Forest Ecology and Management 545 (2023) 121208

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Widespread regeneration failure in ponderosa pine forests of the southwestern United States

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ARTICLE INFO

Keywords:
Conifer
Precipitation
Temperature
Seedling
Disturbance

ABSTRACT

As climate changes in coming decades, ponderosa pine forest persistence may be increasingly dictated by their regeneration. Sustained regeneration failure has been predicted for forests of the southwestern US (SWUS) even in absence of stand-replacing wildfire, but regeneration in undisturbed and lightly disturbed forests has been studied infrequently and at a limited number of locations. We characterized 77 ponderosa pine sites in 7 SWUS locations, documented regeneration occurring over the past ∼20 years, and utilized gridded meteorological estimates and water balance modeling to determine the climate and environmental conditions associated with regeneration failure (R0). Of these sites, 29% were R0, illuminating that regeneration failure in these forests is widespread. R0 sites were distinguished by high above- and belowground heat loading, loss of cool-season climate, and high soil moisture variation. Explanatory variables had high accuracy in identifying R0 sites, and illustrate the climate-driven pathway by which regeneration failure has occurred in the SWUS. Regeneration failure has high potential to increase in a warmer, more hydrologically variable climate, and expand regionally from lower to higher latitudes. Yet, we also found that human management interventions were associated with environmental conditions that avoided regeneration failure. To counteract regeneration-associated forest declines, interventions will need to influence climate-driven environmental change by adjusting forest characteristics at local scales. Regeneration failures are a major threat to ponderosa pine forest persistence, and they have potential to intensify and expand in a changing climate.

1. Introduction

In a future shaped by the transformative effects of climate change and disturbance, regeneration may increasingly determine the persistence of many terrestrial ecosystems (Walck et al., 2011; Martinez-Vilalta and Lloret, 2016). In the southwestern US (SWUS), the future of ponderosa pine (*Pinus ponderosa*) forests may be especially tied to regeneration. Ponderosa pine is a foundational mid-elevation tree species in western North America, and ponderosa pine-dominated forests comprise millions of hectares across the SWUS (Norris et al., 2006). These forests have experienced declines due to enhanced drought, wildfire expansion, and pathogen and insect outbreaks in recent decades, and their future persistence is uncertain in many locations (Dey et al., 2019; Stevens-Rumann et al., 2022; Davis et al., 2023). Forest declines in the SWUS have been increasingly tied to post-wildfire regeneration failure, and attributed to reductions in favorable microclimates, soil hydrophobicity and erosion, loss of seed sources, and competition with recolonizing plant species (DeBano, 2000; Rother and Veblen, 2016; Roccaforte et al., 2012; Korb et al., 2019; Singleton et al., 2021; Marsh et al., 2022). Post-wildfire environments can have higher temperatures and lower soil moisture availability that limit natural regeneration (post-wildfire regeneration, hereafter; see Singleton et al. (2021) and Marsh et al. (2022) for recent examples). Long-term forecasts suggest that post-wildfire regeneration failure may become increasingly

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https://doi.org/10.1016/j.foreco.2023.121208
Received 7 February 2023; Received in revised form 24 April 2023; Accepted 11 June 2023
Available online 12 July 2023
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common and widespread as climate change further increases temperature and moisture stress in these environments (Feddema et al., 2013; Davis et al., 2019; Rodman et al., 2020; Davis et al., 2023). To combat these declines, the United States Executive Order 14072 and REPLANT ACT will commit USD $130–250 MM annually towards forest replanting efforts, and will potentially be the largest sustained ecological restoration effort ever conducted.

If many post-wildfire environments are too hot and dry for successful regeneration, could climate change also limit ponderosa pine regeneration in the absence of severe disturbance? The potential problem of ponderosa pine regeneration failure in undisturbed or lightly disturbed forests (i.e., no stand replacing wildfire or similar severe disturbance in the last 50+ years) has been identified for some time (Schubert, 1969), although it has not been widely recognized. In a modeling study, Petrie et al. (2017) found that declining climatic favorability for seedling survival could begin to restrict natural regeneration in ponderosa pine forests of the SWUS in the later half of the 21st century. However, there have been few studies focused on seedling germination and establishment in undisturbed environments, and there is considerable uncertainty about the environmental conditions both supporting and limiting natural regeneration (Petrie et al., 2016). Ponderosa pines spend an extended period of time as seedlings and small juveniles (often 20+ years of less than 0.5 m height), they do not appear to adjust their ratio of above- and belowground growth to different environments, and their survival and performance is tightly coupled to near surface above- and belowground environmental conditions (Kolb and Robberecht, 1996; Stein and Kimberling, 2003; Pirtel et al., 2021). As a result, seedling mortality is often very high in the first years following germination (Keyes et al., 2007; Flathers et al., 2016). Studies have documented natural regeneration failure in unfavorable microsites and at the lower elevational boundaries of ponderosa pine forests (Kolb and Robberecht, 1996; Stein and Kimberling, 2003; Kolb et al., 2020; Minott and Kolb, 2020), but these earlier studies did not include multiple subregions of the SWUS (see Singleton et al. (2021) for a recent exception). Other commonly used datasets, including the Forest Inventory Analysis (FIA) program [https://www.fia.fs.usda.gov/], do not capture near-term (0–20 year) regeneration, and it has been difficult to attribute ponderosa pine regeneration patterns to environmental conditions using these data (Puhlick et al., 2012; Puhlick et al., 2021). Therefore, although regeneration failure driven by climate change in lightly disturbed forests is a reasonable hypothesis, its potential scale and importance remains poorly defined.

It is widely accepted that natural regeneration of ponderosa pine is promoted by periods of favorable climate and environmental conditions that support the demographic stages of seed production, germination, and seedling establishment (Savage et al., 1996; Brown and Wu, 2005; League and Veblen, 2006; Kolb et al., 2020). According to this model for regeneration, when each of these stages is supported, discrete pulses of regeneration occur, and may occur at high densities. Successful regeneration has been associated with episodic climate events including ENSO and heavy late-summer monsoonal precipitation, which reinforces the pulse model (Brown and Wu, 2005; League and Veblen, 2006; Flathers et al., 2016). It follows that regeneration failure could therefore be common under average climate conditions and average forest and landscape attributes. Some SWUS forest stands exhibit a homogeneous age structure that supports this pulse driven model of regeneration (Savage et al., 1996), whereas others have heterogeneous age structures that do not (White, 1985). Adding to this complexity, of regeneration studies conducted in undisturbed or lightly disturbed forests, most have been located in the same regional locations – northern Arizona, central New Mexico, or the Colorado Front Range (Brown and Wu, 2005; League and Veblen, 2006; Shepperd et al., 2006; Flathers et al., 2016; Francis et al., 2018; Minott and Kolb, 2020; Kolb et al., 2020). It is therefore unclear if the pulse model and its consequences for regeneration failure can be applied to the broader SWUS region. In a future where the extrema of climate and environmental distributions are promoted (Allan and Soden, 2008; Jentsch and Beierkuhnlein, 2008), it is critically important to determine if regeneration failure is controlled by the lack of distinctly favorable climatic periods, or is shaped by the occurrence of specific, highly stressful climate and environmental events. As it stands, the plausible pathways of regeneration failure are numerous, and without mechanistic understanding of these pathways it is unclear where, to what degree, and over what time periods regeneration failure could reduce ponderosa pine forest persistence.

In this study we sought to determine how climatic and environmental conditions influence regeneration failure (R0: 0.0 trees m^{-2}) over the past ~20 years in undisturbed and lightly disturbed ponderosa pine forests of the SWUS. We characterized landscape attributes, over- and understory forest characteristics, and regeneration density for 77 ponderosa pine sites across 7 regional, climatically-variable locations. To our knowledge, this is the first regeneration-focused dataset for undisturbed/lightly disturbed ponderosa pine forests across a large multistate region. Our study sites included unmanaged forests, and managed forests experiencing combinations of overstory basal area thinning, understory thinning, and understory burning. We employed site characteristics and gridded meteorological estimates in an ecosystem water balance model to investigate the role of climatic and environmental variables in regeneration failure. Our objectives were to: (1) investigate the frequency of R0 occurrence over the past two decades in undisturbed/lightly disturbed ponderosa pine forest sites of the SWUS; (2) determine the most explanatory climatic and environmental variables distinguishing R0; (3) determine the multiyear time periods and seasons over which top variables were influential; and (4) contrast the influence of regional climate variation versus site management (none, thinning, burning) on regeneration failure. In total, this study illuminates the under-appreciated problem of R0 in ponderosa pine forests of the SWUS, elucidates the climate-driven pathways shaping R0, and explores how these pathways could change in the future.

2. Site description

Our research focused on ponderosa pine-dominated forests in 7 regional locations in the SWUS: northern Arizona (NAZ in select figures), central Arizona (CAZ), southern New Mexico (SNM), northern New Mexico (NNM), southern Colorado (SCO), the Colorado Front Range (FCO), and southern Nevada (SNV; Fig. 1, Table 1). Climate characteristics have an important influence on resource availability, tree stand health, and recovery from disturbance in these forests (Bradford and Bell, 2017; Davis et al., 2019; Koehn et al., 2021). During the 20 years prior to sampling (Oak Ridge National Laboratory Daymet estimates [https://daymet.ornl.gov/] Thornton et al., 2022), the locations of our study exhibited significant variation in climate variables across the water year (October-September), as well as during the cool season (October-March) and warm season (April-September; Table S1). Northern AZ and southern CO experienced the highest total precipitation [PPT: mm], the slight majority of which occurred during the cool season (~53–55%; Table S1). Southern NV was cool season PPT-dominated (~68%), and received the lowest water year PPT (Table S1). In contrast, central AZ, southern NM, northern NM and Front Range CO experienced intermediate water year PPT totals, and were warm season PPT-dominated (~53–71%; Table S1). March 1 snow water equivalent [SWE: mm] was notably higher in northern AZ, northern NM, southern CO, and southern NV compared to central AZ, southern NM, and Front Range CO (Table S1). Locations at more southern latitudes (~32.7–34.2° N; central AZ, southern NM) often had warmer air temperatures [Ta: °C] and higher Growing Degree Days [GDD: °C] than locations at more northern latitudes (35.9–39.1° N; northern NM, southern CO, Front Range CO; Table 1, S1).

Ponderosa pine forests throughout the SWUS have experienced a legacy of disturbance (logging, wildfire, drought), and human management activities (fire suppression, thinning, burning; Covington and Moore, 1994; Dey et al., 2019; Stevens-Rumann et al., 2022). Sites in our

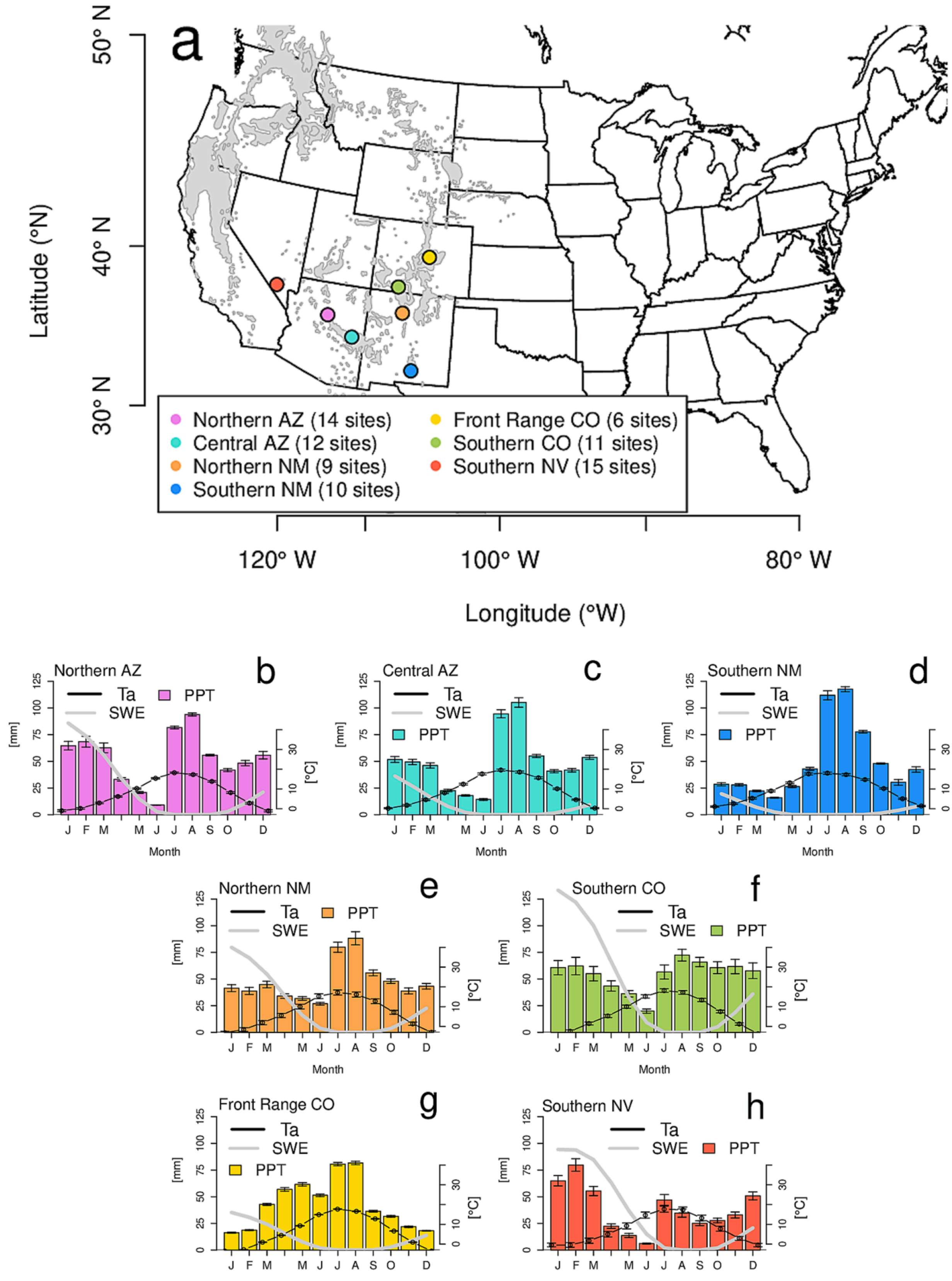

Fig. 1. Map of research locations and number of sites characterized at each location (Panel a), and climate diagrams illustrating average monthly precipitation [PPT: mm], snow water equivalent [SWE: mm], and daily mean air temperature [°C] for research locations (Panels b-h). PPT and Ta values were derived from daily Daymet estimates (1980–2020), and SWE was estimated using the SOILWAT2 model from Daymet forcing. The error bars illustrate variation in monthly mean values (± one standard deviation) across study sites in each location. Statistical differences in meteorological variables between study locations are illustrated in Table S1.

Table 1
Summary of characterization locations, variation in regeneration density [# juveniles < 50 cm height m^{-2}] at characterization sites. Summary values of regeneration density and management are shown at the bottom of the table. Letters designate significant differences in elevation between study locations (ANOVA and Tukey's honest significant differences; $p < 0.05$; sites in Northern AZ, Northern NM, and southern NV combined for each location). We found no significant differences in average regeneration density between study locations.

ID	Location	Average Coordinates	Elevation [m]	Characterization Month/Year	Regeneration min–max	# Sites	# Managed	# R0 sites
					[# m^{-2}]		Sites	[0.0 m^{-2}]
Northern AZ	Coconino National Forest	35.271°N, 111.688°W	2243 ± 40^{b}	6/2021	0.0–0.0032	3	3	1
	NAU Centennial Forest	35.170°N, 111.756°W	–	7/2019; 6/2021	0.0–8.91	11	8	1
Central AZ	Apache-Sitgreaves National Forest	34.167°N, 109.869°W	2217 ± 79^{b}	6/2021	0.0–1.61	12	10	4
Southern NM	Lincoln National Forest	32.697°N, 105.616°W	2391 ± 84^{ab}	6/2021	0.0–0.016	10	6	5
Northern NM	Santa Fe National Forest	35.848°N, 106.609°W	2506 ± 108^{a}	6/2021	0.0–0.018	7	5	1
	Valles Caldera National Preserve	35.893°N, 106.606°W	-	7/2019	0.0014–0.068	2	1	0
Southern CO	San Juan National Forest	37.285°N, 107.097°W	2378 ± 137^{ab}	6/2021	0.0–0.113	11	9	4
Front Range CO	Manitou Experimental Forest	39.111°N, 105.100°W	2394 ± 17^{ab}	7/2019; 6/2021	0.0–6.01	6	6	1
Southern NV	Humboldt-Toiyabe National Forest	36.327°N, 115.630°W	2480 ± 166^{a}	8/2019; 7/2021	0.0–0.548	14	9	4
	Desert National Wildlife Refuge	36.590°N, 115.214°W	-	8/2019	0.0	1	0	1
			2366±149	-	**0.0–8.91**	**77**	**57**	**22**

study were intentionally selected to exclude stand-replacing wildfire or other severe human or natural disturbances occurring in the past ~50 years (1970s–sampling date). They instead were comprised of undisturbed forests, forests that had experienced a natural understory burn, and those that had experienced both over- and understory human management in the form of basal area reduction, understory thinning, and/or understory burning. The characteristics of ponderosa pine forest stands (canopy cover, basal area, and understory) vary across fine spatial scales (100–500 m^{-2}), such that single stands may exhibit a wide variety of microclimate conditions (Reynolds et al., 2013). To maintain consistency in our sampling across sites, we focused on characterizing the transition zone between a moderately sized forest interspace and a higher density area, such that our sampling captured an intermediate condition of the larger forested unit, specifically one that included both lower and higher forest density and canopy cover. We expected that this design (see Pirtel et al. (2021) for specific detail on sampling arrangement) would be most likely to include both more and less sheltered forest microsites, and minimize bias in our sampling sites between locations. Sites were located on shallow slopes (< 10° when feasible), and displayed no obvious influence of topography on surface or subsurface hydrology (surface depressions, run-on or runoff, etc.). These data (see Petrie et al. (2023)) provide a comparative baseline for future research exploring additional settings and fine-scale processes (N-facing and S-facing slopes, large interspaces, influence of lateral subsurface hydrology, etc.).

3. Methods

3.1. Site characterization and regeneration densities

We characterized the overstory, understory, and ponderosa pine regeneration density of 77 ponderosa pine forest sites across 7 regional locations in the SWUS (Table 1, Fig. 1). Of these sites, 17 were sampled in 2019 and 60 in 2021. We sampled each site using a circular plot with a 5.0–20.0 m radius (protocol described and visualized in Pirtel et al. (2021), data available at Petrie et al. (2023)). Field characterizations included landscape characteristics, over- and understory forest structure, vegetation cover and regeneration density, and soil properties (Table S2). Measurements made across the entire plot included regeneration density (number of seedlings < 500 mm in height), adult tree diameter at breast height, basal area, canopy cover, soil properties (0–10 cm depth), slope, and aspect (Pirtel et al., 2021). Across North–South and East–West transects in each plot (4 quadrat measurements along each transect, 8 total per plot), we measured litter attributes (cover, depth), coarse woody debris cover, ponderosa pine cone density, herbaceous vegetation cover, and woody vegetation cover (Pirtel et al., 2021). We categorized sites by density of ponderosa pine seedlings < 500 mm in height counted for the entire plot area (R0: 0.0 trees m^{-2}; R1: > 0.0 to 0.01 m^{-2}; R2: > 0.01 to 0.1 m^{-2}; R3: 0.1+ m^{-2}), and separately by management history (N: no management; T: basal area reduction and/or understory thinning; B: any management including an understory burn; known and estimated management date included in Petrie et al. (2023)). We recognize that these broad management categories include a wide range of forest conditions, management practices, and time since management, and these categories are best viewed as a broad representation of generalized management activities conducted across the SWUS. In 2019 we measured physical soil properties using a sedimentation soil particle size analysis (Bouyoucos, 1962) and soil organic carbon (SOC) using loss on ignition (Abella et al., 2007). In 2019 we quantified physical soil properties and soil nutrient concentrations (SOC, pH, NO_3-N, P, K) utilizing the Soil, Water and Forage Analytical Laboratory (SWFAL) at Oklahoma State University [www.soiltesting.okstate.edu]. All data manipulations, calculations, and statistical analyses were conducted using R-project statistical computing software (R Development Core Team, 2023). We used ANOVA and Tukey's honest significant differences to evaluate differences in site characteristics ($p < 0.05$), and used generalized linear models to evaluate differences in regeneration densities between study locations and regeneration density classifications ($p < 0.05$).

3.2. Meteorological estimates, SOILWAT2 modeling, and analysis variables

To investigate the role of solar radiation, surface and soil temperature, and water balance dynamics in regeneration at our study sites, we simulated these variables using the SOILWAT2 model. SOILWAT2 is a daily time step, one dimensional, multiple soil layer, process-based, water balance simulation model (Schlaepfer and Andrews, 2019; Schlaepfer and Murphy, 2019), and is formulated and operated independently of other water balance and land surface models. Computational water balance models are subject to uncertainty arising from numerous sources, including meteorological drivers, parameterizations, formulations. SOILWAT2 has been tested and used successfully to simulate ecohydrological and temperature dynamics in ponderosa pine forests under a variety of climates and forest stand characteristics (Bradford and Bell, 2017; Petrie et al., 2017; Petrie et al., 2020). The model translates meteorological conditions, landscape characteristics, and ecosystem properties from observations and spatial data products into a full suite of temperature patterns and water balance processes, providing a direct representation of the climate-driven conditions expected to shape regeneration.

We parameterized each study site in SOILWAT2, incorporating elevation, slope and aspect, tree stand characteristics including canopy cover and basal area, understory vegetation (herbaceous, shrub), surface litter and coarse woody debris, and near-surface (0–10 cm) soil properties. We estimated soil properties below 10 cm depth using POLARIS (Chaney et al., 2019). To drive SOILWAT2, we used Oak Ridge National Laboratory Daymet estimates from 1980–2020 at 1 km^2 resolution [https://daymet.ornl.gov/] (Thornton et al., 2022). To develop a more complete perspective of meteorological anomalies we obtained longer-term, less spatially detailed estimates from 1915–2011 at 1/16° resolution for comparison between near-term and long-term values (Livneh et al., 2013; see Renne et al. (2019) for an example where this long-term view was beneficial). Recognizing the substantial changes to forest structure that have occurred over the past century in the SWUS, we did not conduct long term SOILWAT2 simulations using Livneh et al. (2013).

Meteorological estimates in our analysis included PPT and Ta, as well as derived variables including PPT event properties (event timing, magnitude), periods of sequential days with and without PPT (PPT periods), and GDD with base temperatures of 0 °C, 10 °C, and 20 °C (Table S3). We used SOILWAT2 to simulate SWE and tilted solar radiation [MJ m^{-2} day^{-1}] at each study site from meteorological estimates and site characteristics (Table S3). Our analyses of soil moisture focused on the juvenile ponderosa pine rooting zone from 0–20 cm and 20–40 cm depth (see Pirtel et al. (2021)), and included estimates of volumetric soil moisture [VWC: m^3 m^{-3}], soil water potential [SWP: MPa], and soil water availability > -3.0 MPa [SWA: mm] (Table S4). We evaluated surface and soil temperature from 0–20 cm [Ts: °C], and calculated derived measures of the number of dry days (SWA $= 0.0$ mm), the GDD of hot-dry days (GDD when SWA $= 0.0$ mm), and the interaction of water balance variables including evaporation [E: mm], transpiration of all vegetation [T: mm], canopy + litter interception [I: mm], and evapotranspiration [ET: mm; E + T] (Table S4). All meteorological and simulated variables were developed for 4 seasonal time periods: water year (October-September), cool season (October-March), warm season (April-September), and summer (June-August). The exception was SWE, which was evaluated as water year maximum on March 1 (DOY 60) and on April 1 (DOY 91).

3.3. Average, pre-regeneration, and post-regeneration time periods

Our field characterization of regeneration densities only included ponderosa pine seedlings and juveniles < 500 mm in height, which corresponds to trees ~20 years in age (Pirtel et al., 2021). To capture the average climate conditions corresponding to the shared regeneration period for each site, we evaluated meteorological estimates and SOILWAT2 simulations for 20 water years prior to the year of our field characterizations (2019 sampling: 1999–2018 water years; 2021: 2001–2020 water years; Figure S1b,f,g). Based on a site-average tree height and tree diameter, we used tree size and ring number relationships developed by Pirtel et al. (2021) to estimate the year of highest regeneration for each R1–R3 site. For each of these sites, we then evaluated meteorological estimates and SOILWAT2 simulations for each site's pre-regeneration window (-5 years prior to +2 years after estimated regeneration year; Figure S1c,g,k) and post-regeneration window (-2 years prior to +5 years after estimated regeneration year; Figure S1d, h,l). R0 sites were only evaluated using a 20-year window, but were compared to 20-year, pre-regeneration, and post-regeneration windows for R1–R3 sites.

3.4. Explanatory variable illustration

Together, the potential variables explaining R0 included field measurements of site characteristics (Table S2), meteorological estimates (Table S3), and SOILWAT2-simulations (Table S4). Meteorological variables included estimated values from Daymet (see Figure S1a for an example), and meteorological anomalies calculated from Daymet estimates using long-term estimates of the mean and standard deviation of meteorological variables from Livneh (1916–2011; see Figure S1e). R0 20-year values were compared to 20-year, pre-regeneration, and post-regeneration time periods for R1–R3, focusing on water year (October-September), cool season (October-March), warm season (April-September), and summer (June-August) seasonal time periods. To do this, we determined the meteorological and simulated variables that were significantly different between R0 sites and R1-R3 sites (R0 different from all other sites; ANOVA and Tukey's honest significant differences; $p < 0.05$). We scored differences as -1 (R0 lower than R1–R3) or $+1$ (R0 higher than R1–R3) for 20-year, pre-regeneration, and post-regeneration time periods (3 time periods). Combined, the minimum score for each variable was -3 (R0 lower than all other densities for all 3 time periods), and the maximum score was $+3$.

3.5. Top explanatory variables

Using only meteorological and simulated variables where R0 values were significantly different from R1–R3 regeneration densities (ANOVA and Tukey's honest significant differences; $p < 0.05$), we developed groups of non-correlated explanatory variables for meteorological and water balance variables (linear correlations; Pearson's $r < 0.4$, $p < 0.05$). When two variables had a Pearson's $r > 0.4$, we chose the top variable based on its significance in the ANOVA analysis ($p < 0.0001$ chosen over $p < 0.05$, for example). When two variables had a Pearson's $r > 0.4$ but similar p-values in the ANOVA analysis, we included each variable in a different group of explanatory variables. This resulted in 4 different explanatory variable groups for meteorological variables, and 4 different groups for simulated variables. This process differed from other methodologies for top variable selection, but had the benefit of allowing our analyses to better determine the seasonal time periods where top variables were most influential. For example, GDD during the warm season (April-October) and summer (June-August) were both significantly higher for R0 sites in the ANOVA analyses, and were highly correlated to each other. By placing these variables in different groups, we did not predetermine which time period was most indicative of R0, and how its importance compared to other top variables.

After developing non-correlated groups of explanatory variables, we used random forest analyses for each group of explanatory variables to determine the top models and variables associated with R0 sites, all performed in R-project environment for statistical computing and with the *randomForest* and *rpart* packages (R Development Core Team, 2023; Liaw and Wiener, 2002; Therneau et al., 2013). We chose top models and variables based on their: (1) sensitivity (accurate identification of R0 sites); (2) specificity (accurate identification of non-R0 sites), (3) balanced model accuracy (BA: arithmetic mean of sensitivity and specificity); and (4) balanced versus unbalanced Gini Importance among explanatory variables. We chose the top meteorological + water balance model using the top model(s) from the meteorological and SOILWAT2-simulated variable random forests analyses (5 different meteorological + water balance groups). In the random forests model, some explanatory variables are used to classify a site as R0, whereas others are used to classify a site as non-R0. Using a methodology described in Molnar (2022), we used partial dependence plots to determine how model selection of R0 or non-R0 sites changed across the range of explanatory variables, and to visually determine values of these top variables (i.e., thresholds) where model selection most frequently occurred. In cases where the Random Forests model had high balanced accuracy, partial dependence was able to inform the conditions promoting versus inhibiting R0. We describe an explanatory variable used by the model to categorize a site as R0 as one that "promotes" R0, whereas we describe a variable used by the model to categorize a site as non-R0 as one that "inhibits" R0. We used partial dependence in the R-project *rpart.plot* package to estimate the threshold value of each top variable (Milborrow, 2022).

Using the partial dependence for each R0 explanatory meteorological variable, we evaluated over the past 20 years how frequently top variables at each site promoted R0, and how frequently other top variables inhibited R0. To do this, we calculated the percentage of observations at each site over the past 20 years that exceeded the partial dependence threshold value. We then grouped sites by management (None, Thinning, Burning) and separately by location (northern AZ, central AZ, etc.). We then calculated average exceedance for each variable in each group. This analysis addressed the questions of to what degree the sites in each group (management, location) promoted versus inhibited R0, and provided insight on the variables and pathways that led to regeneration failure.

4. Results

4.1. Field characterization and regeneration density across SWUS locations

We found a wide range of regeneration densities (from 0.0 trees m^{-2} to 8.91 m^{-2}) across and within the 7 SWUS locations of our study (Table 1). Only Northern AZ had a significant difference in regeneration density compared to other study locations (generalized linear models, $p < 0.05$; Fig. 2). This difference was also maintained with R0 sites removed (generalized linear models, $p < 0.05$; not shown). Front Range Colorado had high regeneration densities, but a low number of observations ($n = 6$). Of the 77 sites we characterized, 22 of them had no ponderosa pine seedlings or juveniles < 0.5 m in height, and were classified as R0 sites that had experienced no regeneration in the past 20 years (R0: 28.6% of sites; see Pirtel et al. (2021) for height-tree ring relationships; Table 1). Central AZ, southern NM, southern CO, and southern NV had more R0 sites than other locations (Table 1, Table S5). R0 sites had a lower incidence of management (thinning and/or burning) compared to R2 and R3 regeneration densities (Table S5).

R0 sites did not have site characteristics that were significantly different from those of all other regeneration densities (Table S6). However, site characteristics at R0 sites were in some instances significantly different from those of R3 sites. Compared to R3 sites, R0 sites had lower ponderosa pine cone density, higher coarse woody debris cover, and at $p < 0.1$ had lower canopy cover (2-way ANOVA with Tukey's honest significant differences, $p < 0.05$; Table S6).

4.2. Explanatory meteorological and environmental variables for R0 regeneration density

R0 sites were distinguished by meteorological variables associated with higher Ta and greater GDD (Fig. 3). These explanatory variables were most frequently different for R0 sites in the water year and the warm season (April-September; Fig. 3a). Meteorological anomalies were less illustrative, and R0 sites only experienced higher water year GDD 10 °C anomalies compared to those of R1-R3 sites (Figure S2). We observed only small variation in significant meteorological variables for R0 when compared against 20-year, pre-regeneration, and post-regeneration time periods for R1–R3.

R0 sites were distinguished from other regeneration densities by environmental and water balance variables associated with higher soil temperatures in all seasons [Ts: °C], higher cool season ET, more variable VWC and SWA in the water year and cool season, and more negative maximum SWP in summer (Fig. 4).

4.3. Top explanatory variables and SWUS assessment for R0 regeneration density

The top meteorological variable and model for R0 was water year GDD 10 °C (Sens. = 0.864, Spec. = 0.891, BA = 0.877; Table 2a). The top water balance variable model for R0 included the standard deviation of October-March daily volumetric soil moisture (σVWC) from 20–40 cm

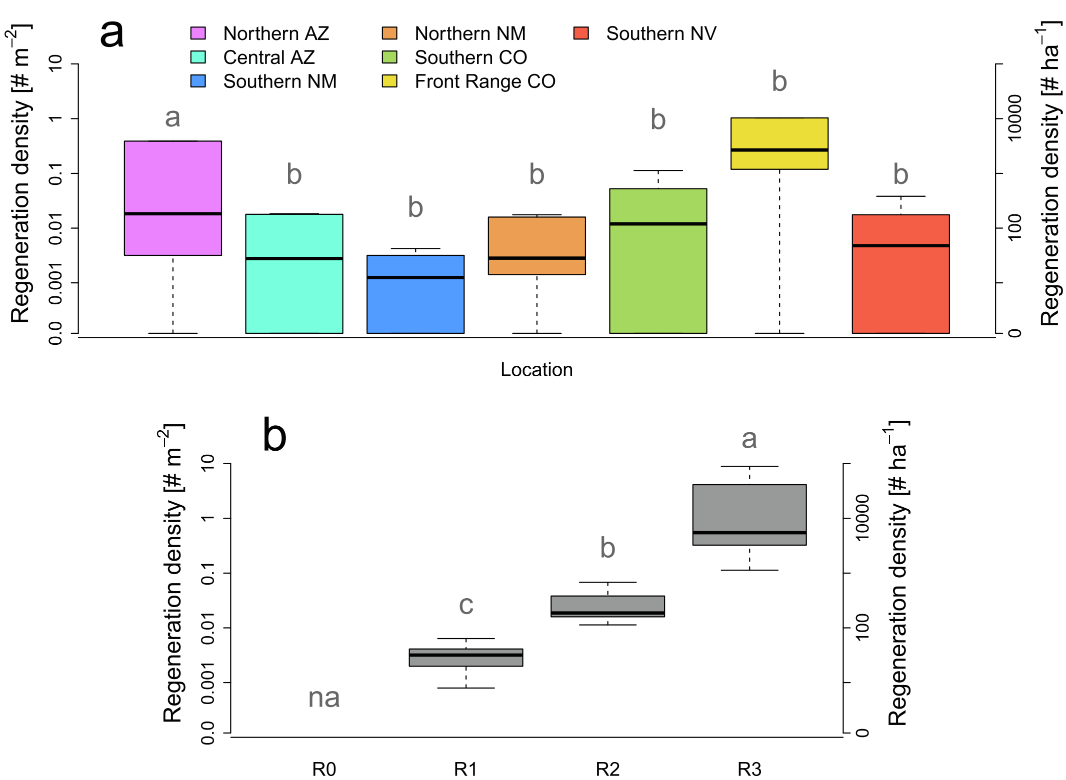

Fig. 2. Boxplots illustrating variation in juvenile ponderosa pine regeneration density [# m^{-2}, # ha^{-1}] between sites in differing regional locations (Panel a), and between different regeneration density classifications (R0–R3; Panel b). Due to wide variation in regeneration density, many sites with no regeneration, and low degrees of freedom for Front Range CO, only Northern AZ had significantly different regeneration density from other study locations (generalized linear models; $p < 0.05$). We found significant differences in regeneration density among R0-R3 classifications (generalized linear models; $p < 0.05$).

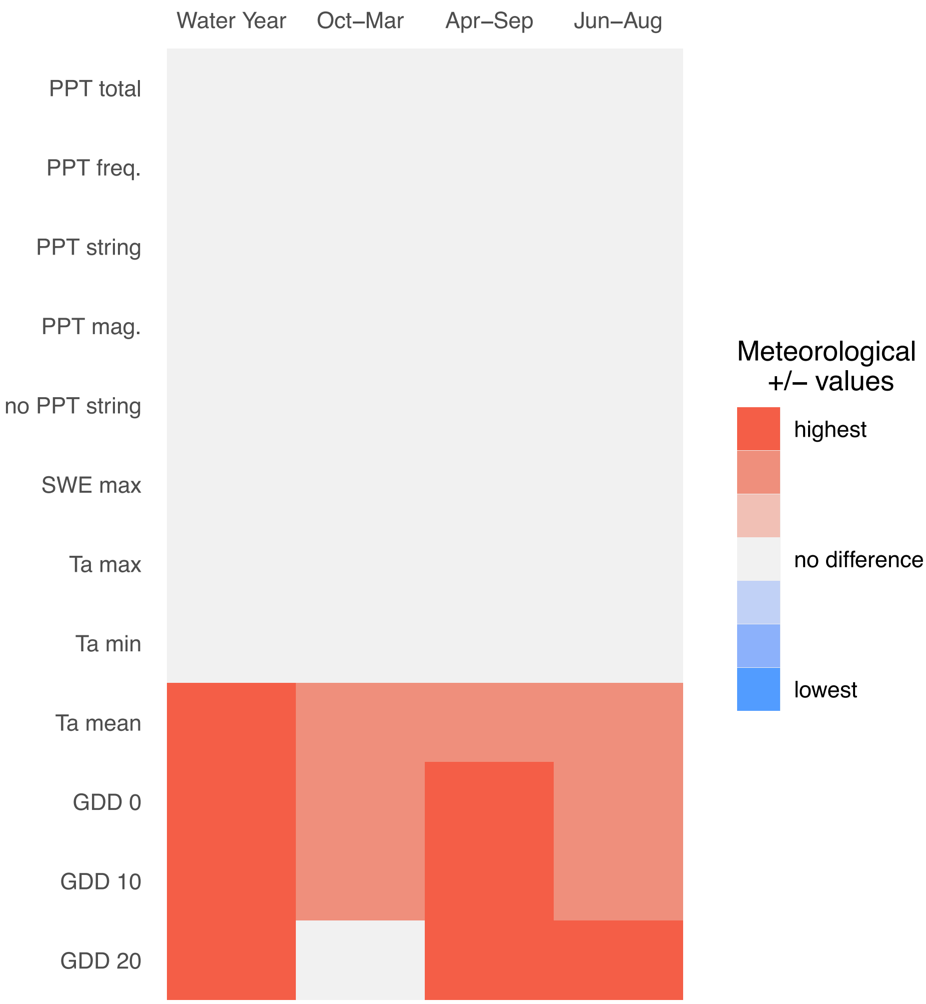

Fig. 3. Visualization of significant differences in meteorological variables for sites with no regeneration [R0: 0.0 m^{-2}, 0.0 ha^{-1}]. The colors in each panel represent a score for each variable, totaled across 3 analysis windows: (1) a 20-year window prior to sampling, (2) a 20-year window prior to sampling at R0 sites compared to a −5 year to +2 year window (pre-regeneration window) surrounding the estimated regeneration year for R1-R3 sites, and (3) a 20-year window prior to sampling at R0 sites compared to a −2 year to +5 year window (post-regeneration window) surrounding the estimated regeneration year for R1-R3 sites. In each analysis we used 2-way ANOVA ($p < 0.05$) to compare each variable across R0, R1, R2 and R3 regeneration levels. To visualize each variable and analysis window, R0 values that were significantly lower than all other values were scored −1, and those that were higher were scored +1. Thus, the highest possible score was +3 and the lowest was −3. A summary of meteorological variables is provided in Table S2.

in the soil profile, water year σVWC from 20–40 cm, and water year maximum Ts from 0–20 cm (Sens. = 1.0, Spec. = 1.0, BA = 1.0; Table 2b). The top meteorological + water balance variable model for R0 included October-March σVWC from 20–40 cm, water year σVWC from 20–40 cm, water year maximum Ts from 0–20 cm, and water year GDD 10 °C (Sens. = 1.0, Spec. = 1.0, BA = 1.0; Table 2c, Fig. 5).

Using partial dependence analysis for the top meteorological and water balance explanatory variables of R0, we evaluated the percentage of months for each management category and each study location that exceeded the boundary value of variables designated as promoting R0, and did the same for variables designated as inhibiting R0 (top model in Fig. 5, other top variables in Figure S3). We found small differences in the promotion and inhibition of R0 by management category – sites with no management had slightly higher than average promotion of R0, sites with thinning had near-average promotion and inhibition, and sites with burning had slightly lower than average promotion of R0 by explanatory variables (Fig. 6). Central AZ and southern NM – the two lowest latitude locations – both had a higher than average R0, higher than average promotion of R0, and much lower than average inhibition of R0 (Fig. 7). In contrast, southern CO and southern Nevada – located at higher latitudes – also had higher than average R0, but with greater variation in promotion and inhibition variables (Fig. 7). Northern AZ, northern NM, and Front Range CO had lower than average R0, underscored by both lower than average promotion of R0 and greater than average inhibition of R0 (Fig. 7).

5. Discussion

A small body of research has explored the problem of natural regeneration failure in undisturbed/lightly disturbed ponderosa pine forests (White, 1985; Kolb et al., 2020; Minott and Kolb, 2020), and has suggested regeneration failure may expand as a result of climate change (Petrie et al., 2017). We found that regeneration failure of ponderosa pine over the past 20 years is widespread across the SWUS. Although sites with regeneration failure were less likely to have experienced management interventions, we found that regeneration failure was most strongly influenced by meteorological and environmental conditions – sustained high air and soil temperatures (heat loading), loss of cool season climate characteristics (i.e., a cool-season transition towards higher GDD and higher soil moisture variability), and high soil moisture variability in both the warm season and cool season. Heat loading has also been identified as an important factor shaping ponderosa pine recruitment in post-wildfire environments, the success of which occurs at a lower rate than the less disturbed forests of our study (Davis et al., 2023). Although the time period of these regeneration failures coincides with sustained regional drought conditions (Cayan et al., 2010; Seager and Ting, 2017), making it difficult to determine if climate-driven pressure on regeneration could be alleviated if drought conditions improve, they nonetheless illustrate the current scale of regeneration failure and its threat to forest persistence. Climate change projections for temperature and moisture availability in the SWUS are interchangeable with the moisture and temperature conditions that distinguish R0 sites (Cayan et al., 2010; Jones and Gutzler, 2016; Bradford et al., 2020), and there is considerable risk for regeneration failure to intensify in the

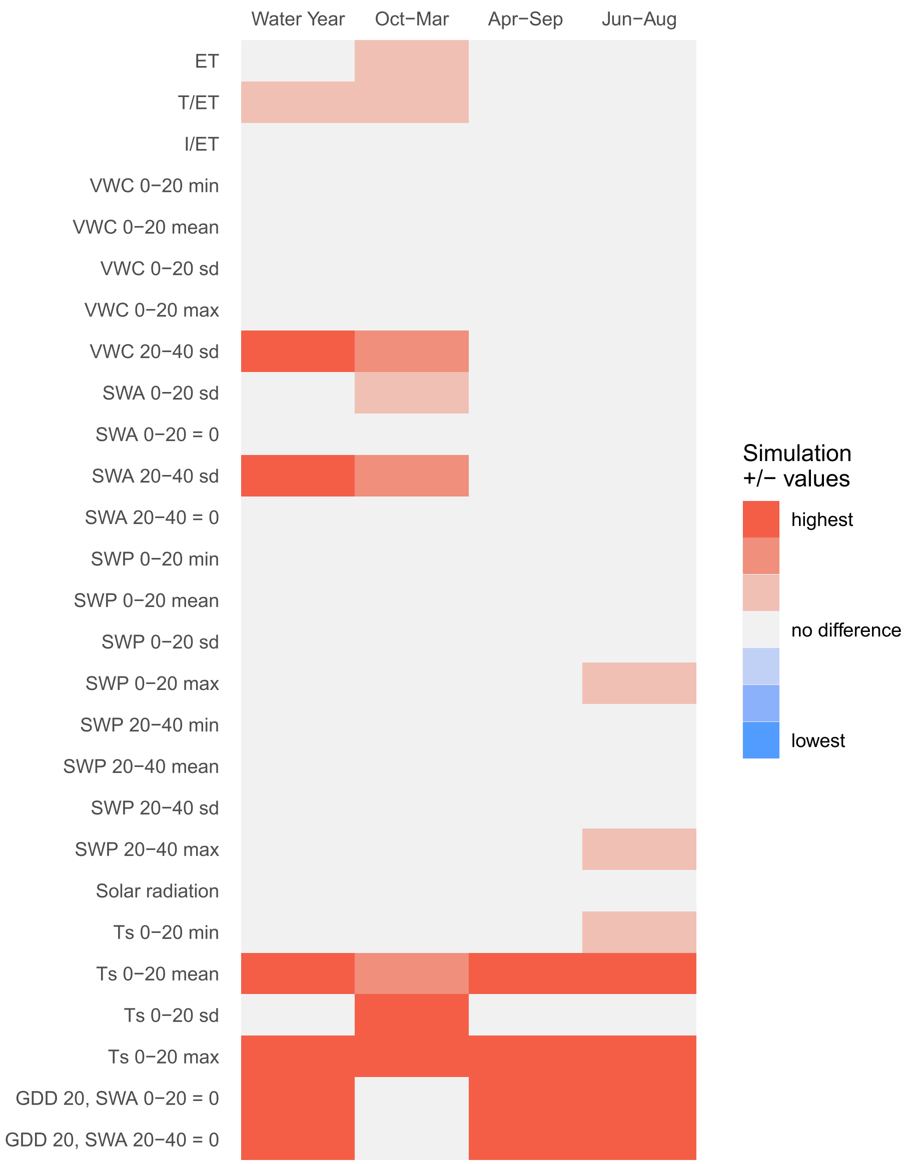

Fig. 4. Visualization of significant differences in SOILWAT2-simulated variables for sites with no regeneration [R0: 0.0 m^{-2}, 0.0 ha^{-1}]. The colors in each panel represent a score for each variable, totaled across 3 analysis windows: (1) a 20-year window prior to sampling, (2) a 20-year window prior to sampling at R0 sites compared to a −5 year to +2 year window (pre-regeneration window) surrounding the estimated regeneration year for R1-R3 sites, and (3) a 20-year window prior to sampling at R0 sites compared to a −2 year to +5 year window (post-regeneration window) surrounding the estimated regeneration year for R1-R3 sites. In each analysis we used 2-way ANOVA ($p < 0.05$) to compare each variable across R0, R1, R2 and R3 regeneration levels. To visualize each variable and analysis window, R0 values that were significantly lower than all other values were scored −1, and those that were higher were scored +1. Thus, the highest possible score was +3 and the lowest was −3. For soil water potential, high values are the most negative, whereas the lowest are the least negative. A summary of SOILWAT2 simulations is provided in Table S3.

future. Similar to the North–South gradient of post-wildfire conifer regeneration in the western United States (Davis et al., 2023), we found that locations at lower latitudes (southern NM, central AZ) exhibited more frequent promotion and less frequent inhibition of regeneration failure, suggesting that future climate-driven regeneration declines may expand from southern to northern latitudes in the SWUS. This pattern may be evidenced by higher than average R0 in southern CO and southern NV, although warm season PPT in southern NV is much lower than other locations of the SWUS, and may be a unique pathway to regeneration failure. In a changing climate, regeneration failure is likely to become more severe in less favorable locations and become an emergent problem in more favorable locations, and management interventions that support regeneration may need to be expanded to include undisturbed and lightly disturbed forests. Natural regeneration failure in undisturbed and lightly disturbed ponderosa pine forests is no longer a plausible threat to forest persistence, it is an active and widespread threat that is poised to increase in scale and severity.

5.1. Natural regeneration provides perspective on wildfire and forest management

The conditions distinguishing R0 sites may help to elucidate how the microclimates of severely disturbed sites also promote regeneration failure. Our results agree with much of the wildfire literature that suggests regeneration in these environments is supported by shading and higher soil moisture availability, and is hindered by higher temperatures and soil moisture deficit (Rother and Veblen, 2016; Haffey et al., 2018; Davis et al., 2019; Marsh et al., 2022; Stevens-Rumann et al., 2022). Although post-wildfire regeneration may be influenced by multiple factors, one of the pathways to successful regeneration is minimizing heat loading and moisture stress in the warm season. This may be realized through multiple years of favorable climate conditions (Brown and Wu, 2005; League and Veblen, 2006), and it is plausible that greater interannual precipitation variability – if it results in more frequent sustained wet periods – could promote post-wildfire recovery. The other climate and environmental pathway to regeneration success is through sheltered microsites and environmental refuges that are more favorable than the surrounding environment (Owen et al., 2017; Marsh et al., 2022). More concerning is the influence of wildfire on the cool season. Although interactions between canopy cover, topography, and snowpack dynamics are complex, the severe reduction forest canopy cover post-wildfire generally promotes earlier snowmelt and greater risk of seedling death from freezing and frost-heaving (Maxwell et al., 2019; Moeser et al., 2020; Wilson et al., 2021), and likely also leads to earlier

Table 2
Summary of Random Forests determination of the top models and variables identifying ponderosa pine sites with no regeneration [R0: 0.0 m^{-2}, 0.0 ha^{-1}]. Top variable determination included meteorological variables from Daymet (Part a), SOILWAT2-simulated variables (Part b), and combined analysis of the top meteorological + simulated variables (Part c). Values include balanced model accuracy evaluated across the entire dataset using a confusion matrix [*BA* : %], model sensitivity (higher values indicate fewer R0 sites misclassified), model specificity (higher values indicate fewer non-R0 sites misclassified as R0), 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 variable denoting the estimated boundary between R0 and other regeneration densities using partial dependence [*VB*]. Models were ranked based on sensitivity, and included non-correlated variables (Pearson's r < 0.4) with a significant difference between R0 and other regeneration densities (ANOVA and Tukey's honest significant differences; $p < 0.05$).

Rank	Model	BA	Sens.	Spec.	p-value	GI	VB
Part a. Meteorological estimates							
1	[1]Water Year: GDD 10 °C	0.877	0.864	0.891	< $1.0e^{-3}$	24.5	R0 less likely below 700 °C
2	[1]Oct-Mar: GDD 10 °C	0.864	0.818	0.909	< $1.0e^{-3}$	13.4	R0 more likely above 25 °C
	[2]Apr-Sep: GDD 0 °C					11.4	R0 less likely below 2600 °C
3	[1]Oct-Mar: GDD 10 °C	0.850	0.773	0.927	< $1.0e^{-3}$	13.2	R0 more likely above 25 °C
	[2]Apr-Sep: Ta ($\bar{x}$ daily)					11.4	R0 less likely below 14 °C
Part b. SOILWAT2 simulations							
1	[1]Oct-Mar: VWC 20–40 cm ($\bar{\sigma}$ daily)	1.0	1.0	1.0	< $1.0e^{-11}$	11.5	R0 more likely above 0.019 m^3 m^{-3}
	[2]Water Year: VWC 20–40 cm ($\bar{\sigma}$ daily)					10.1	R0 more likely above 0.035 m^3 m^{-3}
	[3]Water Year: Ts 0–20 cm (maximum daily)					9.4	R0 less likely below 15.0 °C
2	[1]Oct-Mar: VWC 20–40 cm ($\bar{\sigma}$ daily)	1.0	1.0	1.0	< $1.0e^{-11}$	12.1	R0 more likely above 0.019 m^3 m^{-3}
	[2]Water Year: VWC 20–40 cm($\bar{\sigma}$ daily)					10.1	R0 more likely above 0.035 m^3 m^{-3}
	[3]Oct-Mar: Ts 0–20 cm ($\bar{\sigma}$ daily)					8.8	R0 more likely above 3.75 °C
Part c. Meteorological + SOILWAT2 top model							
1	[1]Oct-Mar: VWC 20–40 cm ($\bar{\sigma}$ daily)	1.0	1.0	1.0	< $1.0e^{-11}$	10.8	R0 more likely above 0.019 m^3 m^{-3}
	[2]Water Year: VWC 20–40 cm ($\bar{\sigma}$ daily)					8.2	R0 more likely above 0.035 m^3 m^{-3}
	[3]Water Year: Ts 0–20 cm (maximum daily)					6.6	R0 less likely below 15.0 °C
	[4]Water Year: GDD 10 °C					5.2	R0 less likely below 700 °C

soil moisture depletion later in the year (Koehn et al., 2021). It is unclear to what degree microclimate and environmental refuges can ameliorate cool season impacts, which differ markedly from the conditions limiting regeneration in less disturbed forests.

Forest managers are tasked with developing interventions that minimize wildfire hazard, minimize competition among trees, and support the health of adult trees. Many forest interventions reduce forest basal area to increase availability of deeper, cool season-derived soil moisture for adult trees (Bigelow et al., 2011; Kerhoulas et al., 2013; Bradford and Bell, 2017; Belmonte et al., 2022), and it is expected that basal area reductions will support regeneration and seedling growth by increasing access to both soil moisture and light (Bigelow et al., 2011; Flathers et al., 2016). High cone production in thinned forests suggests that healthy adult trees are more likely to produce large regeneration pulses when favorable conditions occur (Flathers et al., 2016). However, low canopy cover may limit regeneration by increasing near-surface temperatures and evapotranspiration (Kolb and Robberecht, 1996; Gray et al., 2005; Minott and Kolb, 2020; Marsh et al., 2022). Together, these findings allude to specific ranges of basal area and canopy cover that can both promote adult tree health and support natural regeneration. Due to differences in solar radiation, precipitation, and temperature among our SWUS study locations, it is likely that these basal area conditions are location- and site-specific, and may require future evaluation to account for topography and edaphic properties, human-grown versus natural seedlings, and climate change.

Our study reinforces that effective management for regeneration may need to be customized at sub-regional scales. The managed sites of our study had lower incidence of regeneration failure compared to unmanaged sites, but only exhibited small differences in variables promoting or inhibiting regeneration failure. It is possible that management may influence regeneration through the climate-adjusting properties of over- and understory forest characteristics (light, soil moisture, temperature), or through different pathways (soil nutrients, soil chemistry, soil parent material, biological associations; Remke et al., 2020; Puhlick et al., 2021; Marsh et al., 2022) and over different timescales (Wasserman et al., 2022). Although we found that variation in soil properties, soil nutrients, and soil parent material were difficult to link to regeneration across our regional study area, their variation has been found to exert a meaningful influence on regeneration in other studies (Puhlick et al., 2021; Wasserman et al., 2022). From the perspective of climate and environment, we postulate that the potential positive effects of management on regeneration are not realized uniformly across heterogeneous climates and landscape settings, such that management pathways to regeneration success and failure are realized at the location or even stand scale. Thus, while a management action may be beneficial in aggregate, its effects on the environment where regeneration occurs may not be uniform across locations. In a rapidly changing climate that is

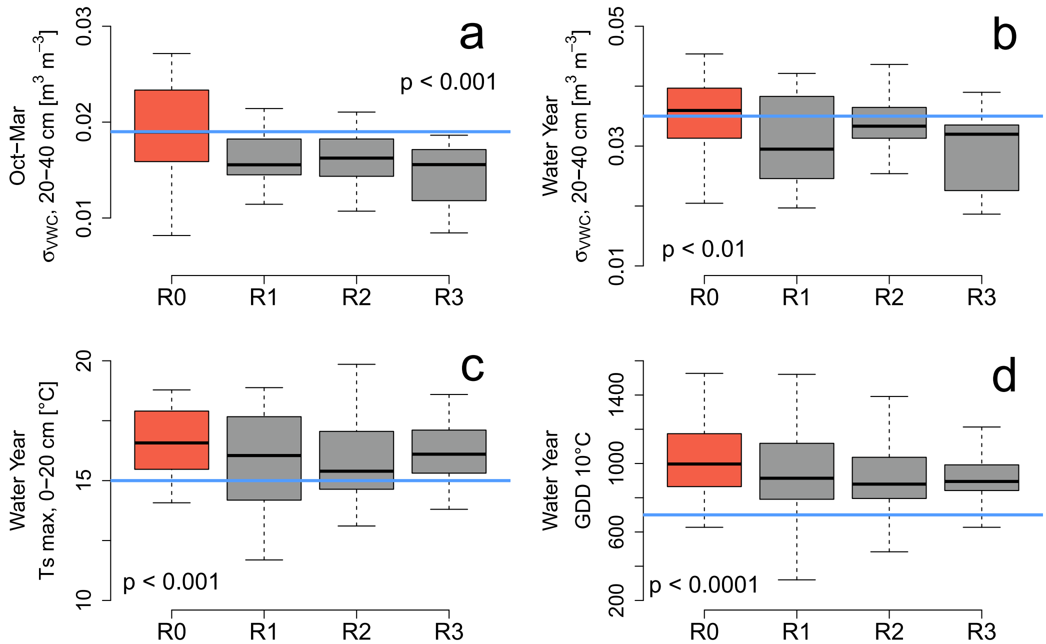

Fig. 5. Summary of meteorological and SOILWAT2-simulated variables differentiating sites with no regeneration [R0: 0.0 m^{-2}, 0.0 ha^{-1}] from sites with all other regeneration densities. Variables include October-March standard deviation (σ) of average daily volumetric soil moisture [VWC: m^3 m^{-3}] from 20–40 cm in the soil profile (Panel a), water year σ of average daily VWC from 20–40 cm in the soil profile (Panel b), water year average maximum daily Ts from 0–20 cm in the soil profile (Panel c), and water year growing degree days calculated using a base temperature of 10 °C [GDD: °C] (Panel d). In each panel, the p-value designates the significance level of R0 values from all other regeneration levels (R1-R3; 2-way ANOVA, Tukey's honest significant differences). The horizontal blue line in each panel designates the boundary of each variable used to differentiate R0 from R1-R3 using partial dependence from a random forests analysis (see Table 2 for an explanation of boundary values). Additional explanatory variables not included in the top model are illustrated in Figure S3.

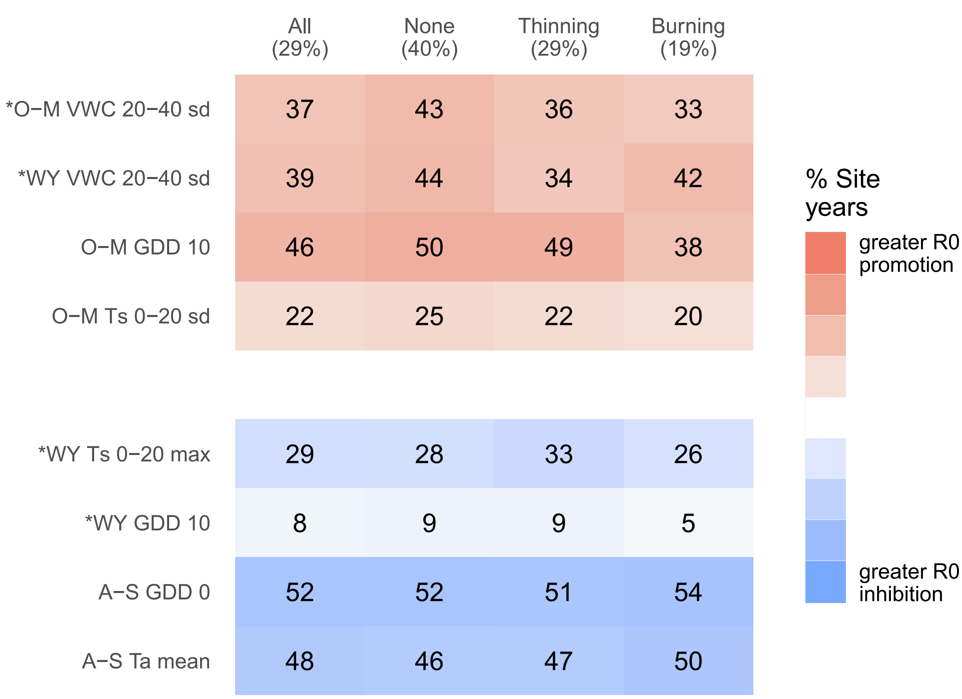

Fig. 6. Evaluation of explanatory meteorological and SOILWAT2-simulated variables associated with greater promotion or greater inhibition of no regeneration [R0: 0.0 m^{-2}, 0.0 ha^{-1}] for all study sites (All), and for sites experiencing no management (None), understory and/or basal area thinning (Thinning), or any management including understory burning (Burning). Top variables are indicated by a star (*). In each box, the value and color indicate the percentage of years/seasons for 20 years prior to the sampling date (2019 sampling: 1999–2018; 2021 sampling: 2001–2020) exceeding the the boundary value of each variable, used to differentiate R0 from R1-R3 using partial dependence from a random forests analysis (see Table 2 for an explanation of boundary values). The percentage values below each management action indicate the percentage of sites with no regeneration (R0).

poised to increasingly restrict natural regeneration, we propose that the best next steps are to evaluate the long-term trajectories of the key variables promoting and inhibiting regeneration failure, to determine how management interventions can alter the specific near-surface microclimates that influence regeneration, and to evaluate these alterations against interventions that support healthy stands of adult trees and other ecosystem services.

5.2. Belowground variability and uncertainty

We found that higher soil moisture variation from 20–40 cm in the soil profile promoted R0. In the SWUS, the rooting depth of 5–15 year old ponderosa pine seedlings is ~40 cm, and the rooting depth of younger 0–3 year old seedlings is ~10–20 cm (Pirtel et al., 2021). In mid-elevation coniferous forests of the SWUS, near surface soil moisture is strongly influenced by precipitation and evaporation throughout the warm season, and is more variable than deeper soil moisture largely

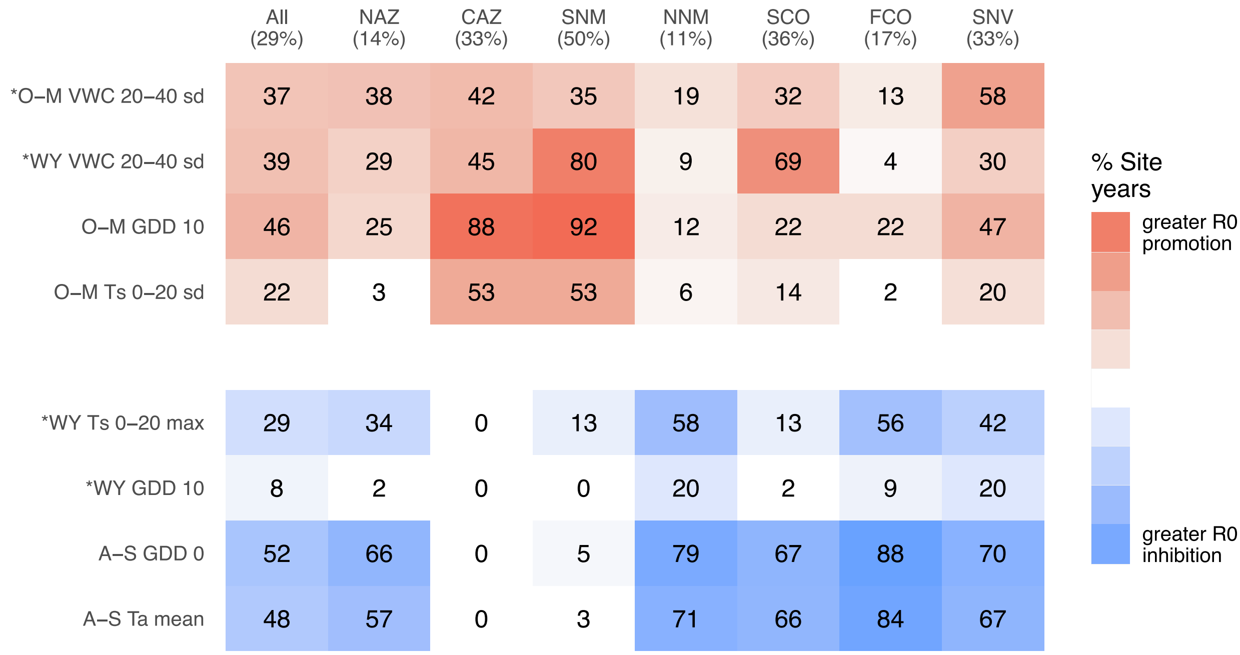

Fig. 7. Evaluation of explanatory meteorological and SOILWAT2-simulated variables associated with greater promotion or greater inhibition of no regeneration [R0: 0.0 m^{-2}, 0.0 ha^{-1}] for all study sites (All), and for sites within different locations of the southwestern US. Top variables are indicated by a star (*). In each box, the value and color indicate the percentage of years/seasons for 20 years prior to the sampling date (2019 sampling: 1999–2018; 2021 sampling: 2001–2020) exceeding the boundary value of each variable, used to differentiate R0 from R1-R3 using partial dependence from a random forests analysis (see Table 2 for an explanation of boundary values). The percentage values below each location indicate the percentage of sites with no regeneration (R0).

derived from cool-season precipitation (Loik et al., 2004; Kerhoulas et al., 2013; Koehn et al., 2021). It is understandable why 20–40 cm was the depth of the explanatory moisture variables in our random forests analyses, because this depth represents water availability at the rooting depth of older seedlings, and dry soils at intermediate depths are indicative of dry shallow soils as well (Koehn et al., 2021). It is less clear, however, why soil moisture variability was the top moisture variable, and not more direct representations of soil water availability.

Linking soil moisture dynamics to ecological change is the focus of a great deal of contemporary research effort (see Dorigo et al. (2011), Bradford et al. (2020), and Llamas et al. (2020) for examples), and simulating soil moisture in computational models requires a direct representation of the processes influencing water balance dynamics. Errors can arise from inaccuracies in model formulations, from physical processes that cannot be fully resolved, and from errors in the measurement, estimation, and averaging of driving variables and site parameters (see Strachan and Daly (2017),Chaney et al. (2019), and Schwinning et al. (2020) for examples). Using our study as a hypothetical example, if 10 consecutive days of soil water potential below −4.0 MPa is a condition that kills ponderosa pine seedlings, small errors in soil porosity parameterizations could result in over- or underrepresentation of regeneration failure in a water balance model, especially across a large number of simulated sites. However, if higher soil moisture variation is a unique characteristic of soil drying, measures of variability may be a general indicator of the occurrence of a regeneration-limiting condition, even when it is not able to be resolved accurately. We postulate that this is the reason soil moisture variability is the top moisture variable in our analyses. This finding may have utility in other research working to resolve the mechanisms of moisture-driven ecological change to ecosystems – measures of variability may offer advantages in indicating the occurrence of conditions and events that are difficult to identify and/or resolve mechanistically.

6. Conclusions

Regeneration failure (R0) threatens the persistence of ponderosa pine forests in the southwestern US (SWUS). Better understanding of the climate and environmental conditions that influence R0 can help to identify threats to the future sustainability of these forests. We characterized and documented natural regeneration at 77 undisturbed ponderosa pine sites in 7 regional locations in the SWUS, and utilized gridded meteorological estimates and computational water balance modeling to elucidate the climate and environmental conditions leading to R0. Almost a third (29%) of sites experienced no natural regeneration (R0) over the past two decades. These R0 sites experienced higher seasonal heat loading, loss of cool season climate, and higher variation in soil moisture compared to sites with regeneration (R1-R3). In a warmer and more variable climate, we can expect increasing heat loading, warmer winters, and enhanced precipitation variability to increase the potential for R0 across the SWUS. Our results suggest that climate-driven impacts to R0 are likely to expand from lower to higher latitudes in the future, and that forest management practices designed to minimize regeneration failures may be successful if they can create canopy structures that combat these changes at the microsite scale. The problem of natural regeneration failure is widespread in undisturbed/lightly disturbed ponderosa pine forests, has great potential for regional expansion, and should be considered alongside wildfire as a major threat to ponderosa pine forest persistence.

CRediT authorship contribution statement

M.D. Petrie: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing - original draft, Writing - review & editing. **R.M. Hubbard:** Conceptualization, Funding acquisition, Methodology, Writing - review & editing. **J.B. Bradford:** Conceptualization, Funding acquisition, Methodology, Writing - review & editing. **T.E. Kolb:** Conceptualization, Methodology, Formal analysis, Writing - review & editing. **A. Noel:** Conceptualization, Writing - review & editing. **D.R. Schlaepfer:** Formal analysis, Software, Writing - review & editing. **M.A. Bowen:** Investigation, Resources, Writing - review & editing. **L.R. Fuller:** Investigation, Resources, Writing - review &

editing. **W.K. Moser:** Investigation, Resources, Writing - review & editing.

Declaration of Competing Interest

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

Data availability

Data and model simulations are published online, are publicly available, and are referenced in the manuscript,

Acknowledgments

This research was supported by grants from the USDA Forest Service, Western Wildlands Environmental Threat Assessment Center (20-JV-11221634–190), and the US Geological Survey Southwest Climate Adaptation Science Center (G20AC00440-01). We would like to acknowledge the contributions of USDA Forest Service personnel towards permitting and site selection, including Gennaro Falco (Santa Fe NF), Matthew Tuten and Jason Lawhon (San Juan NF), Paula Fornwalt and Steven Alton (Manitou EF), and James Hurja, Kathryn Gulley and Deborah MacNeill (Humboldt-Toiyabe NF). We thank UNLV technicians Nikki Pirtel, Shelley Porter, Carolyn Koehn, and Gabriel Rodriguez for field support. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. This research was supported by the USDA Forest Service, Rocky Mountain Research Station.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, athttps://doi.org/10.1016/j.foreco.2023.121208.

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