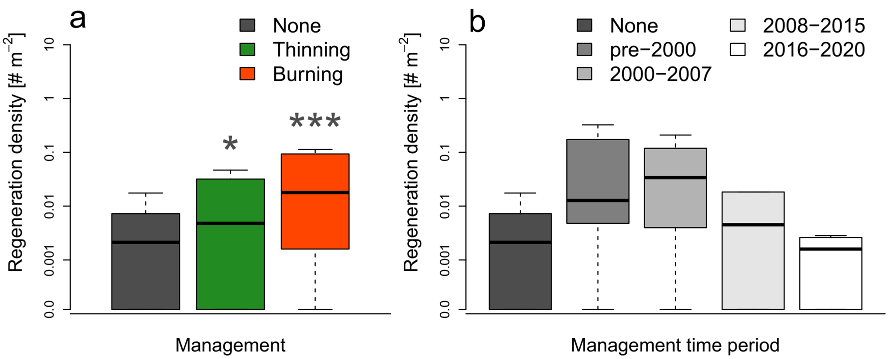

Fig. 3 Boxplots comparing ponderosa pine regeneration density between management treatments (Unmanaged, Thinning, Burning; Panel a), and between management time periods (Unmanaged, before 2000, 2000-2008, 2009-2016, 2017-2020; Panel b). Significant differences were determined using Gaussian generalized linear models (GLM; *: $p = 0.047$; ***: $p = 0.003$) and between main effect coefficients (ME; Burning–Unmanaged: $p = 0.048$; Burning–Thinning: $p = 0.043$; Thinning–Unmanaged: not significant

a higher percentage of R450 regeneration densities and a lower proportion of R0 densities (Fig. 2c). On average, the estimated regeneration year occurred ~5 years following the estimated treatment date at thinned sites, and ~10 years following the estimated treatment date at burned sites (Table 2).

Site characteristics

Management treatments were conducted differently across the SWUS, resulting in considerable variation in forest overstory and understory characteristics within unmanaged, thinned, and burned sites (Supplementary material S1: Table S1). Management treatments were therefore associated with only a small number of significant differences in site characteristics variables. Thinned and burned sites had significantly lower adult tree densities [# ha^{-1}], and adult trees with significantly larger average diameter at breast height [DBH: cm] than those at unmanaged sites ($p < 0.0001$; Table 3). Burned sites had significantly higher litter cover than thinned and unmanaged sites ($p < 0.04$), and burned sites had significantly lower litter density than thinned sites ($p < 0.02$; ANOVA with Tukey's Honest Significant Differences; Table 4). Recently managed sites (2009-2016, 2017-2020) in some cases had significantly lower basal

Table 3 Summary of significant differences in site characteristics between management treatments (Unmanaged, Thinning, Burning), management time periods (Unmanaged, before 2000, 2000-2008, 2009-2016, 2017-2020), and ponderosa pine regeneration density (R0, R75, R300, R450)

Category	Basal Area [m^2 ha^{-1}]	Adult trees [# ha^{-1}]	Canopy [%]	DBH_{mean} [cm]
	ns	$p < 0.0001$	ns	$p < 0.0001$
Unmanaged	-	668 ± 235^{a}	-	20.8 ± 6.9^{b}
Thinning	-	282 ± 209^{b}	-	31.9 ± 8.6^{a}
Burning	-	263 ± 149^{b}	-	34.4 ± 9.7^{a}
	$p < 0.03$	$p < 0.05$	$p < 0.02$	$p < 0.01$
Unmanaged	23.0 ± 8.3^{ab}	668 ± 235^{a}	47.0 ± 14.4^{a}	20.8 ± 6.9^{b}
Before 2000	27.7 ± 8.0^{a}	434 ± 194^{ab}	56.7 ± 13.5^{a}	27.9 ± 11.5^{ab}
2000–2008	19.8 ± 7.2^{ab}	260 ± 158^{bc}	46.8 ± 13.8^{a}	35.7 ± 9.5^{a}
2009–2016	19.3 ± 6.2^{ab}	250 ± 195^{bc}	43.9 ± 16.4^{ab}	31.5 ± 7.8^{a}
2017–2020	14.6 ± 12.3^{b}	214 ± 195^{c}	26.4 ± 15.5^{b}	30.6 ± 3.6^{ab}
	ns	ns	$p < 0.08$	ns
R0	-	-	39.5 ± 13.5^{b}	-
R75	-	-	44.1 ± 16.2^{ab}	-
R300	-	-	52.2 ± 13.4^{ab}	-
R450	-	-	52.6 ± 16.6^{a}	-

Significant differences were determined using ANOVA and Tukey's Honest Significant Differences ($p < 0.05$; differences at $p < 0.1$ shown for reference). Only significant differences are shown. See Supplementary material S1: Table S3 for a list of measured variables

Table 4 Summary of significant differences in site characteristics between management treatments (Unmanaged, Thinning, Burning), management time periods (Unmanaged, before 2000, 2000-2008, 2009-2016, 2017-2020), and ponderosa pine regeneration density (R0, R75, R300, R450)

Category	Cone density [# m^{-2}]	Debris [%]	Litter [%]	Litter depth [cm]	Litter density [g cm^{-3}]
	ns	ns	$p < 0.04$	ns	$p < 0.02$
Unmanaged	-	-	76.8 ± 19.0^{b}	-	0.13 ± 0.09^{ab}
Thinning	-	-	77.2 ± 18.8^{b}	-	0.14 ± 0.09^{a}
Burning	-	-	88.1 ± 6.6^{a}	-	0.10 ± 0.06^{b}
	ns	ns	$p < 0.08$	$p < 0.05$	ns
Unmanaged	-	-	76.8 ± 19.0^{ab}	2.2 ± 1.1^{ab}	-
Before 2000	-	-	88.9 ± 11.2^{a}	3.0 ± 1.2^{a}	-
2000–2008	-	-	87.7 ± 6.5^{a}	2.4 ± 0.9^{a}	-
2009–2016	-	-	74.8 ± 19.2^{ab}	1.6 ± 0.8^{b}	-
2017–2020	-	-	67.2 ± 22.8^{b}	1.8 ± 0.8^{ab}	-
	$p < 0.05$	$p < 0.01$	$p < 0.08$	ns	ns
R0	2.4 ± 3.2^{b}	20.4 ± 16.1^{a}	74.1 ± 21.8^{b}	-	-
R75	2.9 ± 3.6^{b}	14.0 ± 13.0^{a}	80.5 ± 15.4^{ab}	-	-
R300	1.1 ± 0.7^{b}	16.2 ± 11.0^{a}	86.2 ± 8.0^{ab}	-	-
R450	6.9 ± 8.6^{a}	6.5 ± 8.4^{b}	88.2 ± 8.8^{a}	-	-

Significant differences were determined using ANOVA and Tukey's Honest Significant Differences ($p < 0.05$; differences at $p < 0.1$ shown for reference). Only significant differences are shown. See Supplementary material S1: Table S3 for a list of measured variables

area, adult tree density, canopy cover, litter cover, and litter depth compared to unmanaged and less recently managed sites (before 2000, 2000-2008; ANOVA with Tukey's Honest Significant Differences; Tables 3 and 4). Soil sand and silt content differed significantly among management treatments (∼10-12% difference), reflecting spatial variation in the most common treatments conducted across our regional study locations ($p < 0.02$; ANOVA with Tukey's Honest Significant Differences; Supplementary material S1: Table S2).

There were a small number of significant differences in site characteristics between regeneration densities. R450 sites had significantly higher ponderosa pine cone densities ($p < 0.05$) and lower coarse woody debris cover ($p < 0.01$) than R0, R75, and R300 sites (ANOVA with Tukey's Honest Significant Differences; Table 4). At the $p < 0.1$ level, R450 sites had significantly higher canopy cover ($p < 0.08$) than R0 sites, and R450 and R300 sites had significantly higher litter cover than R0 sites ($p < 0.07$; ANOVA with Tukey's Honest Significant Differences; Tables 3 and 4).

Other tree species

Our GLM model for the density of adults of other tree species (response variables) between management treatments (categorical explanatory variables) performed sig-

Table 5 Summary of significant differences in the density of adults of other tree species between management treatments (Unmanaged, Thinning, Burning), management time periods (Unmanaged, before 2000, 2000-2008, 2009-2016, 2017-2020), and ponderosa pine regeneration density (R0, R75, R300, R450)

Management	Higher elevation adults [# 0.1 ha^{-1}]	Piñon adults [# 0.1 ha^{-1}]	Juniper adults [# 0.1 ha^{-1}]
	$p < 0.02$	$p < 0.03$	$p < 0.002$
Unmanaged	13.3 ± 23.7^a	2.9 ± 8.6^a	5.6 ± 10.2^a
Thinning	4.0 ± 10.6^b	0.0 ± 0.0^b	0.5 ± 2.3^b
Burning	0.0 ± 0.0^b	0.0 ± 0.0^b	0.3 ± 1.1^b

Significant differences were determined using Gaussian generalized linear models (GLM) and main effect coefficients (ME). Unmanaged sites were the sole significant predictor for each species type (Higher elevation (HE): p = 0.002; Piñon: p = 0.025; Juniper: p = 0.001). Significant differences in main effect coefficients included those between unmanaged and burned sites (N–B; Higher elevation: p = 0.001; Piñon: p = 0.025; Juniper: p = 0.002), and between unmanaged and thinned sites (N–T; Higher elevation: p = 0.02; Piñon: p = 0.02; Juniper: p = 0.001). Only significant differences are shown. See Supplementary material S1: Table S3 for a list of measured variables

nificantly better than the null model (LR: p = 0.0), but our GLM models for seedlings of other tree species did not. Unmanaged sites were the sole significant predictor of the density of higher elevation tree species (p = 0.002), piñon pines (p = 0.025), and junipers (p = 0.001; Table 5). Significant differences in main effect coefficients included those between unmanaged and burned sites (N–B; Higher elevation: p = 0.001; Piñon: p = 0.025; Juniper: p = 0.002), and between unmanaged and thinned sites (N–T; Higher elevation: p = 0.02; Piñon: p = 0.02; Juniper: p = 0.001).

High density regeneration (R450)

Meteorological and water balance values over the past 20 years were better explanatory variables of R450 compared to pre-regeneration and post-regeneration time periods, and meteorological estimates were better explanatory variables of R450 compared to meteorological anomalies. The top meteorological random forest model for R450 sites included summer PPT event magnitude, cool and warm season daily minimum Ta, and consecutive PPT days in summer (Sensitivity = 0.864, Specificity = 0.891, BA = 0.877; Table 6). Three groups of simulated variables were ranked as top models (Sens. = 1.0, Spec. = 1.0, BA = 1.0), and each of these models could additionally include warm season total evapotranspiration [ET: mm] as an additional non-correlated variable (Table 6). The top meteorological + simulated variable model for R450 sites included warm season solar radiation, cool season σVWC, warm season total evapotranspiration, and cool season minimum daily Ta (Sens. = 1.0, Spec. = 1.0, BA = 1.0; Table 6).

Using partial dependence, the majority of variables in the top model were those used to select against (inhibit) the determination of R450 sites (Table 6). Across all explanatory variables, most locations exhibited variation in the variables both pro-

Table 6 Summary of random forest determination of the top models and variables identifying ponderosa pine sites with high density ponderosa pine regeneration densities [R450: > 450 TPA]

Model Rank	Variable	BA	Sens.	Spec.	p-value	GI
Meteorology	Jun-Aug: PPT event magnitude	0.878	0.864	0.891	$< 1.0e^{-3}$	7.5
1	Oct-Mar: Ta (minimum daily)					7.0
	Apr-Sep: Ta (minimum daily)					5.4
	Jun-Aug: PPT (consecutive days)					4.6
Meteorology	Oct-Mar: Ta (minimum daily)	0.864	0.818	0.909	$< 1.0e^{-3}$	6.7
2	Water Year: PPT event magnitude					6.3
	Apr-Sep: Ta (minimum daily)					5.9
	Jun-Aug: PPT event frequency					5.6
SOILWAT2	Apr-Sep: Solar radiation	1.0	1.0	1.0	$< 1.0e^{-6}$	12.0
1a	Jun-Aug: Soil water potential 0-20cm ($\overline{x}$ daily)					9.6
SOILWAT2	Water Year: Solar radiation	1.0	1.0	1.0	$< 1.0e^{-6}$	11.6
1b	Jun-Aug: Soil water potential 0-20cm ($\overline{x}$ daily)					9.5
SOILWAT2	Oct-Mar: VWC 0-20cm ($\overline{\sigma}$ daily)	1.0	1.0	1.0	$< 1.0e^{-6}$	10.7
1c	Water Year: Solar radiation					10.5
1a-c	Apr-Sep: Evapotranspiration (total)	1.0	1.0	1.0	$< 1.0e^{-6}$	-
Meteorology +	Apr-Sep: Solar radiation	1.0	1.0	1.0	$< 1.0e^{-6}$	6.8
SOILWAT2	Oct-Mar: VWC 0-20cm ($\overline{\sigma}$ daily)					5.9
1	Apr-Sep: Evapotranspiration (total)					4.1
	Oct-Mar: Ta (minimum daily)					4.1

VB

Water Year: PPT event magnitude: R450 more likely above 5.0 mm & below 9.0 mm event^{-1}

Water Year: Solar radiation: R450 more likely below 14.5 MJ m^{-2} d^{-1}

Oct-Mar: Ta (minimum daily): R450 more likely below -18.0°C

Oct-Mar: VWC 0-20cm ($\overline{\sigma}$ daily): R450 less likely above 0.023 m^3 m^{-3}

Apr-Sep: Ta (minimum daily): R450 more likely below -7.5°C

Apr-Sep: Solar radiation: R450 less likely above 19.5 MJ m^{-2} d^{-1}

Apr-Sep: Evapotranspiration (total): R450 less likely below 315 mm

Jun-Aug: PPT event magnitude: R450 more likely above 4.0 mm & below 10.0 mm event^{-1}

Jun-Aug: PPT (consecutive days): R450 more likely above 7.5 days

Jun-Aug: PPT event frequency: R450 more likely above 0.325 events day^{-1}

Jun-Aug: Soil water potential 0-20cm ($\overline{x}$ daily): R450 less likely below -2.0 MPa

Top explanatory variable determination included meteorological variables from Daymet (Meteorology; Thornton et al. 2022), SOILWAT2-simulated water balance variables (SOILWAT2), and combined analysis of the top meteorological + water balance variables (Meteorology + SOILWAT2). Values include balanced model accuracy evaluated across the entire dataset using a confusion matrix [BA: %], model sensitivity (higher values indicate fewer R450 sites misclassified), model specificity (higher values indicate fewer non-R450 sites misclassified as R450), a p-value designating a significant difference in accuracy between the random forest model and a no information control, the mean decrease Gini Importance for the variables in the model [GI], and the values of each explanatory variable denoting the estimated boundary between R450 and other regeneration densities using partial dependence [VB]. Models were ranked based on sensitivity, specificity, and balanced model accuracy moting and inhibiting model selection of R450 (Supplementary material S1: Fig. S2). The exceptions to this were southern New Mexico and southern Nevada, which had variables that infrequently promoted R450 determination and more frequently inhibited R450 determination. This pattern corresponds to the low percentage of R450 sites found at these locations. In contrast, at Front Range Colorado, in which 83% of sites were R450, explanatory variables frequently promoted the determination of R450, and less frequently inhibited R450 determination (Supplementary material S1: Fig. S2). Between management treatments, unmanaged and thinned sites more infrequently promoted model determination of R450, and unmanaged sites more frequently inhibited model determination of R450 (Supplementary material S1: Fig. S3). Burned sites more frequently promoted R450 determination (Supplementary material S1: Fig. S3). Density distributions of raw and scaled R0 and R450 scores suggested that our R0 scoring captured a wider variety of conditions supporting and inhibiting regeneration failure (R0) compared to our R450 scoring, where the majority of sites exhibited conditions inhibiting R450, and a smaller number of sites exhibited conditions promoting R450 (Supplementary material S1: Fig. S4).

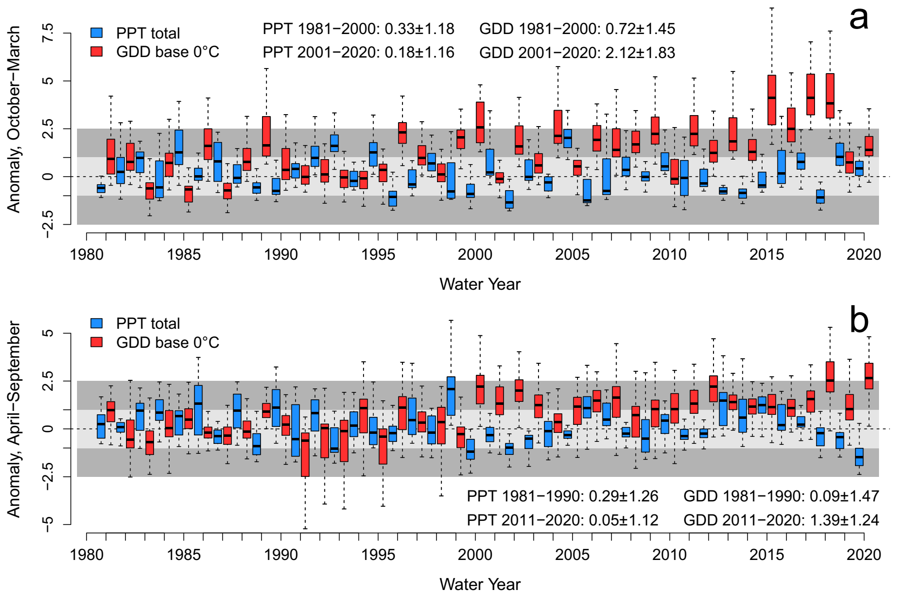

Fig. 4 Cool season (October-March; Panel a) and warm season (April-September; Panel b) anomalies of total precipitation (PPT) and total growing degree days calculated from a base temperature of 0°C (GDD) for the 77 forest sites of our study from 1981-2020. Anomaly values for PPT and GDD were calculated independently for each site and season as (observed - long-term mean)/long-term standard deviation. We used Oak Ridge National Laboratory Daymet estimates as observed values (Thornton et al. 2022), compared to the mean and standard deviation of longer-term estimates from 1915-2011 (Livneh et al. 2013). The average ± one standard deviation of PPT and GDD is shown in each panel, summarized between 1981-2000 and 2001-2020 time periods

R0 and R450 in the context of 1981-2020 meteorological change

Using anomaly values of total PPT and GDD with a base temperature of 0°C, we found that the cool season (October-March) from 1981–2020 across our study sites was characterized by large temperature increases since 2000, and further amplification

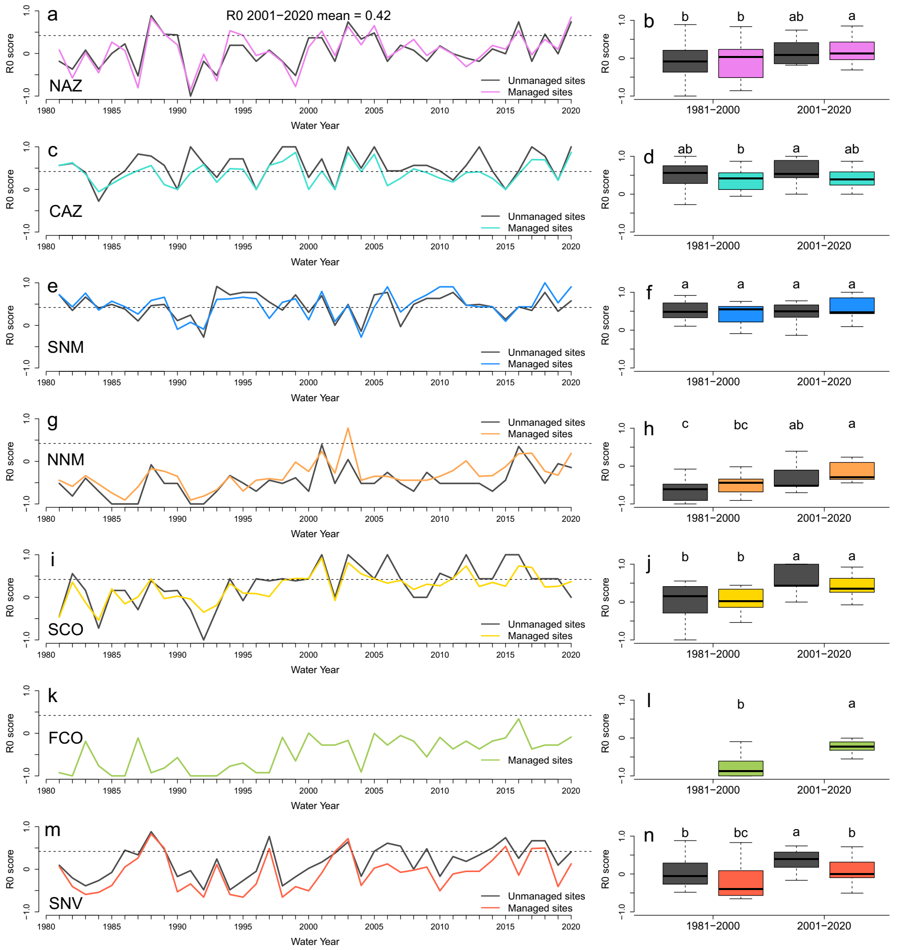

Fig. 5 Timeseries of the estimated ponderosa pine regeneration failure potential (R0 score) of managed and unmanaged ponderosa pine sites (1981–2020), and boxplots illustrating significant differences in the R0 score for managed and unmanaged sites between 1981-2000 and 2001-2020 time periods. Locations include northern Arizona (NAZ: Panels a,b), central Arizona (CAZ: Panels c,d), southern New Mexico (SNM: Panels e,f), northern New Mexico (NNM: Panels g,h), southern Colorado (SCO: Panels i,j), Front Range Colorado (FCO: Panels k,l), and southern Nevada (SNV: Panels l.m). The R0 score was estimated in each year, and was scaled from a minimum of -1.0 (lowest failure potential) to a maximum of +1.0 (highest failure potential). The mean R0 score of R0 sites from 2001-2020 is illustrated by the horizontal line in the timeseries panels. In the boxplot panels, significant differences in R0 scores were determined using ANOVA and Tukey's Honest Significant Differences ($p < 0.05$)

beginning in 2015 (Fig. 4a). The warm season (April-September) was characterized by smaller temperature increases since 2000, and 3 periods of low regional PPT from 2000-2005, 2008-2012, and 2018-2020 (Fig. 4). The potential for regeneration failure (R0 score) increased significantly from 1981–2020 across many of our study sites (Fig. 5, Supplementary material S1: Table S6). Since 2001, mean R0 scores in central Arizona, southern New Mexico, and southern Colorado have consistently approached and exceeded the 0.42 average of R0 sites from 2001-2020 (Fig. 5, Supplementary material S1: Table S6). From 2001-2020, only in southern Nevada was the R0 score of managed sites lower than that of unmanaged sites (Fig. 5n, Supplementary material S1: Table S6). R450 scores were inconclusive due to low observation of variables promoting R450 (Supplementary material S1: Fig. S4).

Discussion

We sought to understand how management treatments in ponderosa pine forests of the SWUS were associated with natural regeneration over the past two decades, and specifically the occurrence of short-term regeneration failure (R0) and high regeneration densities (R450). We found a wide variety in forest management across the SWUS – the treatments conducted, their influence on over- and understory forest characteristics, and the time periods in which they occurred. As a result of this variety, we did not find simple relationships between natural regeneration and measures of climate, tree stand attributes, or silvicultural prescription across the sites of our study. This finding corroborates other research findings that relationships between management and natural regeneration are varied and often localized; other studies have reported positive relationships, negative relationships, and neutral relationships (Thomas and Waring 2015; Flathers et al. 2016; Francis et al. 2018; Kolb et al. 2020; Wasserman et al. 2022). Our results illustrate that management treatments produce a wide variety of effects to forest overstory and understory conditions in the SWUS. They also provide a broad perspective on management and natural regeneration, showing that forest management treatments – especially those that incorporated thinning and prescribed understory burning – helped sustain or promote regeneration in forests of the SWUS over a recent 20 year time period. In support of these conclusions, R0 and R75 sites were ~30% less likely to have been managed than R300 and R450 sites, and were ~50% less likely to have been burned. Compared to unmanaged forests, managed forests more frequently experienced natural regeneration within a broad range of desired seedling densities (R300) or at undesirable high densities (R450). Indeed, ~90% of R300 and R450 sites had been managed. Thus, while management treatments helped to avoid short-term natural regeneration failure over the past two decades, potentially problematic low regeneration (R75) and high regeneration (R450) densities constituted the majority of the managed sites in our study.

A recent review by Wasserman et al. (2022) reports relatively low natural regeneration response of ponderosa pine in the first 10 years following management, higher regeneration in years 11-20, and declining regeneration after year 20. Although it is difficult to disentangle the influence of multiyear to decadal climate variation from the influence of management on natural regeneration, our results corroborate delayed regeneration response for managed forests of the SWUS reported by Wasserman et al. (2022), and more broadly corroborate the sustained influence of both thinning and prescribed burning on the structure and function of ponderosa pine forests (Thomas and Waring 2015; Stoddard et al. 2021; Wion et al. 2023). We found a ~10-year delay in natural regeneration at burned sites, and a ~5-year delay in regeneration at thinned sites, albeit with high across-site variability. This illuminates an important question about regeneration response – what is the relative importance of post-management change to forest stand characteristics versus post-management climate conditions in shaping natural regeneration? Although we cannot fully resolve this question, we explore its components in the following sections.

Management influence on natural regeneration

Forest management treatments can support natural regeneration by altering forest stand characteristics to make climate-driven environmental conditions more favorable (Bigelow et al. 2011; Flathers et al. 2016; Andrews et al. 2020). In central Arizona and southern Nevada, managed sites had environmental conditions that were less likely to result in short-term regeneration failure. However, we also found that the non-climatic pathways by which management treatments support natural regeneration may be equally important. The most notable of these pathways may include the alteration of understory forest litter and debris cover, and reducing the cover of competitive tree species at both lower and higher elevations. Variation in soil parent material, management-associated nutrient transformations, and potential phenotypic variation in the stress tolerance of ponderosa pine populations could be additional influences on regeneration that were not captured by our sampling (Kolb et al. 2016; Puhlick et al. 2021). We hypothesize that understanding these potential non-climatic pathways can be improved by longer-term research quantifying biotic and abiotic attributes of forest stands pre- and post-management treatments, utilizing nearby unmanaged stands as a reference.

If a warming climate in the SWUS restricts natural ponderosa pine regeneration in coming decades (Petrie et al. 2017), forest managers may have increasing difficulty meeting targets for tree stand density. The majority of managed forest sites in our study were managed after 2000, and overlap in time with considerable warm season and cool season temperature increases, multiyear warm season drought, and short-term regeneration failure (Seager and Ting 2017; Petrie et al. 2023b). The potential for regeneration failure increased at many of our study locations between 1981-2000 and 2001-2020 time periods. Yet, we also found that management may promote natural regeneration even during these two decades (2001-2020) of unfavorable conditions through modification of overstory and understory forest environments. Yet, if management effects on tree stand attributes continue to be maintained over multiple decades, as documented in our study and by others (Thomas and Waring 2015; Stoddard et al. 2021; Mott et al. 2021), managed forests are likely to experience sequences of differing multiyear weather and environmental conditions alongside increasing temperatures. This adds additional uncertainty in evaluating both lower (R75, for example) and higher (R300, R450) regeneration densities, since both regeneration and seedling mortality rates will be shaped by increasingly non-analog meteorological conditions. In response, forest managers may seek to implement treatments that seek to enhance favorable high precipitation periods (or reduce the effects of less favorable periods) to influence natural regeneration.

High density regeneration

High density regeneration can result in seedling densities that exceed desired stocking levels, and enhance fire risk by increasing ladder fuels (Battaglia et al. 2009; Westlind and Kerns 2017). In the SWUS, natural regeneration has been most frequently documented as high density germination and establishment events (i.e., regeneration pulses) that are associated with favorable climatic periods (Savage et al. 1996; Brown and Wu 2005; League and Veblen 2006; Kolb et al. 2020). Yet, of the sites in our study that had natural regeneration, 76% of them experienced it at lower than R450 densities, and often with a wide range of estimated regeneration years. In interpreting these results, it is important to note that preferred stocking levels differ among forest districts of the SWUS, and in some instances both R450 and a subset of R300 regeneration densities may exceed these levels. Despite this uncertainty, our results show that high density regeneration is not the only form of natural regeneration in the SWUS – regeneration may also occur at lower densities and relatively higher frequency that may potentially resemble the uneven age structure of historical ponderosa pine forests (see White 1985 for similar findings). In northern Arizona and Front Range Colorado – locations where the majority of regeneration research has been conducted in the SWUS – we found that high density regeneration was more common (77% of R450 sites in our study; Brown and Wu 2005; League and Veblen 2006; Flathers et al. 2016; Kolb et al. 2020). Thus, the occurrence of high density regeneration is not common across the entire SWUS, but may be more common in the region's most studied locations.

Our research corroborates findings that favorable climate and environmental conditions – moderate solar radiation, cool temperatures, and consistent near-surface soil moisture availability – are associated with high density regeneration (Gray et al. 2005; League and Veblen 2006; Keyes et al. 2007; Wasserman et al. 2022; Fertel et al. 2022). Although our random forest approach was able to identify R450 sites with high accuracy, it was challenging to elucidate variation in R450 scores through time, or to tease apart the contributions of climate versus management influence on R450. We hypothesize three potential reasons for this difficulty. First, in contrast to our R0 scoring, our evaluation of the distribution of R450 scores suggests that our 77 sites did not accurately capture diversity in the meteorological and water balance conditions promoting high density regeneration. That is, the sample size of R450 sites was too small, and R450 sites were predominantly located in only two locations (northern Arizona and Front Range Colorado). Although the random forest model had high accuracy in identifying R450 sites, it was largely doing so by determining climatic differences between SWUS locations. Second, although it was clear that the conditions supporting R450 differ from those supporting other regeneration densities, we were only able to observe the outcome and did not observe the process. In research quantifying a high density regeneration pulse in New Mexico, Savage et al. (2013) and Feddema et al. (2013) suggest that natural regeneration pulses result from environmental conditions supporting multiple demographic stages of adult tree flowering, seed production, germination, and seedling survival. In our analyses, we had little success in disentangling pre-regeneration and post-regeneration climatic and environmental conditions at R450 sites from the broader patterns occurring over the past two decades. More complete observation and attribution of the multiple stages of natural regeneration *in situ* may help to improve understanding of high density regeneration.

Finally, in contrast to the climate- and microclimate-driven conditions promoting short-term regeneration failure (Petrie et al. 2023b), R450 regeneration appears to respond to the combined effects of climate variation and tree stand attributes. As a result, our location-averaged scores for R450 were inconclusive and unhelpful. In addition to favorable climate conditions, we found that R450 sites were more likely to be managed, which corroborates other studies illustrating variation in natural regeneration response at the stand scale (Thomas and Waring 2015; Flathers et al. 2016; Kolb et al. 2020). Our results suggest that understory litter and debris cover, and adult tree density are potential stand scale influences of management on high density regeneration. Indeed, many management treatments increase litter cover, reduce tree stand density, and reduce coarse woody debris. In addition, stand density reductions also increase moisture availability and growth of adult ponderosa pines (Kerhoulas et al. 2013; Thomas and Waring 2015; Flathers et al. 2016; Andrews et al. 2020), which may allow adults to take greater advantage of favorable periods for masting and cone production (Keyes and Gonzalez 2015). The R450 sites of our study had cone densities that were significantly higher than those of all other regeneration densities, supporting other work that has identified cone production as an important precursor to high density regeneration (Feddema et al. 2013; Flathers et al. 2016). More broadly across the SWUS, natural regeneration outcomes vary across landforms and soil parent material, but locally important topographic and edaphic factors are difficult to apply to regeneration in other subregions (Francis et al. 2018; Puhlick et al. 2021; Marsh et al. 2022). Our sampling design sought to minimize topographic and edaphic differences between sites, but we did find that high soil phosphorus (P) in northern Arizona, which resulted in significantly higher soil P for R450 sites because a large percentage of R450 sites were located in northern Arizona. Together, our findings attest to – although they do not fully elucidate – the multiple factors and processes associated with high density regeneration.

Conclusions

We conducted a field and water balance modeling study of managed and unmanaged ponderosa pine forests across 7 regional locations of the southwestern US (SWUS), with the primary goal of elucidating to what degree forest management treatments have influenced natural regeneration. We found that thinning and prescribed understory burning supported natural regeneration by altering both the forest structural characteristics that shape environmental conditions, and in a separate pathway by influencing understory forest biomass and reducing the cover of competing tree species. However, management treatments have not been uniformly applied across the SWUS, and regeneration outcomes are further influenced by variation in regional climate conditions. Natural regeneration has on average occurred 10 years post-management, and the most recent two decades in the SWUS have been especially limiting to regeneration in both managed and unmanaged forests. Forest managers may wish to consider the potential for sequences of both favorable and unfavorable climate-driven conditions to influence natural regeneration following management, and to continue to plan for follow-up treatments to ameliorate problematic lower and higher seedling densities that can occur ~5-10 years following their activities. Our results provide novel insight on management and natural regeneration over a recent 20 year time period in the SWUS, but determinations of short-term regeneration failure (R0) and high density regeneration (R450) require further interpretation in the context of long term forest demography and stand dynamics. In a changing regional environment, management treatments have the potential to support natural ponderosa pine regeneration through both climatic and non-climatic pathways, with planning, assessment, and revision through time.

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Author Contributions MDP, RMH, JBB, and TEK designed the study. MAB, LRF, and WKM assisted with site selection, permitting, and analysis. DRS and JBB developed model simulations. AN conducted data archival. MDP conducted the study and data analysis, and wrote the original draft of the manuscript. All authors contributed to manuscript edits and revisions.

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Declarations

Conflicts of interest/Competing interests The Authors declare no conflicts of interest or competing interests.

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