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Soil properties and climate drive ponderosa pine seedling presence in the southwestern USA

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ABSTRACT

A continual improvement of our understanding about factors that influence tree regeneration is needed to inform landscape-scale restoration efforts across the western USA. This is increasingly important because changing climate and disturbance regimes will influence where restoration efforts should be implemented across landscapes. In this study, we used Forest Inventory and Analysis (FIA) data to model ponderosa pine (*Pinus ponderosa* C. Lawson var. *scopulorum* Engelm.) seedling presence across FIA plots in Arizona and New Mexico, USA. Additionally, we analyzed archived soil samples from FIA plots for percent clay, silt, and sand; samples were collected from the upper 20 cm of the mineral soil. Soil particle size is correlated with soil parent material, which has been shown to influence ponderosa pine regeneration. We used structural equation modeling to determine the relative importance of direct and indirect factors affecting ponderosa pine seedling presence. For the 0–10 cm depth increment of the mineral soil, soils with high inorganic C (carbonate) concentrations, a low percentage of coarse fragments (>2 mm) in the mineral soil, a low percentage of sand in the fine fractions (<2 mm) of the mineral soil, and low average May minimum temperature had the greatest probability of ponderosa pine seedling presence. Average annual precipitation also influenced pine regeneration through its negative correlation with inorganic C concentration. A partial explanation for the latter correlation could be that carbonates in the upper soil horizons leach into lower layers over time in areas with greater precipitation. Inorganic C concentration was also associated with soil parent material and was correlated with the soil cation exchange capacity and several macronutrient concentrations. Overall, our results indicate that soils and climate are key drivers of tree regeneration in the southwestern USA. Other factors such as the forest overstory, including the presence of seed trees, and the herbaceous plant community can also influence ponderosa pine regeneration. However, these factors were not statistically significant in the current study, likely because a small subset of FIA plots were used in the analyses. As soils are collected on additional FIA plots, new models of tree regeneration based on the current structural equation model could be evaluated and refined. Our results also indicate that information about the soil series associated with FIA plots would be useful for modeling tree regeneration, especially because soil series are commonly used by land managers in decision-making processes.

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1. Introduction

Improved predictions of ponderosa pine (*Pinus ponderosa* C. Lawson var. *scopulorum* Engelm.) regeneration are needed to inform landscape-scale restoration efforts across the western United States. For example, predictions of ponderosa pine seedling presence would be useful for planning where to strategically implement silvicultural methods for regenerating ponderosa pine across landscapes (Long et al., 2018). These predictions could also inform decisions about where to plant ponderosa pine in landscapes where high-severity wildfires are becoming more common (Owen et al., 2017; Davis et al., 2019). Prior modeling efforts (Puhlick et al., 2012) used USDA Forest Service, Forest Inventory and Analysis (FIA) data to identify key factors (elevation, temperature, precipitation, overstory basal area, and the presence of a *Muhlenbergia* association) affecting ponderosa pine regeneration in Southwestern ponderosa pine forests which cover millions of hectares of land in Arizona and New Mexico. While soil variables associated with FIA plots were not available at the time, Puhlick et al. (2012) speculated that soil texture was a key driver of ponderosa pine regeneration at the regional scale. In other regions, soil and physiographic variables have been shown to explain much of the variability in plant communities across complex landscapes that contain numerous ecosystem types (Palik et al., 2000). The present study uses particle size analysis recently acquired from archived FIA soil samples and the current FIA soil database to evaluate the influence of soil attributes on ponderosa pine regeneration across the southwestern USA while simultaneously considering climatic drivers. Improving our knowledge of conditions that influence ponderosa pine regeneration will be crucial to planning and implementing management activities, such as prioritizing locations to be naturally regenerated or planted across landscapes, and to provide a framework for how FIA soils data can be used to evaluate ecological processes at regional scales.

Soil texture, which reflects the parent material of soils and the degree of pedogenic development over time, is a principal factor in the arrangement of ecosystem types across the landscape and the types of plants that occur within certain ecosystem types (Abella and Covington, 2006). For example, on the Coconino National Forest in northern Arizona, Goodwin (2004) and Puhlick et al. (2012) found that ponderosa pine regeneration densities were greater on sandy loams and cobbly loams derived from sedimentary parent material than on clay loams derived from basalt parent material. Ponderosa pine seedlings growing on fine-textured soils (i.e., soils with high silt and clay contents) derived from basalt have been shown to be highly susceptible to frost heaving and drought (Haasis, 1923; Schramm, 1958; Heidmann and Thorud, 1976). In a study by Heidmann and King (1992), available soil moisture to ponderosa pine seedlings in a clay loam became limiting when gravimetric water content dropped below 10%. In contrast, available soil moisture did not become limiting to ponderosa pine in a sandy loam until gravimetric water content dropped below 1.5%. In sandy loams, the water potential (i.e., energy needed to pull water from the soil) is less than clay loams; therefore, water is more available to seedlings. In other regions, soil texture has been used to estimate available soil moisture to plants and to predict plant communities across the landscape (Palik et al., 2000).

Soil nutrients also influence tree regeneration establishment and growth, and the relative amounts of soil nutrient stocks and concentrations are often associated with the soil parent material and the percentage of coarse fragments (>2 mm) in the mineral soil. For example, Abella and Covington (2006) found that $CaCO_3$ equivalent was variable but highest on xeric limestone soils where leaching rates of exchangeable base cations were likely lower compared to mesic sites. On coarse-textured soils, the percentage of coarse fragments in the mineral soil can be negatively correlated with tree growth (Childs and Flint, 1990) and forest C stocks (Puhlick et al., 2016), and could also constrain tree regeneration by influencing root growth and nutrient supply. However, for clay loam and loamy clay soils derived from basalt, Pearson (1933) found that areas of stands that were well stocked with ponderosa pine regeneration tended to occur on soils with more gravel and stone. In soils with high amounts of coarse fragments, the fine earth fraction cannot pack as closely to the coarse fragments as it can to itself (Stewart et al., 1970). This creates larger pore spaces in the soil, which increases soil aeration and potentially water availability to seedlings. Haasis (1923) also suggested that greater amounts of organic matter in rocky loam soils causes them to hold greater amounts of water in comparison to stony clay, and gravelly soils.

Pine germination and establishment is highly dependent on local precipitation and temperature conditions (Schubert, 1974; Savage et al., 1996; Stein and Kimberling, 2003), with locally variable summer rains also influencing the distribution of seedling establishment (Pearson, 1950; Schubert, 1974; Kolb et al., 2020). Successful regeneration establishment in areas that receive high precipitation is likely due to increased availability of soil moisture. Flathers et al. (2016) found that high soil water content at a depth of 15–30 cm favored pine survival and growth. Additionally, Nepal et al. (2020) found that water availability to plants up to a depth of 150 cm was positively correlated with pine stocking. Climate may also indirectly influence pine regeneration through effects on overstory structure and herbaceous plant communities (Puhlick et al., 2012). Mortality of overstory ponderosa pine can be caused by drought, which can trigger infestations of bark beetles (*Dendroctonus* sp. and *Ips* sp.). Climate events such as drought can also have a persistent effect on overstory species composition and may reduce herbaceous cover, which can potentially increase soil erosion (Allen and Breshears, 1998; Allen et al., 2002). Drought conditions also increase the likelihood of moderate- to high-severity wildfires, and post-wildfire ponderosa pine regeneration establishment can be limited, even when seed sources are present (Stoddard et al., 2018).

The overall goal of this study was to evaluate the relative importance of the many direct and indirect factors affecting ponderosa pine regeneration across the southwestern USA. Our primary objective was to develop a regional model of ponderosa pine seedling presence that considered the influence of soils, climate, forest structure, and herbaceous understory. We discuss the results in the context of informing ecological restoration strategies at regional scales.

2. Methods

2.1. Study system

The ponderosa pine forest ecosystem spans over 2.3 million hectares of land across uplands in the southwestern USA (O'Brien, 2002, 2003). We conducted our study across forest stands in Arizona and New Mexico with live or dead ponderosa pine trees, or that were part of ecological communities that could include ponderosa pine (see the Data Collection section). Ponderosa pine is associated with numerous forest types, but primarily occurs within the ponderosa pine forest type in montane areas on broad plateaus and at elevations between 2040 and 2680 m (USDA, 1997). Ponderosa pine forms extensive pure stands but often occurs with Gambel oak (*Quercus gambelii*), quaking aspen (*Populus tremuloides*), and alligator juniper (*Juniperus deppeana*). Common plant associations include Arizona fescue (*Festuca arizonica*), mountain muhly (*Muhlenbergia montana*), blue grama (*Bouteloua gracilis*), and screwleaf muhly (*M. virescens*) (USDA, 1997). Ponderosa pine also occurs on a wide variety of soil parent materials including basalt, volcanic cinders, benmoreite (a sodium-rich variety of trachyandesite), mixed igneous rock, limestone, and mixed limestone/sandstone (Shaw et al., 1991). In Arizona and New Mexico, stands with no recent (>50 years) tree cutting or major disturbance (e.g., severe crown fire) typically have high overstory tree densities and altered understory structure due to fire exclusion, past tree cutting, and heavy livestock grazing (Covington and Moore, 1994; Moore et al., 2004; Bakker and Moore, 2007). Increasing forest densities over the last century have reduced pine regeneration rates, but stand conditions are rapidly changing as forest restoration treatments are applied across large landscapes. Given these relatively recent (since ~ the 1990s) management strategies, which include thinning to reduce fuel loads and silvicultural methods to create or maintain uneven-aged stand structure, it is important to understand their effects on pine regeneration.

2.2. Data collection

We used data (USDA, 2015) from the FIA database (USDA, 2014a; O'Connell et al., 2015) that included the forest inventory of permanent plots across forest types and landowners in Arizona and New Mexico. Each plot consisted of four, circular subplots (radius = 7.32 m) spaced 36.6 m apart in a triangular arrangement with one subplot in the center (O'Connell et al., 2015). FIA crews inventoried all trees (live and standing dead) with a diameter at breast height (dbh) ≥ 12.7 cm on forested subplots. Tree species of the forest canopy were also recorded on subplots; the forest canopy included the crowns of trees rooted within or adjacent to subplots (USDA, 2014b). Within each subplot, a circular microplot (radius = 2.07 m) was offset 3.66 m from subplot center for measuring live trees with a dbh ≥ 2.5 and < 12.7 cm. Tree seedlings ≥ 15.2 cm in height and < 2.5 cm in dbh were also inventoried on microplots. Bechtold and Patterson (2005), O'Connell et al. (2015), USDA (2014a), and USDA (2014b) provide more complete details regarding the FIA sample design, plot protocols, and data management.

To obtain a subset of plots that could have ponderosa pine seedlings (based on overstory tree attributes and ecological classifications) and yield an adequate sample size for modeling ponderosa pine regeneration, we restricted our analyses to plots with the following attributes: (1) presence of a live ponderosa pine with a dbh ≥ 2.5 cm or a standing dead ponderosa pine with a dbh ≥ 12.7 cm dbh, (2) presence of ponderosa pine within the forest canopy (USDA, 2014b), (3) having a primary or secondary habitat type within the ponderosa pine series (USDA, 1997), and (4) being classified as a ponderosa pine forest type by FIA field crews (O'Connell et al., 2015). We included plots in our analyses that met one or more of these attributes for any inventory conducted from 2001 and 2015. Additionally, subplots and microplots within plots had to have at least one accessible forest land condition as delineated by FIA field crews (O'Connell et al., 2015). Accessible conditions included portions of plots that could be inventoried safely (i.e., no hazards) and where landowner access was not denied. While our plot selection criteria resulted in some plots without ponderosa pine overstory trees, it is conceivable that overstory pines could have occurred immediately adjacent to FIA subplots in stands with scattered overstory pines. Of the 1,981 plots that met our plot selection criteria: 1,905 plots met attribute number one, 626 plots met attribute number two, 1,219 plots met attribute number 3, and 1,219 plots met attribute number four. Of these 1,981 plots, FIA crews collected forest floor samples on 105 plots and mineral soils on 73 plots. For each inventory of plots, three forest floor samples were collected using a circular sampling frame with a radius of 15.2 cm (USDA, 2011, 2014a). FIA crews also measured the depth of the forest floor and depth to a restrictive layer at these sample locations; a restrictive layer included rock fragments and bedrock that prevented a soil probe from being inserted into the soil and was evaluated to a maximum depth of 51 cm (USDA, 2014b; O'Connell et al., 2015). Mineral soil samples were collected at one location from two depth increments (0–10 cm and 10–20 cm) using an impact-driven soil corer with a 5 cm diameter (USDA, 2011, 2014a).

We used the most recent inventories of seedlings, from 2006 to 2015, to calculate pine seedling presence at the plot level. We evaluated seedling presence at the plot level instead of the subplot level because most of the explanatory variables used in statistical analyses were determined at the plot level. To evaluate the influence of soil properties on the presence of ponderosa pine seedlings, we used data from laboratory analysis conducted on sampled soils (USDA, 2015). For both mineral soil depth increments, soil properties included: total C, total N, inorganic C (carbonate) concentration, the percentage of coarse fragments (≥2 mm) in the mineral soil, soil pH in a 1:1 soil/water suspension, effective cation exchange capacity, and exchangeable Ca^{++}, Mg^{++}, and K^{+} (USDA, 2011, 2014a). For plots that had soil samples collected in multiple years, we calculated the mean value for each soil property by depth increment. For forest floor samples collected from the same plot, we calculated the mean value for soil properties which included forest floor depth, depth to a restrictive layer, soil bulk density, total C, and total N (USDA, 2011, 2014a). A complete list of the forest floor and mineral soil properties evaluated in this study are included in USDA (2014a).

For this study, soil texture was determined using archived soil samples; currently, particle size analysis is not conducted on FIA soil samples as part of standard procedures, which is why information on soil texture is not reported in the FIA database. Of the 73 plots from which mineral soils were collected and that met our study criteria, we located archived samples from the 0–10 cm depth increment for 47 plots (Fig. 1). We also located samples from the 10–20 cm depth increment for 40 plots; many of these samples were from the same plots as the archived samples for the 0–10 cm depth increment. Particle size analysis of forest soils has been traditionally done mechanically, but this method requires ~40 g of mineral soil, is labor intensive, and can yield variable results (Jedari et al., 2020). Because many of the FIA archived samples weighed < 40 g and there were concerns about using all the archived material, particle size analysis was done by laser diffraction (Mastersizer 3000E, Malvern PANalytical Ltd., Malvern, UK). This relatively new method for determining particle size has been used and explained in studies by Di Stefano et al. (2010) and Jedari et al. (2020).

Besides soils, numerous factors that could influence regeneration establishment and recruitment were also evaluated for inclusion in statistical models (Table 1). These factors included elevation, heat load (an index of temperature based on latitude, steepness of slope and aspect about a northeast-southwest line), precipitation, temperature, tree density, basal area, quadratic mean diameter, percentage of the total basal area that was represented by ponderosa pine trees, seed tree presence, *Muhlenbergia* presence, and percent graminoid cover. For each plot, elevation was determined from FIA plot tables. Plot locations were used to derive 1981–2010 climate normals using the Parameter-Elevation Regressions on Independent Slopes Model (PRISM) Data Extractor (PRISM Climate Group, http://www.prism.oregonstate.edu/). PRISM is an interpolation method that uses climate-elevation regression analysis to derive climate values for digital elevation grid cells that have a spatial resolution of 800 m (Daly et al., 2008). Data from weather stations are used in the analysis and assigned weights based on the physiographic similarity of the station to the grid cell. PRISM also weights station data to account for proximity to coastlines, the location of temperature inversions and cold air pools, and measures of terrain complexity (Daly and Bryant, 2013). In regions of the western USA with mountainous areas and large elevation gradients, PRISM has been shown to yield better predictions of climate variables than other spatial climate data sets (Daly et al., 2008). Mean annual precipitation and mean annual temperature had strong correlations with ponderosa pine seedling presence. However, we used average May minimum temperature in statistical models instead of mean annual temperature because ponderosa pine germination and growth rates may be more favorable in areas that have warmer May temperatures (Savage et al., 1996). For each FIA subplot, we used trees ≥ 2.54 cm in dbh to calculate tree density, basal area, quadratic mean diameter, and percent ponderosa pine. For these variables, subplot values were averaged to obtain plot-level values. We used FIA tree data to identify seed trees, which were considered to be open grown, dominate, or co-dominate ponderosa pines with a dbh ≥ 50 cm and having an uncompacted live crown ratio ≥ 30% (Puhlick et al., 2012). We also used FIA vegetation data on species and structure to identify *Muhlenbergia* species and to determine percent graminoid cover. For percent graminoid cover, subplot average values (based on three 1 m^2 quadrats) were averaged to obtain plot-level values. A ponderosa pine seed tree and a *Muhlenbergia* species were

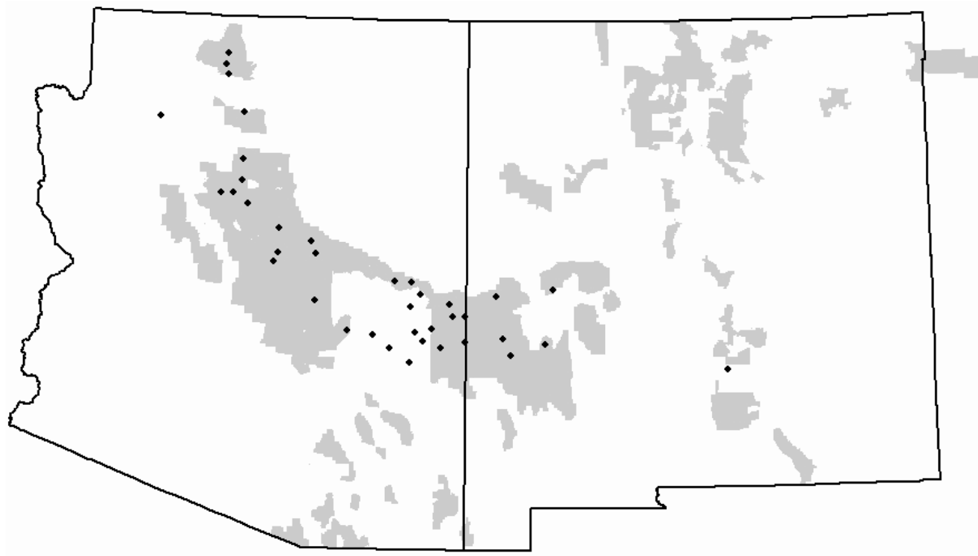

Fig. 1. Approximate forest inventory and analysis plot locations in Arizona and New Mexico, USA used to conduct structural equation modeling. Shaded areas represent National Forest boundaries.

Table 1
Continuous variables considered for inclusion in the structural equation model of ponderosa pine seedling presence. Mineral soil fine fractions (<2 mm) composed of sand, coarse fragments (≥2 mm) in the mineral soil, and mineral soil inorganic C (carbonate) concentration are for the 0–10 cm depth increment. Live tree attributes are for trees ≥ 2.5 cm diameter at breast height.

Variable	Average	SD	Minimum	Maximum
Percent sand (%, 0–100)	69	9	53	85
Coarse fragments > 2 mm (%, 0–100)	27	16	0	60
Depth to a restrictive layer (cm)	15	14	1	51
Forest floor thickness (cm)	3	2	0	7
Carbonate concentration (%, 0–100)	0.23	0.11	0.05	0.58
Elevation (m)	2220	270	1756	2774
Heat load	0.96	0.06	0.73	1.04
Mean annual precipitation (cm)	61	10	44	93
May minimum temperature (degrees C)	2.8	1.8	0.0	7.6
Tree density (trees ha^{-1})	899	761	104	3173
BA (m^2 ha^{-1})	24	11	5	43
Quadratic mean diameter (cm)	23	8	14	55
Ponderosa pine BA (% of total BA)	44	34	0	100
Graminoid cover (%)	8	7	1	27

SD = standard deviation. BA = basal area.

considered present at the plot-level if they were detected on at least one subplot.

2.3. Data analysis

Prior to developing structural equation models, we used binomial generalized linear mixed effects modeling to evaluate the probability of ponderosa pine seedlings on FIA plots. We did not model ponderosa pine seedling density because ponderosa pine seedlings were either absent across microplots associated with a given plot, or the number of ponderosa pine seedlings across microplots almost always summed to one and did not exceed three for the plots used in this study. Because most seedling counts were zero or one, binomial modeling was more appropriate for this study. We evaluated all the explanatory variables and their interactions with other variables for inclusion in the binomial models as fixed effects. We also considered the inclusion of administrative unit (i.e., specific national forests and a classification for private lands) as a random effect in the models to account for variation in regeneration probability among sites that was not attributable to the fixed effects. Separate models were developed using soil properties from the forest floor, 0–10 cm depth increment of the mineral soil, and 10–20 cm depth increment of the mineral soil. We considered a single model with data from the forest floor and both mineral soil depth increments but data for all three groups were not always available for the same plot. Plots with extremely high values for inorganic C concentration in the mineral soil and plots on silt loam soils were excluded from analyses; only two plots occurred on silt loam soils. We also excluded plots without values for inorganic C concentration. For modeling ponderosa pine presence using soil properties from the 0–10 and 10–20 cm depth increment of the mineral soil, this reduced the number of plots to 38 and 30 plots, respectively. Correlated explanatory variables were not used in the same model and we assessed collinearity through bivariate plots, correlation coefficients, and variance inflation factors (VIF). If two or more explanatory variables were highly correlated (our standard was $r \geq 0.7$), we only included the explanatory variable that was the most strongly correlated with pine presence. Additionally, if some the explanatory variables had VIF values > 3, we removed the variable with the highest VIF, recalculated the VIF values, and repeated the process until all variables had VIF values < 3 (Zuur et al., 2009). We determined the optimal models in terms of fixed effects based on an evaluation of the z-statistics associated with model parameters and analysis of deviance tests (Zuur et al., 2009). We used the glm function in the stats package and the glmer function in the lme4 package in R (R Development Core Team, 2014) to fit the models. Akaike's Information Criteria (AIC) (Akaike, 1972) suggested that inclusion of the administrative unit random effect did not result in improved models, so the random effect was dropped from the models.

We performed structural equation modeling (SEM) using data associated with the 0–10 cm depth increment of the mineral soil because preliminary analyses showed that variables from this depth increment explained more variation in ponderosa pine seedling presence than variables associated with the forest floor and 10–20 cm depth increment. We used the psem function in the piecewise package (Lefcheck, 2016) in R (R Development Core Team, 2014) to conduct the analysis. Piecewise SEM can incorporate a wide variety of model structures, distributions, and assumptions in a single causal network for simultaneously testing multiple hypotheses (Lefcheck, 2016). We used tests of directed separation to evaluate whether the model structure fit the observed data. Good-fitting models yield *P*-values > 0.05. We also used tests of directed separation to identify missing pathways, and pathways were added to the model only if they were theoretically justified. We considered variables for inclusion in the model that were not correlated with pine seedling presence but that we hypothesized influenced other predictors. For example, elevation was not significantly correlated with pine seedling presence, but it was correlated with the climate variables. Hence, we included it in the model because of its indirect effect on pine seedling presence mediated through the climate variables. The piecewise SEM included four component models of the following response variables: ponderosa pine presence, mean annual precipitation, average May minimum temperature, and inorganic C concentration. We used the gls function and the corRatio function in the nlme package (Pinheiro et al., 2014) in R (R Development Core Team, 2014) to fit generalized linear models of the latter three response variables and to account for spatial dependence, which was detected in variograms of the residuals (these models are referred to as gaussian models in Table 2). The values of each response variable were normally distributed and their relationships with the explanatory variables were linear. The frequency distributions of response variable values were assessed using histograms and linear relationships were evaluated using bivariate plots and correlation coefficients. We also included in the piecewise SEM the optimal binomial model of ponderosa pine presence described in the preliminary analysis and in Table 2. Pathways from the percentage of coarse fragments (>2 mm) in the mineral soil, the percentage of sand (0.05–2.0 mm) in the fine fraction of the mineral soil, and average May minimum temperature to ponderosa pine seedling presence had *P*-values of 0.073, 0.069, and 0.064 (Table 2). We retained these pathways in the final SEM because our interest was more in obtaining a good fitting structural equation model rather than only retaining 'significant' paths. Finally, we presumed that the relationship between soil texture and inorganic C concentration was not causal and unidirectional, but rather as being driven by underlying drivers such as climate and parent material which influence pedogenesis and thus both inorganic C and texture. Hence we modeled the relationship between these variables as correlated error (Lefcheck, 2016).

3. Results

Ponderosa pine seedlings were present on 29% of the plots ($n = 38$) for which particle size analysis was performed on archived mineral soil samples from the 0–10 cm depth increment. For the 0–10 cm depth increment of the mineral soil, the best model of ponderosa pine presence included soil inorganic C (carbonate) concentration, percentage of coarse fragments in the mineral soil, percentage of sand in the fine fraction of the mineral soil, and average May minimum temperature (Table 2; the parameter estimate, standard error, and *P*-value for the intercept of the binomial model were 6.225, 3.935, and 0.114, respectively). While the *P*-values associated with the parameter estimates for some of these variables were > 0.05 (Table 2), analysis of deviance tests suggested that the variables be retained in the model. These variables explained 35.7% of the deviance in ponderosa pine presence. The model indicated that soils with high carbonate concentrations, low percentage of coarse fragments, low percentage of sand in the fine fraction of the mineral soil, and low average May minimum temperatures had a greater probability of ponderosa pine seedling presence (Fig. 2). For instance, while holding other explanatory variables in the model constant at their mean values, a soil with 55% sand was associated with a 47% probability of ponderosa pine seedling presence versus a soil with 80% sand which exhibited a 5% probability of ponderosa pine seedling presence. Three of the 38 plots used to model ponderosa pine seedling presence had no overstory ponderosa pine trees but included other overstory tree species (Table 1). *Muhlenbergia* species and ponderosa pine seed trees were present on 26% and 32% of the 38 plots, respectively. However, live tree and herbaceous explanatory variables were not statistically significant in the final model of ponderosa pine seedling presence. Also, the correlation between the percentage of sand in the fine fraction of the mineral soil and the percentage of coarse fragments was low ($r = -0.03$).

Many of the explanatory variables in the model of ponderosa pine presence were correlated with other variables in the system. Average May minimum temperature was negatively correlated with elevation ($r = -0.71$), with low elevations tending to have high average May minimum temperatures. For the 0–10 cm depth increment of the mineral soil, carbonate concentration was positively correlated with the percentage of sand in the fine fraction of the mineral soil ($r = 0.32$), total C ($r = 0.35$), total N ($r = 0.40$), soil pH ($r = 0.53$), effective cation exchange capacity ($r = 0.55$), and exchangeable K ($r = 0.46$), Mg ($r = 0.49$), and Ca ($r = 0.53$). The percentage of coarse fragments in the mineral soil had low correlations ($r < 0.30$) with other soil variables. The percentage of sand in the fine fraction of the mineral soil was positively correlated with total C ($r = 0.39$), total N ($r = 0.38$), soil pH ($r = 0.41$), effective cation exchange capacity ($r = 0.37$), and exchangeable K ($r = 0.34$) and Ca ($r = 0.36$).

Soil variables from the 10–20 cm depth increment of the mineral soil and that were from the 30 plots that had data on soil particle size were not statistically significant predictors of ponderosa pine seedling presence. However, when using all plots where FIA crews collected mineral soils ($n = 73$), we found that the probability of ponderosa pine seedling presence was greater on soils with high carbonate concentrations. Carbonate concentration of the 10–20 cm depth increment explained 7.7% of the deviance in ponderosa pine presence. For this model, the parameter estimates and standard errors (in parentheses) for the intercept and slope were – 2.317 (0.673) and 6.038 (2.549), respectively. For the 105 plots where crews recorded forest floor depths while collecting soil samples, the depth of the forest floor and depth to a restrictive layer were not statistically significant predictors of ponderosa pine seedling presence. For 80 of these plots with complete soil physical and chemical data, forest floor bulk density, total C, total N, and C/N ratio were not significant predictors of pine seedling presence.

The initial SEM included all the pathways shown in Fig. 3 except for the pathway from mean annual precipitation to carbonate concentration. While the initial model fit the data well (Fisher's C = 18.481, df = 18, $P = 0.424$), the addition of a pathway from mean annual precipitation to carbonate concentration was included based on the theoretically justified effect of precipitation on mineral soil carbonate concentration. The addition of this pathway resulted in a model that showed good consistency with the data (Fisher's C = 20.947, df = 20, $P = 0.4$) and explained 50% of the deviance in ponderosa pine seedling presence. This final model indicated that the probability of ponderosa pine seedling presence was highest where (1) soil carbonate concentration was highest, (2) the percentage of coarse fragments in the mineral soil was lowest, (3) the percentage of sand in the fine fraction of the mineral soil was lowest, and (4) average May minimum temperature was lowest. Mean annual precipitation had a negative indirect effect on ponderosa pine seedling presence mediated through soil carbonate

Table 2
Parameter estimates, standard errors (SE), and *P*-values for pathways in the final structural equation model (SEM). Single-headed arrows point from explanatory to response variables and two-headed arrows present correlated error. The piecewise SEM included four component models of the following response variables: ponderosa pine presence, mean annual precipitation, average May minimum temperature, and inorganic C concentration.

Pathway	Estimate	SE	*P*-value
Pathways related to the binomial model			
Pine presence ← Carbonates	14.6830	5.6506	0.0094
Pine presence ← Coarse fragments	–0.0624	0.0348	0.0730
Pine presence ← Percent sand	–0.1119	0.0615	0.0690
Pine presence ← Temperature	–0.7020	0.3789	0.0639
Pathways related to Gaussian models			
Temperature ← Elevation	–0.0034	0.0001	0.0008
Precipitation ← Elevation	0.3579	0.0518	<0.0001
Carbonates ← Precipitation	–0.0004	<0.0001	0.0111
Correlated error			
Carbonates ↔ Percent sand	0.3244	0.3244	0.0251

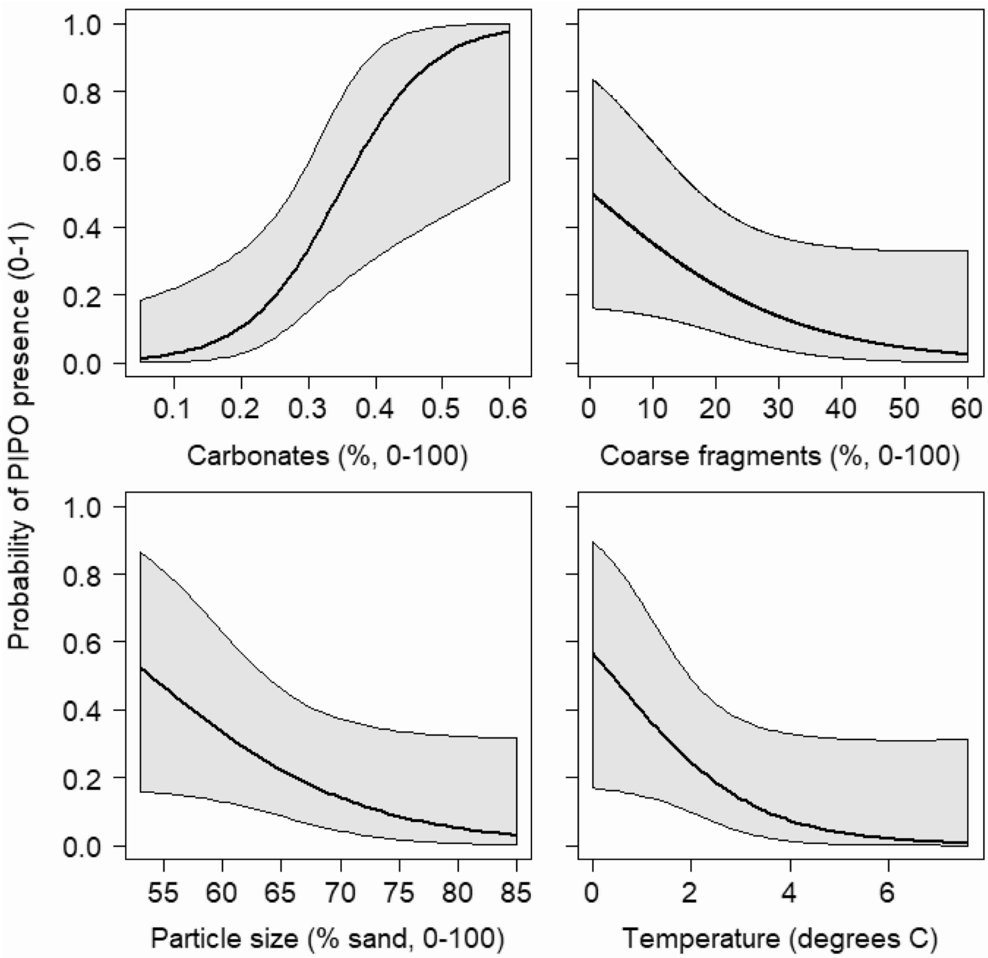

Fig. 2. Predicted probabilities (0–1; thick black line) and 95% confidence interval (gray shading) of ponderosa pine seedling presence on Forest Inventory and Analysis plots while holding other explanatory variables constant at their mean values [inorganic C (carbonate) concentration (%, 0–100) = 0.23%, coarse fragments (≥2 mm) in the mineral soil (%, 0–100) = 27%, fine fractions (<2 mm) composed of sand (%, 0–100) = 69%], average May minimum temperature (2.8 degrees C). The mineral soil variables are for the 0–10 cm depth increment.

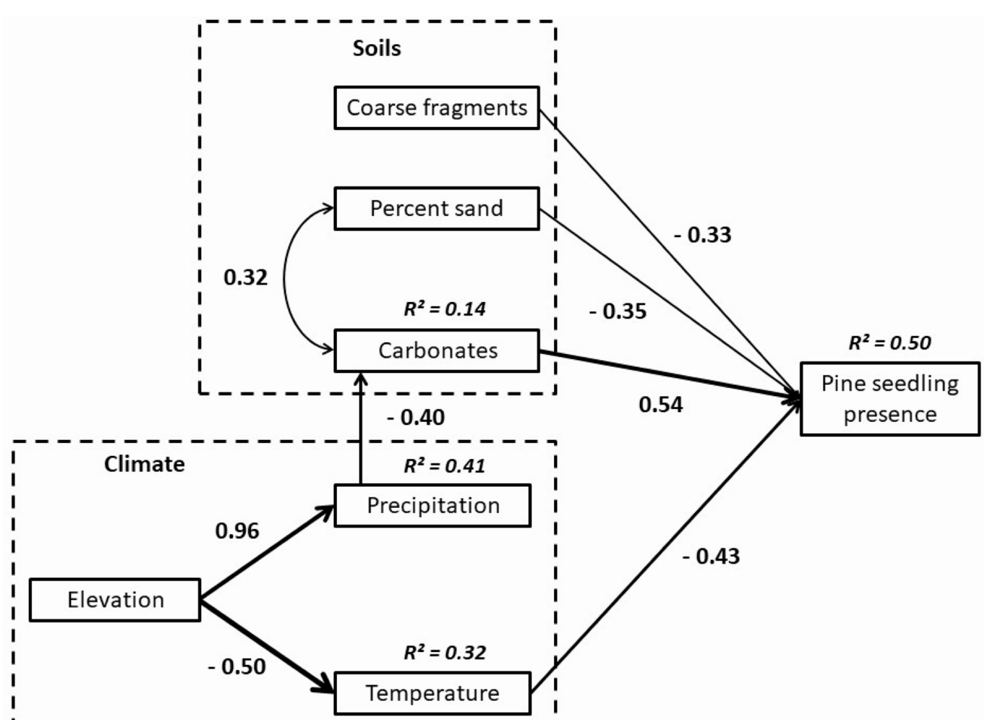

Fig. 3. Final structural equation model (Fisher's C = 20.947, df = 20, $P = 0.4$) with standardized path coefficients (range from −1 to 1).

concentration. Elevation had a net positive relationship with ponderosa pine seedling presence mediated through two pathways: one through average May minimum temperature and another through mean annual precipitation and soil carbonate concentration.

4. Discussion

4.1. Key findings

Our study used a modeling approach that simultaneously considered the influence of numerous factors on ponderosa pine regeneration, which suggested that elevation, climate, and soils were key regional drivers of ponderosa pine seedling presence across forests of Arizona and New Mexico. Areas that received high precipitation had low soil carbonate concentrations, which may indicate that carbonates were leached from the upper soil horizons in areas with greater precipitation over time. Carbonates in xeric limestone soils can be greater than those in soils on mesic sites (Abella and Covington, 2006), which may affect the amount of nutrients that are available for pine establishment. For instance, in the current study, carbonate concentration was correlated with other soil variables such as total N and exchangeable K, Mg, and Ca. One must also consider the indirect effect that elevation had on ponderosa pine seedling presence, which was partially mediated through precipitation. Our results indicated that areas that received high precipitation and had low May minimum temperatures were associated with high elevation sites. High elevation sites had a greater probability of ponderosa pine seedling presence than low elevation sites. For plots used to develop the SEM, the median value for elevation was 2217 m and 82% of plots with ponderosa pine seedlings occurred at elevations above this median value. This could be related to marginal precipitation and temperature conditions for ponderosa pine establishment at woodland-forest ecotone and low-elevation forest sites, and these conditions could be accentuated with severe droughts and warming temperatures (Minott and Kolb, 2020). After high-severity wildfires, Haffey et al. (2018) also found that low-elevation, xeric sites were more limiting to conifer regeneration than high-elevation, mesic sites.

The greater probably of ponderosa pine seedling presence on soils with high carbonate concentrations was likely associated with soil parent material and the correlation of carbonate concentration with other soil properties. For example, we identified soils for plots with particle size data to series or subgroups using plot coordinates in the public FIA database, Natural Resource Conversation Service soil surveys, and the Terrestrial Ecological Unit Inventory for the Southwestern region (USDA, 2019). Soils with high (>0.3%) carbonate concentrations included the Blamer, Hogg, Pocomate, and Pinntank series, which are primarily derived from limestone, cherty limestone, shale, or sandstone. These results are in agreement with research that has shown that ponderosa pine regeneration densities are typically greater on soils derived from sedimentary parent material than on soils derived from basalt parent material (Ffolliott and Baker, 1977; Goodwin, 2004; Puhlick et al., 2012). Furthermore, carbonate concentration was positively correlated with effective cation exchange capacity and several macronutrient concentrations, which were likely beneficial to pine establishment and growth. While soil pH was also positively correlated with carbonate concentration, soils derived from sandstone can have lower pH values than soils derived from limestone, and pine seedling densities can be high on both parent materials (Puhlick et al., 2012). The wide range of soil pH values for the plots of this study with particle size analysis (5.5–7.9) was similar to that reported by Pearson (1950) and Schubert (1974) for highly productive sites with pine (4.5–7.5), which suggests that ponderosa pine may be less sensitive to pH than other factors in the system.

Our results indicated that soils with a high percentage of sand in the fine fraction (<2 mm) of the mineral soil were negatively correlated with ponderosa pine seedling presence. This finding may seem counterintuitive because fine-textured soils derived from basalt parent material typically have lower ponderosa pine regeneration densities than coarse-textured soils derived from sedimentary parent material (Ffolliott and Baker, 1977; Goodwin, 2004; Puhlick et al., 2012). However, the plots of the present study had sand percentages as high as 70–85%, which are less favorable for tree growth than medium-textured, loam soils (Schubert, 1974). Using the results from the particle size analysis and the USDA soil triangle, the texture of the soils of our study are loamy sand and sandy loam. On the Coconino National Forest, Puhlick et al. (2012) found that basalt-derived soils contained an average of 21% clay and 32% sand, while sedimentary-derived soils contained an average of 13% clay and 50% sand. Likewise, Goodwin (2004) found basalt-derived soils contained an average of 20% clay and 46% sand while limestone soils contained an average of 20% clay and 53% sand. The sand percentages of the soils in the present study are similar to those found by Abella and Covington (2006) for cinder and limestone ecosystems with sandy loam soils. The high sand percentages of the soils of this study could also be attributed to methodologies used to infer soil particle size. The other studies mentioned used traditional methods to infer soil particle sizes (i.e., hydrometer method), while the present study used laser diffraction. However, both methods can yield similar sand percentages (the particle size used in the SEM), while the hydrometer method tends to yield greater clay percentages compared with laser diffraction analysis (Di Stefano et al., 2010).

The relative volume of coarse fragments in the mineral soil was negatively correlated with ponderosa pine presence. A high percentage of coarse fragments in the mineral soil can limit biomass production, and potentially seedling establishment, by reducing the volume of the mineral soil fine fractions that could in turn reduce the available nutrient supply (Childs and Flint, 1990; Poesen and Lavee, 1994). However, this assumes that the concentrations of available nutrients such as N, P, Ca, Mg, and K in the fine fraction of the mineral soil are not significantly influenced by coarse fragment content. This may not always be the case. For example, some studies have shown that C and essential nutrients become more concentrated in the fine fraction of the mineral soil as coarse fragment content increases (Childs and Flint, 1990; Schaetzl, 1991). However, we did not find any significant correlations between the percentage of coarse fragments in the mineral soil and nutrient concentrations. A high percentage of coarse fragments in the mineral soil may have also reduced the volume of the mineral soil fine fractions that were necessary for adequate establishment and growth of root systems. Abella and Covington (2006) found that ponderosa pine growth rates were greater in mesic basalt ecosystems than rocky or xeric basalt ecosystems, partially because mesic basalt ecosystems had fewer coarse fragments in the mineral soil which increased the volume of the soil for roots to be established. Haasis (1923) noted that soil texture and coarse fragments influenced the depth of ponderosa pine seedling rooting and lateral branching. Specifically, stony clay and gravelly soils supported seedlings with deeper rooting but less lateral branching than seedlings on rocky loam soils, and shallower rooting but more lateral branching than seedlings on clay soils. Deeper rooting and more lateral branching may provide more anchorage and minimize seedling mortality due to frost heaving. Haasis (1923) also suggested that high amounts of organic matter in rocky loam soils causes them to hold large amounts of water in comparison to stony clay and gravelly soils. In our study, soils were coarse-textured and higher percentages of coarse fragments in these soils could have increased the infiltration rates of water by increasing large pore spaces, thereby making water less available to seedlings. This could further explain the negative relationship between the percentage of coarse fragments in the mineral soil and ponderosa pine seedling presence on coarse-textured soils.

4.2. Study limitations

While we were able to identify numerous factors that influenced ponderosa pine regeneration, this study has several limitations. First, the sample size of FIA plots used to develop the SEM was relatively small (*n*

= 38). In Arizona and New Mexico, a total of 392 plots were visited for soil sampling and only a portion of those plots met our plot selection criteria. Second, soil properties at depths below 20 cm from the top of the mineral soil may have directly or indirectly affected tree regeneration. For example, overstory trees utilize resources at soil depths below 20 cm and overstory tree conditions can influence the herbaceous community and ponderosa pine regeneration dynamics (Stein and Kimberling, 2003; Laughlin et al., 2006; Sánchez Meador et al., 2009). Also, the carbonate concentration signal may be more pronounced at deeper depths due to leaching of carbonates from the upper profile of soils (Abella and Covington, 2006). A caveat of the study is that elevation was one of many variables used by PRISM to derive the climate variables that were used in our analyses. Hence, the strength of correlations between elevation and the climate variables presented in the SEM may be partially due to the methods used derive the climate variables. However, we chose to retain elevation in the model to examine the strength of these correlations (while keeping in mind the limitations), and because other variables besides elevation were used to derive the climate variables. Also, the relationship between elevation and precipitation is well known, so it was included in the SEM for completeness. While there are limitations with the soil sampling that is conducted across the region, soil sampling on FIA plots is important for monitoring soil conditions over time and their influence on long-term tree regeneration dynamics and other ecological processes.

4.3. Management implications

Our results can also inform ecological restoration activities that include strategically regenerating and managing pine based on assessments of elevation, macroclimate, and soil properties. For example, the Terrestrial Ecological Unit Inventory could be used to identify locations with soil attributes (e.g., high carbonate concentration) that were found to be favorable for pine regeneration in this study. Abella and Covington (2006) and Rodman et al. (2017) also found these units to be useful in making recommendations about the management of ponderosa pine across the broader landscape. Additionally, efforts to map soils to series with more specific information would improve the ability of managers to identify optimal areas for managing ponderosa pine. Currently, map units for most National Forest lands in Arizona and New Mexico only include the soil subgroup, each of which contains multiple series. Also, the results of this study reinforce the recommendation by Fulé (2008) that restoration treatments should be prioritized in high elevation, mesic sites that are likely to maintain forest cover under changing climate conditions. This is especially important because seedling survival is likely to decrease in the late 21st century due to climate change, which may restrict the persistence and expansion of ponderosa pine forests (Petrie et al., 2017).

On sites with limited opportunities for ponderosa pine seedlings to establish after wildfires, planting of seedlings could also be prioritized by the likelihood of their success based on assessments of elevation, macroclimate, and soil properties. This will become increasingly important as more forest area is burned due to increasing fire activity and climate change, and as increased fire severity leads to fewer opportunities for seedlings to become established (Owen et al., 2017; Davis et al., 2019). Additionally, Stevens-Rumann et al. (2018) found that annual moisture deficits from 2000 to 2015 corresponded to lower seedling densities and increased regeneration failures compared with seedling recruitment from 1985 to 1999. Using provenances that are adapted to harsh environments within burns may also increase the likelihood of seedling survival (Kolb et al., 2019). Wildfires can also influence the post-fire soil nutrients that are available to the plant community. While available P was not statistically significant in the SEM of this study, Owen et al. (2020) found that available P had a positive correlation with pine seedling growth after wildfire. This was likely due to a short-term increase in available P, which could increase survival and growth of planted seedlings on burned sites. Also, in a review of studies of ponderosa pine regeneration following wildfires, Korb et al. (2019) found that cooler, moister environments enhanced regeneration. Overall, strategies that focus on improving seedling success will be important as more planting will likely occur across burned areas in the southwestern USA.

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.

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