

Regeneration patterns reveal contraction of ponderosa forests and little upward migration of pinyon-juniper woodlands

Justin A. Minott^a, Thomas E. Kolb^{b,*}

^a School of Forestry, Northern Arizona University, Flagstaff, AZ, United states

^b School of Forestry, Northern Arizona University, Building 82 Southwest Forest Science Complex, 200 East Pine Knoll Drive, Flagstaff, AZ 86011, United states



ARTICLE INFO

Keywords:

Arizona
Climate change
Juniperus
Pinus edulis
Pinus ponderosa
Seedling establishment

ABSTRACT

A recent severe drought caused widespread mortality of ponderosa pine (*Pinus ponderosa*) and pinyon pine (*Pinus edulis*) in forests and woodlands in the southwestern United States. The sustainability of these tree species in the region depends on adequate regeneration and perhaps movement to more climatologically favorable locations. We investigated tree regeneration and species migration along elevation gradients in three community types (pinyon-juniper woodlands, woodland-forest ecotones, and ponderosa pine forests) and three soil parent materials (sedimentary, flow basalt, and volcanic cinder) at 27 sites in northern Arizona. We measured stand characteristics, historic cone production, and density of tree regeneration and small trees. All species produced cones at sites with cinder soil parent material but had little regeneration. Woodlands and woodland-forest ecotones had regeneration of pinyon pine and juniper despite earlier mortality of some mature pinyon trees. Regeneration of ponderosa pine was nearly absent in woodland-forest ecotones, suggesting eventual loss of ponderosa pine and transition to pinyon-juniper woodland. Forests had little regeneration and few small trees of any tree species, indicating little upward migration of pinyon pine and juniper. Occurrence of pinyon pine and juniper regeneration was associated with a suite of biotic and abiotic factors, including a negative relationship with temperature and a positive relationship with precipitation. Regeneration failure of ponderosa pine at woodland-forest ecotone and low-elevation forest sites coupled with limited upward migration of pinyon pine and juniper portends future losses of tree cover as climate continues to warm.

1. Introduction

Forests and woodlands of the southwestern United States are expected to be significantly impacted by climate change (Williams et al. 2010; Breshears et al. 2013). This region experiences periodic severe droughts that amplify tree mortality from disturbances such as wildfire and bark beetle attacks (Gaylord et al., 2013; Hicke et al., 2015; Kolb et al., 2019a; Westerling et al., 2006). As climate warms, these droughts and episodes of high tree mortality are expected to become more severe due to elevated atmospheric moisture demand (Williams et al. 2013; Breshears et al. 2013; McDowell et al. 2015). A recent severe drought resulted in high mortality of ponderosa pine and pinyon pine across the region via intensification of wildfire and bark beetle attacks (Negrón et al. 2009; Hicke et al. 2015; Singleton et al. 2019). In pinyon-juniper woodlands, pinyon pines had greater mortality than co-occurring junipers (Mueller et al. 2005; Breshears et al. 2009; Floyd et al. 2009) and in woodland-forest ecotones, ponderosa and pinyon pines had greater mortality than junipers (Koepke et al. 2010). The recent high mortality

of ponderosa and pinyon pines has raised concern about the future of these species in the southwestern United States as climate continues to warm (Adams et al. 2009; McDowell et al. 2015; Allen 2016). Sustainability of these species depends on successful reproduction under changing climate conditions. Despite broad concern over drought-induced mortality in forests and woodlands of the southwestern United States, few empirical studies have investigated reproduction in drought-impacted stands (Redmond and Barger 2013; Redmond et al. 2015) or potential tree species migration.

To better understand the fate of forests and woodlands of the southwestern United States under warming climate conditions, we studied tree reproduction patterns in three community types and three soil parent materials. For ponderosa pine, we hypothesized that regeneration would be abundant in ponderosa-dominated forests, but sparse in woodland-forest ecotones where earlier drought-related mortality and dieback of mature trees occurred (Koepke et al. 2010). For pinyon pine, we hypothesized little regeneration in both pinyon-juniper woodlands and woodland-forest ecotones due to its high

* Corresponding author.

E-mail addresses: jam2528@nau.edu (J.A. Minott), tom.kolb@nau.edu (T.E. Kolb).

<https://doi.org/10.1016/j.foreco.2019.117640>

Received 25 July 2019; Received in revised form 16 September 2019; Accepted 17 September 2019

Available online 17 December 2019

0378-1127/ © 2019 Elsevier B.V. All rights reserved.

susceptibility to drought stress and death of many seed trees in earlier droughts (Breshears et al. 2009; Redmond and Barger, 2013; Redmond et al. 2015). For juniper, we hypothesized abundant regeneration in both woodlands and woodland-forest ecotones given its high drought resistance and low mortality in recent droughts (Mueller et al., 2005; Koepke et al. 2010). Additionally, we hypothesized little pinyon pine and juniper regeneration in forests because of constraints to migration from slow seed spread and ecological differences between woodland and forest niches (Chambers et al. 1999; Laughlin et al. 2011). Lastly, we hypothesized that regeneration of all species would vary over soil parent materials (sedimentary > basalt > cinder) due to the more negative matrix potentials of basalt-derived soils and lower water-holding capacity and hotter surface of cinder-derived soils (Heidmann et al., 1990; Heidmann and King 1992; Cobb et al. 1997; Looney et al. 2012). Our results bolster understanding of woodland and forest regeneration and inform management efforts to sustain them.

2. Materials and methods

2.1. Study area

We conducted this study in the Coconino National Forest near Flagstaff, Arizona at elevations ranging from 1716 m to 2215 m above sea level. The climate in this region is temperate and semi-arid. Precipitation is bimodal with a majority of precipitation occurring in the summer and winter (Sheppard et al. 2002). We studied three common tree-dominated communities of the southwestern United States: pinyon-juniper woodland, ponderosa-dominated forest, and the woodland-forest ecotone (hereafter, ecotone) where these two communities mix. Pinyon-juniper woodlands in the Coconino National Forest are dominated by pinyon pine (*Pinus edulis*) and two juniper species: one-seed juniper (*Juniperus monosperma*) and Utah juniper (*Juniperus osteosperma*). Woodlands generally occur on warmer, drier sites at lower elevations than forests. Forests in the study area are dominated by ponderosa pine (*Pinus ponderosa*) with a variety of other tree species present in the understory and in forest openings. We focused our study on nine ecotone sites where Koepke et al. (2010) reported about 15% mortality for each of pinyon pine and ponderosa pine in 2004 following a severe drought between 1996 and 2004. These ecotone sites were equally divided among three soil parent materials (SPM). To provide a broader context for assessing the future composition of these ecotone communities, we matched each ecotone site with a nearby higher-elevation site in ponderosa-dominated forest and another nearby lower-elevation site in pinyon-juniper woodland. This resulted in each community being sampled on each SPM three times, for a total of 27 sites: 3 communities \times 3 SPMs \times 3 replicate sites = 27 sites (Fig. 1). By matching a woodland site and a forest site to each previously established ecotone site, we formed nine triads of sites. We matched each triad of sites based on proximity, soil parent material, and similarity in slope and aspect. We used Google Earth satellite imagery to find locations with the desired community types. Access from roads or trails was another, lesser, consideration in establishing new sites.

In each site, we established ten 50-m transects, systematically positioned in a 20 ha area. All transects were oriented south to north and were least 100 m apart. We used the ends of each transect as sample points to make overstory tree measurements using the point-centered quarter method (described below). Along each transect, we established ten 1-m \times 1-m plots at five-m intervals to sample canopy cover, cone density, regeneration density, and regeneration nurse status.

2.2. Overstory composition

We used basal area and tree density to describe the composition of overstory trees in each site. We considered trees \geq 140 cm tall to be overstory, and those < 140 cm tall to be regeneration. We defined

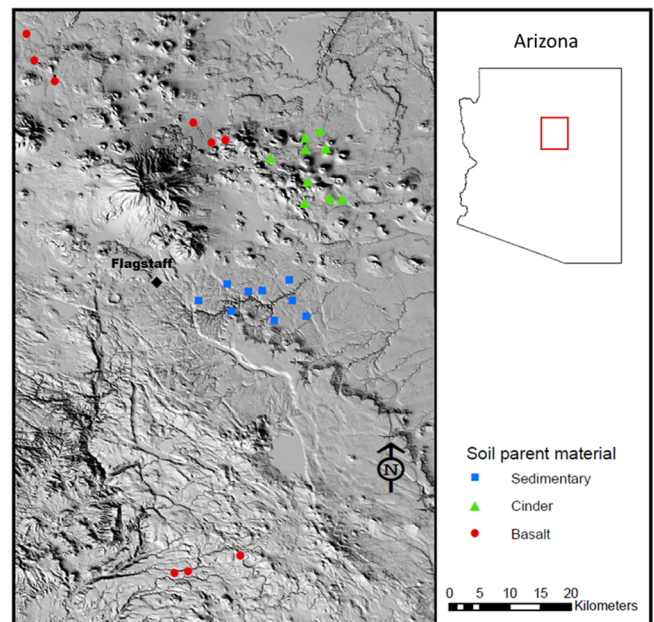


Fig. 1. Shaded relief map displaying study site locations (left) and study area within the state of Arizona (top right). Study site locations are coded by color and shape to indicate the soil parent material.

overstory trees under 10 cm diameter at breast height (dbh) as small trees. We sampled trees using the point-centered-quarter method (Mitchell 2007) and calculated basal area and density on a per-hectare basis for each site. The point-centered-quarter method is a plotless sampling method that can be implemented quickly, measures density and basal area, and is effective for sampling of trees with multiple stems (see Appendix A for details). Because pinyon pine and junipers often fork below breast height, we measured their stem base diameter and converted these values to dbh using equations developed for the southwestern United States by Chojnacky (1999) to facilitate comparison with other tree species. Using the point-centered-quarter method and the diameter conversion method described above, basal area and density per hectare were calculated based on 80 observations per site.

2.3. Abiotic characteristics

We obtained historical mean annual precipitation (MAP) and mean annual temperature (MAT) data for each site from PRISM (PRISM Climate Group, 2019). Values of MAP and MAT were 30-year averages at an 800-m² spatial resolution. We obtained soil data for each site at a 250-m² spatial resolution from SoilGrids.org v0.5.3 (Hengl et al. 2017). We recorded values of soil pH, clay content (%), and volumetric water content at wilting point (WWP) for a point at the center of each site. We acquired topographic data for each site using Arc GIS 10.6.1. We calculated average elevation, slope, and aspect for each site based on a 10-m resolution digital elevation map and topographic maps.

2.4. Site characteristics

Within each triad of sites, elevation was consistently lowest in pinyon-juniper woodlands, intermediate in ecotones, and highest in ponderosa pine-dominated forests (Table 1). Slopes were mild, ranging from 2.0% to 7.4% among sites. Aspect was similar within a site triad, but varied among triads. Within each site triad, MAP was lowest in woodlands, intermediate in ecotones, and highest in forests. MAT had the opposite trend, with highest values in woodlands. Soil clay content ranged from 19% to 29% over sites. Sites with cinder-derived soil tended to have lower soil clay content than other SPMs. Soil pH ranged from 6.4 to 7.8 among sites, with lowest values in forests and highest

Table 1

Biotic and abiotic characteristics of our 27 study sites. Each triad of sites is listed by name with their corresponding soil parent material and community type.

Soil parent material	Site name	Community	Elevation (m)	Slope (%)	Aspect	MAP (cm)	MAT (°C)	Soil % clay	Soil pH	WWP	Ponderosa basal area (m ² /ha)	Pinyon basal area (m ² /ha)	Utah + One-seed juniper basal area (m ² /ha)	Average canopy cover (%)
Basalt	89N	Pinyon-Juniper	2037	4.5	96.7	40.6	9.0	22	7.5	20	0	0.1	7.5	16.0
Basalt	89N	Ecotone	2105	4.3	30.0	42.7	8.5	22	7.3	21	3.6	0.3	1.8	19.1
Basalt	89N	Ponderosa	2180	6.6	312.3	45.0	7.9	25	7.1	24	8.4	0.3	0.3	23.6
Basalt	RM	Pinyon-Juniper	2012	2.7	90.8	44.5	9.3	23	7.4	24	0	0.5	5.9	11.7
Basalt	RM	Ecotone	2093	5.9	60.0	47.5	8.8	25	7.1	25	0.8	2.5	4.2	26.0
Basalt	RM	Ponderosa	2215	6.0	352.5	50.6	7.9	25	6.6	25	29.2	1.5	1.2	57.7
Basalt	SL	Pinyon-Juniper	1716	4.5	259.0	57.5	12.1	29	6.9	26	0	0.8	10.4	34.8
Basalt	SL	Ecotone	1819	3.6	280.3	59.4	11.3	25	6.9	24	0	1.7	7.8	19.1
Basalt	SL	Ponderosa	2129	3.9	226.4	64.4	8.6	27	6.4	26	29.8	0	0.0	52.4
Cinder	CH	Pinyon-Juniper	1819	6.0	64.1	33.9	11.2	24	7.6	27	0	2.2	5.6	11.7
Cinder	CH	Ecotone	1924	6.0	131.6	38.0	10.2	22	7	25	1.9	3.8	0.4	10.5
Cinder	CH	Ponderosa	2015	4.4	128.1	41.9	9.5	25	6.5	28	13.9	0	0.0	36.3
Cinder	HWF	Pinyon-Juniper	1748	5.6	119.0	29.3	11.8	25	7.8	26	0	0.9	1.8	10.7
Cinder	HWF	Ecotone	1791	2.3	90.0	32.1	11.4	19	7.4	26	2.9	2.9	3.2	14.2
Cinder	HWF	Ponderosa	2070	3.3	89.3	44.8	9.0	22	7	28	14.5	0	0.0	23.4
Cinder	PDV	Pinyon-Juniper	1810	5.9	83.0	32.8	11.3	22	7.5	26	0	2.9	1.7	9.2
Cinder	PDV	Ecotone	1894	7.4	83.3	35.7	10.6	24	7.1	28	4.8	6.9	0.8	22.8
Cinder	PDV	Ponderosa	2111	4.7	62.6	42.1	8.7	22	7	27	12.4	0.2	0.8	24.3
Sedimentary	CC	Pinyon-Juniper	1987	4.0	124.1	44.8	9.8	26	7.2	22	0	1.1	6.5	23.9
Sedimentary	CC	Ecotone	2044	3.3	92.3	48.1	9.3	27	7	23	0	0.9	4.2	24.0
Sedimentary	CC	Ponderosa	2103	6.0	161.2	51.7	8.7	24	6.5	23	14.0	0	0.3	43.1
Sedimentary	WE	Pinyon-Juniper	1990	3.2	114.1	44.4	9.8	25	7.1	21	0	0.1	7.1	12.2
Sedimentary	WE	Ecotone	2024	6.9	60.0	46.9	9.5	26	7.2	22	0.5	1.6	3.9	19.8
Sedimentary	WE	Ponderosa	2092	2.6	63.5	49.8	8.9	26	7	23	11.1	0	1.0	31.0
Sedimentary	WW	Pinyon-Juniper	1964	3.2	241.5	43.4	10.1	26	7.3	22	0	1.6	2.4	10.9
Sedimentary	WW	Ecotone	2048	5.7	335.0	47.9	9.3	26	6.9	23	14.6	0.8	1.2	40.1
Sedimentary	WW	Ponderosa	2140	2.0	330.0	52.7	8.3	24	6.5	23	19.0	0	0.0	42.9

values in woodlands. Values of WWP ranged between 20 and 29 over sites. Ponderosa pine basal area was usually highest in forests and lowest in ecotones. No mature ponderosa trees were observed in woodlands. Pinyon pine basal area was lowest in forests (often zero), and higher in ecotones and woodlands. Juniper basal area was generally highest in woodlands and lowest in forests.

2.5. Regeneration, cones, and microsite

We established plots by placing a 1-m × 1-m frame every five m along each of ten 50-m transects per site. We used 1-m × 1-m-plots to measure regeneration because they facilitated collection of several types of data (cones, regeneration, canopy cover) in the same plot. This sampling approach produced 100, 1-m² plots per site (0.01 ha) and 2,700 plots across all sites. Our decision to use this approach is based on tradeoffs among time available for sampling; sampling intensity; the likelihood of detecting all regeneration within a plot, which is higher in smaller plots; use of plots for multiple measurements; and statistical considerations.

In each plot, we counted regeneration (< 140 cm height) by species, measured the height of each individual, and determined whether each individual was nursed. We considered regeneration to be “nursed” if it was within a predefined distance from a potential nurse object (rock, log, shrub, tree bole) or directly beneath a low tree canopy. We defined nurse distances as: a) within a horizontal distance of 1.5 times the height of the nurse object up to a maximum distance of 1.5 m, or b)

within one vertical meter of a tree or shrub canopy.

We counted cones on the ground by species in each plot as an index of past reproductive output. This method does not assess production of viable seed, but is a quantitative metric of historical cone production (Flathers et al. 2016). In most cases, we counted all cones within each plot. In some instances, subsampling of juniper cones was necessary, as thousands sometimes occurred in a plot. In these cases, we counted cones in four 0.1-m × 0.1-m squares (one in each corner of the plot) and multiplied by 25 to obtain the number of cones/m². We measured canopy cover in each plot using a spherical densiometer. We held the densiometer 1 m above the ground in the center of the plot facing south to measure a consistent index of canopy-based solar protection.

2.6. Statistical analysis

We used a variety of models in the statistical program R (R Core team 2019) to determine the influence of community and SPM on cone counts/ha, regeneration counts/ha, and small tree density/ha at the site level. We often observed site-level values of zero, resulting in zero-inflated data with non-normal distributions. Consequently, we analyzed these data using zero-inflated models as needed. For cone and regeneration data, we used negative binomial, zero-inflated negative binomial, or zero-inflated Poisson models to determine the influence of SPM, community, and the SPM × community interaction, and the Wald chi square statistic (WCS) to determine the importance of each model factor. Our sample size in these analyses was 27 (3 SPMs × 3

communities \times 3 sites for each SPM-community combination). In some cases, a factor level (9 sites) composed entirely of zero values resulted in models with excessively high standard errors of model coefficients and unrealistic predicted values. We excluded such factor levels (thereby reducing the sample size from 27 to 18) to improve model fit. We used the R package “pscl” (R Core team 2019) to fit zero-inflated Poisson and zero-inflated negative binomial models to the data. The underlying distributions of modeling procedures used in each analysis were: ponderosa cones - negative binomial, pinyon cones - negative binomial, juniper cones - zero-inflated negative binomial, pinyon regeneration - zero-inflated Poisson, juniper regeneration - zero-inflated negative binomial. We selected models based primarily on the minimization of the Akaike Information Criterion (AIC). In some cases, large standard errors of model coefficients prompted us to discard the procedure that produced the lowest AIC value. In these cases, we selected a model with a higher AIC value that did not have inflated standard errors on model coefficients. We did not conduct this analysis for ponderosa regeneration because the data were too scarce for statistical analysis (see Results).

For small tree data, we used models based on Tweedie distributions to determine the influence of SPM, community, and the SPM \times community interaction. Tweedie distributions are a class of exponential distributions that can be used to model continuous data with a large proportion of zero values (Dunn and Smyth, 2001). The “tweedie” package in R allowed us to adjust the underlying distributions to match the distributions of the data for each model. As with regeneration and cone analyses, the sample size was 27 unless a factor level that was composed entirely of zeros was excluded from an analysis.

We used binomial logistic regression to model the probability of regeneration occurrence of each tree species at the 1-m² plot spatial scale ($n = 2,700$). Abiotic predictor variables were: MAT, MAP, aspect, soil clay content (%), volumetric water content at wilting point (WWP), and soil pH. Biotic predictors were canopy cover, cone counts of ponderosa pine, pinyon pine, and juniper species, and basal area of each major overstory tree species (ponderosa pine, pinyon pine, and juniper species). We used the “best.glm” package in R to assess all possible models containing these predictor variables. This R package selects the 10 best-fitting models for each species based on the minimization of AIC. As an additional measure of model fit, we calculated Nagelkerke’s pseudo R^2 for each of the ten best models (Nagelkerke 1991). We used the variance inflation factor to assess collinearity among predictor variables. We considered a variance inflation factor > 5 to be excessively collinear, which prompted the removal of a problematic variable (Craney and Surles 2002). Aspect and elevation were not included in models of any species because they consistently displayed collinearity with MAP and MAT.

We assessed the importance of nurse objects for regeneration of each species using paired z-tests. We compared the observed proportion of nursed to non-nursed regeneration of each species to a null hypothesis of evenly proportioned nursed to un-nursed regeneration, representing no nurse effect.

3. Results

3.1. Regeneration counts

Ponderosa pine regeneration was scarce at most sampling locations, with the exception of many young seedlings (< 1 year-old, still possessing cotyledons) in some forests (Fig. 2). Over a total of 2,700 m² of sampling (100 m² per site), we counted 230 ponderosa seedlings, of which 223 were < 1 year old, and only seven were > 1 year old. Most pinyon and juniper regeneration was > 1 yr old (based on number of whorls and height). We counted 38 pinyon individuals (three < 1 year old), and 86 juniper individuals (one < 1 year old; Fig. 2). Subsequent results for regeneration focus on pinyon pine and

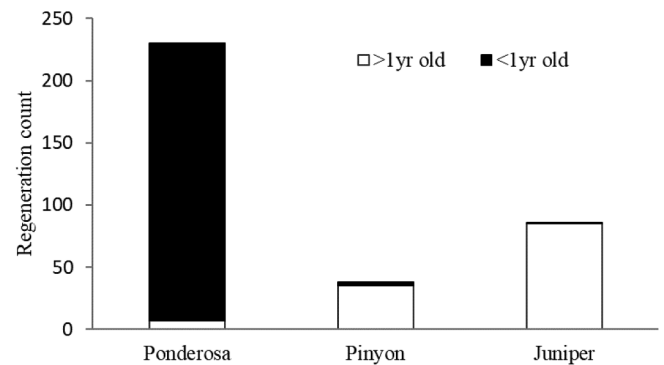


Fig. 2. Counts of ponderosa pine, pinyon pine, and juniper regeneration totaled over all 27 study sites. Dark shading indicates regeneration < 1 year old, no shading indicates regeneration > 1 year old.

juniper > 1 year old because regeneration < 1 year old was rare (Fig. 2). We do not present further results for ponderosa regeneration because individuals > 1 year old were too scarce to assess statistically (7 total: 6 in forests, 1 in ecotones).

3.2. Ponderosa pine cones

To improve model fit, we omitted ponderosa cone data from woodland sites, which were entirely zero values. Both community ($P = 0.033$, $WCS = 4.57$) and SPM ($P = 0.031$, $WCS = 6.96$) had a significant effect on ponderosa cone density, and their interaction was not significant (Fig. 3a). Ponderosa cone density was highest in forests and at sites with cinder SPM. Forests in cinder SPM had cone density three times higher than other SPMs, which was significantly higher than any other site (Bonferroni-adjusted P -value < 0.05).

3.3. Ponderosa small trees

To improve model fit, we omitted ponderosa small tree data (< 10 cm dbh) from woodland sites, which were entirely zero values. Community ($P = 0.089$, $WCS = 2.90$) and the SPM \times community interaction ($P = 0.062$, $WCS = 5.55$) had marginal effects on ponderosa small tree density. Ponderosa small tree density tended to be lower in ecotones than forests (Fig. 3b).

3.4. Pinyon pine cones

To improve model fit, we omitted pinyon cone data from forest sites, which were entirely zero values. The SPM \times community interaction had a significant effect on pinyon cone density ($P = 0.019$, $WCS = 7.96$). Pinyon cone density was significantly lower in woodlands with basalt SPM compared with all other SPMs in woodlands and ecotones (Fig. 4a, Tukey adjusted $P < 0.05$).

3.5. Pinyon regeneration

Pinyon regeneration density was significantly affected by community ($P = 0.047$), but not by SPM or the SPM \times community interaction SPM (Fig. 4b). Pinyon regeneration density was significantly lower in forests than other communities. Pinyon regeneration density in forests and on cinder SPM was often zero. Paired z-tests revealed a significant proportion (0.74) of pinyon pine regeneration was nursed ($P = 0.02$). Nurse objects included logs, tree canopies (pinyon pine and juniper), and shrubs (*Fallugia paradoxa* and *Purshia stansburiana*).

The strongest model of pinyon regeneration occurrence over the 2700 plots was based on canopy cover, ponderosa pine basal area, soil clay percentage, WWP, MAP, and MAT (Table 2). All ten top models had similar support (ΔAIC_c within 2.02, Nagelkerke’s pseudo R^2 0.196

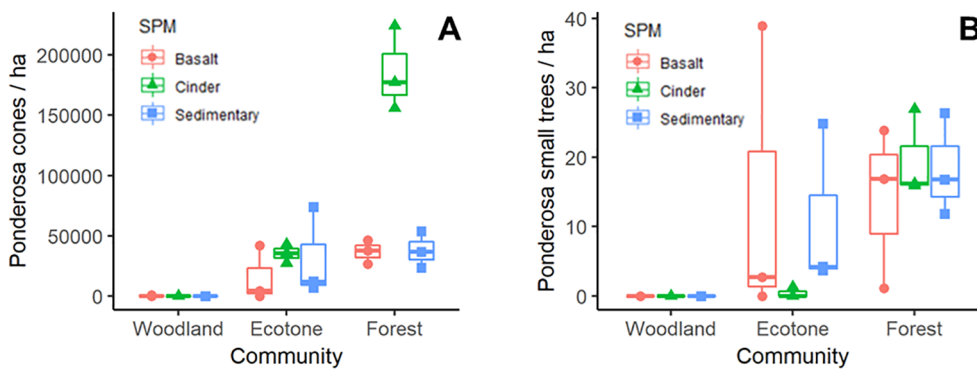


Fig. 3. Box and whisker plots showing ponderosa cone (A) and small tree (B) densities in three communities (woodland, ecotone, forest) and three soil parent materials (SPMs: basalt, cinder, and sedimentary). P-values from Wald chi square tests are: for cone density ($n = 27$) community $P = 0.033$, SPM $P = 0.031$, SPM \times community $P = 0.346$; for small tree density ($n = 18$) community $P = 0.089$, SPM $P = 0.675$, SPM \times community $P = 0.062$.

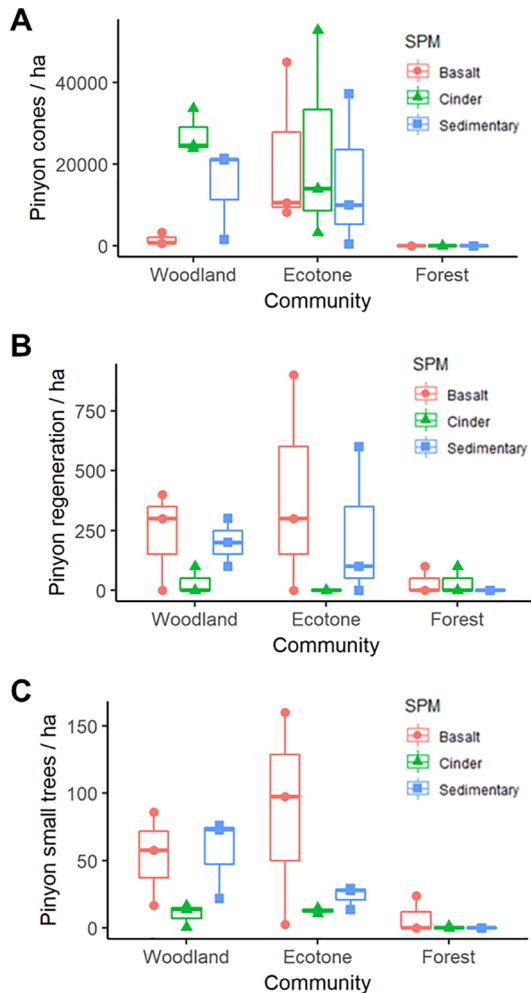


Fig. 4. Box and whisker plots showing pinyon pine cone (A), regeneration (B), and small tree (C) density in three communities (woodland, ecotone, forest) and three soil parent materials (SPMs: basalt, cinder, sedimentary). P-values from Wald chi square tests are: for cone density ($n = 27$) community $P = 0.135$, SPM $P = 0.126$, SPM \times community $P = 0.019$; for regeneration density ($n = 27$) community $P = 0.047$, SPM $P = 0.164$, SPM \times community $P = 0.857$; for small tree density ($n = 27$) community $P < 0.001$, SPM $P < 0.001$, SPM \times community $P = 0.0624$.

to 0.203). Canopy cover, mature ponderosa basal area, mean annual precipitation (MAP), and mean annual temperature (MAT) were highly significant ($P < 0.01$) components in all 10 top models of pinyon regeneration occurrence. Canopy cover and MAP were positively associated with pinyon regeneration occurrence, whereas mature ponderosa basal area and MAT were negatively associated. Most models also

include a significant ($P < 0.05$) positive influence of WWP on pinyon regeneration occurrence.

3.6. Pinyon small trees

Pinyon small tree (< 10 cm dbh) density was significantly affected by both SPM and community ($P < 0.001$, $WCS = 21.48$ and 34.78 , respectively), with a marginally significant SPM \times community interaction ($P = 0.062$). Pinyon small tree density was lower in forests, where it was often zero, than in woodlands and ecotones (Fig. 4c, Tukey adjusted $P < 0.05$). Pinyon small tree density was lower in cinder SPM than in other SPMs. Pinyon small tree density was highly variable in ecotone communities in basalt SPM, with values ranging from zero to 160 trees/ha.

3.7. Juniper cones

Community had a significant effect on juniper cone density ($P < 0.001$, $WCS = 28.50$), whereas SPM and the SPM \times community interaction did not (Fig. 5a). Cone density was significantly lower in forests, where it was often zero, than in other communities (Tukey-adjusted $P < 0.05$). Juniper cone density was similar in ecotones and woodlands.

3.8. Juniper regeneration

To improve model fit, we omitted juniper cone data from forest sites, which were entirely zero values. For the other sites, community had a significant effect on juniper regeneration density ($P < 0.001$, $WCS = 11.65$), with less regeneration in forests than ecotones and woodlands (Fig. 5b). The effects of SPM and the interaction between community and SPM were not significant. Paired z-tests revealed a significant proportion (0.76) of juniper regeneration was nursed ($P < 0.001$). Nurse objects included tree canopies (ponderosa, pinyon, and juniper), logs, rocks, and shrubs (*Purshia stansburiana* and *Hymenoxys richardsonii*).

The strongest model of juniper regeneration occurrence over the 2700 plots was based on canopy cover, juniper cone count, ponderosa pine basal area, juniper basal area, pinyon pine basal area, MAP, and MAT (Table 3). Two other models had similar support ($\Delta AICc$ within 2, Nagelkerke's pseudo R^2 0.270 to 0.279) with a similar suite of factors, including a weak positive influence of juniper basal area and soil clay percentage. Canopy cover, juniper cone count, mature ponderosa basal area, mature pinyon basal area, and MAT were highly significant ($P < 0.01$) components in all of the top 10 models predicting juniper regeneration occurrence. Canopy cover, juniper cone count, and mature pinyon basal area were positively associated with juniper regeneration occurrence, whereas mature ponderosa basal area and mean annual temperature were negatively associated. Most models also included a significant ($P < 0.05$) positive influence of MAP on juniper regeneration.

Table 2

Models predicting pinyon pine regeneration occurrence based on environmental predictors ranked by ΔAICc (corrected Akaike's information criterion). Colors indicate the direction of influence based on model coefficients (blue +, red-) and p-value of coefficients in the model is indicated by size and bolding ($P > 0.05$, $P < 0.05$). Model factors are abbreviated as: Canopy = plot canopy cover, PIPO_BA = ponderosa basal area per hectare, PIED_BA = pinyon basal area per hectare, Juniper_BA = juniper basal area per hectare, Soil_Clay = soil clay content (%), WWP = volumetric water content at wilting point, MAP = mean annual precipitation, MAT = mean annual temperature.

Predictors in Models of Pinyon Seedling Occurrence	Pseudo R^2	ΔAICc
Canopy + PIPO_BA + Soil_Clay + WWP+ MAP + MAT	0.201	0.00
Canopy + PIPO_BA + WWP+ MAP + MAT	0.195	0.06
Canopy + PIPO_BA + PIED_BA + Soil_Clay + MAP + MAT	0.197	1.33
Canopy + PIED_Cones + PIPO_BA + Soil_Clay + WWP+ MAP + MAT	0.203	1.36
Canopy + PIED_Cones + PIPO_BA + WWP+ MAP + MAT	0.197	1.42
Canopy + PIPO_BA + PIED_BA + Soil_Clay + WWP + MAP + MAT	0.203	1.59
Canopy + PIPO_BA + Juniper_BA + Soil_Clay + WWP+ MAP + MAT	0.202	1.89
Canopy + PIPO_BA + Soil_Clay + pH + WWP + MAP + MAT	0.202	1.91
Canopy + PIPO_BA + Juniper_BA + WWP+ MAP + MAT	0.202	1.93
Canopy + PIPO_BA + pH + WWP+ MAP + MAT	0.196	2.02

3.9. Juniper small trees

Both community and SPM had a significant effect on juniper small tree density ($P < 0.001$, $\text{WCS} = 13.49$ and 38.14 , respectively), whereas the $\text{SPM} \times \text{community}$ interaction was not significant. The density of small junipers (Fig. 4c) was significantly higher in woodlands than in forests (Tukey-adjusted $P < 0.05$). Juniper small tree density in cinder SPM sites was often zero, and significantly lower than the other SPMs (Tukey-adjusted $P < 0.05$).

4. Discussion

We found evidence that ponderosa forests in northern Arizona are contracting on their lower elevation edge. Consistent with our hypothesis, ponderosa pine regeneration was low in woodland-forest ecotones where it occurs at the lowest elevation of its local distribution. Ponderosa regeneration was usually absent from ecotones and small tree densities were consistently lower than those in higher elevation forests. Contrary to our hypothesis, ponderosa reproduction was also low in forest with abundant ponderosa overstory, and small tree density averaged less than half of that from reconstructions of pre-settlement-period forests in the region (Reynolds et al. 2013). We also found evidence that ecotones are in transition to pinyon-juniper woodlands, and that current reproduction patterns may support continued codominance of pinyons and junipers. Consistent with our hypothesis, juniper reproduction was abundant in woodlands and woodland-forest ecotones. Juniper regeneration and small tree densities were similar in these two communities, and similar to those reported in a study of nearby woodlands before recent severe drought (Redmond et al. 2015). Contrary to our hypothesis, pinyon pine reproduction was abundant in both woodlands and ecotones. Pinyon regeneration and small tree densities were similar to those of juniper, and to those reported by Redmond et al. (2015) in nearby sites before drought-related overstory mortality. If these young pinyon pine trees survive to maturity, woodlands and ecotones will retain a component of pinyon pine. Consistent with our hypothesis, pinyon and juniper reproduction were low in forests, indicating little upward migration of these species. Also as hypothesized, regeneration of all species was low in cinder SPMs, likely due to the hot and dry conditions on the surface of cinder-covered soils.

4.1. Low-elevation range contraction of ponderosa pine forest

Our results indicate that woodland-forest ecotone communities are losing ponderosa pine. We only observed ponderosa regeneration > 1 year old at one of nine ecotone sites. Ponderosa small tree density in ecotones was also low; mean small tree density (8.4/ha) in ecotones was about half that in forests (17.3/ha) and less than a quarter of the value reported for reconstructions of pre-settlement conditions in northern Arizona at elevations similar to those at our sites (approx. 37/ha; Reynolds et al. 2013). Other study sites in the region experienced a pulse of ponderosa seedling establishment during a wet period in 2013–2014 (Flathers et al. 2016), but there was no sign of this pulse in our ecotone sites. The severe drought period that ended in 2004 was associated with 15% mortality of ponderosa pine at these ecotone sites (Koepeke et al. 2010). Continued mortality of ponderosa pine and little reproduction will eventually lead to the loss of ponderosa pine from these woodland-forest ecotone sites.

We also found evidence of a paucity of ponderosa reproduction in forests. Ponderosa small tree density was 47% of the density reported for trees of this size class (< 10 cm dbh) in reconstructed pre-settlement-period ponderosa forests in the study site region (Reynolds et al. 2013). Interestingly, the density of ponderosa small trees was lower in ecotones than forests despite similar cone density. This suggests a constraint to ponderosa reproduction at ecotones between seed production and seedling establishment. The ponderosa pine cone density values (mean 87 k/ha) suggest ample historical seed production (Krannitz and Duralia 2004), although we could not assess historic seed viability. Some sites had abundant ponderosa germinants (regeneration < 1 year old, still possessing cotyledons), showing that a favorable environment for germination occurred in the year of our observations. Established ponderosa pine regeneration was sparse (0–100/ha), pointing to mortality between the time of germination and development into the small tree stage as the limitation to ponderosa regeneration. This is the life stage when ponderosa seedlings are highly vulnerable to a variety of biotic and abiotic mortality agents (Schubert 1974; Stein and Kimberling 2003; Shepperd et al. 2006).

Some likely causes of the low amount of ponderosa pine regeneration on these sites are excessive shading, soil texture, soil moisture, and aridity. Excessive shading and other stresses of competition resulting from high stand density can limit regeneration survival (Schubert 1974; Flathers et al. 2016). Shading likely restricted seedling establishment in ponderosa forests on sedimentary and basalt SPMs where overstory

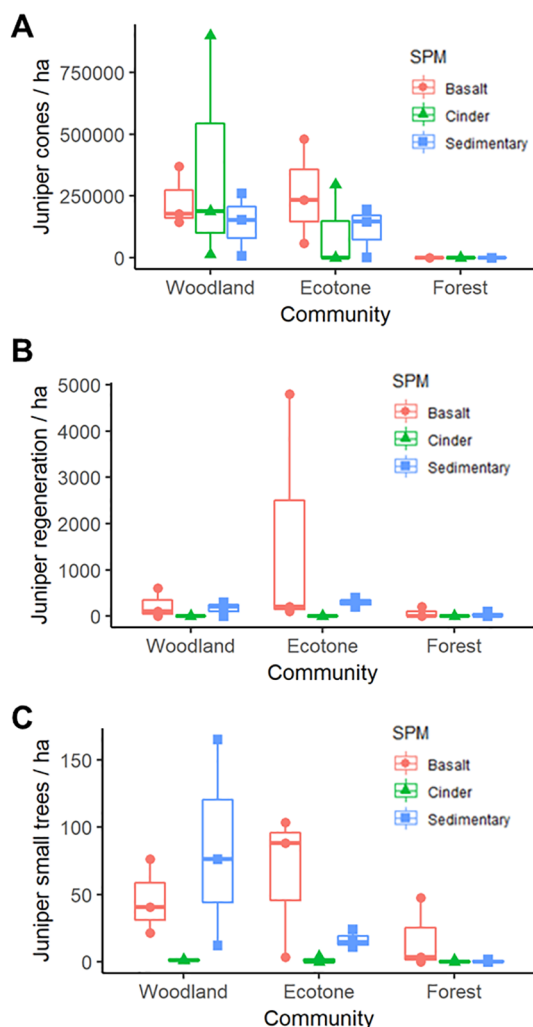


Fig. 5. Box and whisker plots showing juniper cone (A), regeneration (B), and small tree (C) densities in three communities (woodland, ecotone, forest) and three soil parent materials (SPMs: basalt, cinder, sedimentary). P-values from Wald chi square tests are: for cone density ($n = 27$) community $P < 0.001$ SPM $P = 0.920$, SPM \times community $P = 0.845$; for regeneration density ($n = 18$) community $P = 0.026$, SPM $P = 0.545$, SPM \times community $P = 0.219$; for small tree density ($n = 27$) community $P < 0.001$, SPM $P < 0.001$, SPM \times community $P = 0.149$.

Table 3

The ten strongest logistic regression models of juniper regeneration occurrence in $1 \text{ m} \times 1 \text{ m}$ plots ($n = 2,700$) based on climatic and biotic factors, ranked by ΔAICc (corrected Akaike's information criterion). Colors indicate the direction of influence based on model coefficients (blue +, red -), and p-value of coefficients in the model is indicated by size and bolding ($P > 0.05$, $P < 0.05$). Model factors are abbreviated as: Canopy = plot canopy cover, Juniper_Cones = plot juniper cone count, PIPO_BA = ponderosa basal area per hectare, PIED_BA = pinyon basal area per hectare, Juniper_BA = juniper basal area per hectare, Soil_Clay = soil clay content (%), WWP = volumetric water content at wilting point, MAP = mean annual precipitation, MAT = mean annual temperature.

Predictors in Models of Juniper Regeneration Occurrence	Pseudo R^2	ΔAICc
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + Juniper_BA + MAP + MAT	0.278	0.00
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + MAP + MAT	0.274	0.30
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + Soil_Clay + Juniper_BA + MAP + MAT	0.279	1.61
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + Juniper_BA + WWP + MAP + MAT	0.278	2.01
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + Soil_Clay + MAP + MAT	0.274	2.05
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + WWP + MAP + MAT	0.274	2.29
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + Juniper_BA + Soil_Clay + WWP + MAP + MAT	0.279	3.61
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + Soil_Clay + WWP + MAP + MAT	0.274	4.04
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + Juniper_BA + Soil_Clay + MAT	0.274	4.60
Canopy + Juniper_Cones + PIPO_BA + PIED_BA + Juniper_BA + Soil_Clay + WWP + MAT	0.270	6.29

density and canopy cover (91–635 trees/ha and 31–58%, respectively) are considerably higher than pre-settlement reference conditions for the region (27–159 trees/ha and 10–22%; Reynolds et al. 2013). Aridity is another possible limitation to regeneration at our study sites. Warmer, drier conditions can decrease soil moisture and increase atmospheric moisture demand, leading to drought stress and seedling mortality (Kolb and Robberecht 1996; Savage et al. 2013; Petrie et al. 2016). At our study sites, mean annual temperature in the post-drought period (2005–2017) was 0.85°C warmer than during the 100-year period before the drought and mean annual precipitation was 9.8 mm lower (PRISM Climate Group 2019). Soil texture is another factor that may have affected regeneration survival. Density of ponderosa regeneration > 1 year old in our study averaged 67/ha on sedimentary SPM, 33/ha on basalt SPM, and 0/ha on cinder SPM. Ponderosa pine regeneration density tends to be lower on basalt SPM than on sedimentary SPM (Ffolliott and Baker 1977; Goodwin 2004) due to more frost heaving and more negative matric potential that reduces water availability (Heidmann and King 1992; Heidmann and Thorud 1976). Cinder SPM has a gravelly, dark-colored, hot surface, and low water holding capacity (Sthultz et al. 2007; Looney et al. 2012), which inhibit seedling establishment.

We found little evidence of migration of the pinyon-juniper community into forests. We detected pinyon regeneration in only two of nine forest sites, and only at low density (100/ha). Pinyon small trees occurred in only two forest sites, both at low density (1.2 and 23.8 per ha). Likewise, juniper regeneration occurred in only two of nine forest sites, both at low density (100 and 200/ha). Juniper small tree density in forest was usually zero, or very low (1.2 to 3.4/ha), with the exception of one forest site which had 47.7 small trees/ha. The logistic regression models indicate a negative relationship between both pinyon and juniper seedling occurrence and mature ponderosa basal area. They also indicate a negative relationship with mean annual temperature, and a positive relationship with both mean annual precipitation and canopy cover. These relationships suggest that pinyon and juniper regeneration should grow well in the climate of forest sites, but they are inhibited by constrained seed dispersal and other factors associated with mature ponderosa trees.

4.2. Ecotone transition to pinyon-juniper woodland

Our results show that woodland-forest ecotone communities are transitioning to pinyon-juniper-dominated woodlands. Mature ponderosa trees in these communities are not being replaced due to low regeneration. Pinyon pine and junipers, however, have regenerated in ecotones, and should become the dominant overstory trees as

ponderosa pines die and are not replaced. In woodlands on sedimentary and basalt SPMs, pinyon regeneration density averaged 217/ha and juniper regeneration density averaged 200/ha. In woodland-forest ecotones on the same SPMs, pinyon regeneration density averaged 317/ha and juniper regeneration density averaged 1000/ha. These densities are similar to those reported by Redmond et al. (2015) in the same region between 1998 and 2001, before widespread drought-induced pinyon pine mortality (pinyon pine regeneration: 220/ha, juniper regeneration: 62/ha). Redmond et al. (2015) found a decrease in pinyon regeneration between pre-drought and post-drought samplings, and higher survival of juniper regeneration, suggesting a future shift toward a juniper-dominated ecosystem (Redmond et al. 2015). We found similar densities of pinyons and junipers at both the regeneration stage and the small tree stage, which suggests codominance in the near future on our sites. This trajectory may change, however, under projected climate for the southwestern United States because pinyon pine is more susceptible to drought than junipers (Adams et al. 2009; Breshears et al. 2009; Williams et al. 2010; Floyd et al. 2015). Woodland and ecotone sites with cinder SPM had much lower regeneration and small tree density than basalt and sedimentary SPMs, despite having similar cone densities. Under recent warm climatic conditions, and even warmer projected climate conditions, pinyon-juniper woodlands on cinder SPM likely will fade due to low reproduction.

4.3. Climate and future reproduction

Future climate warming is projected to result in warmer droughts, more frequent mortality events, further restriction of regeneration, and continued contraction of ponderosa pine's range (Hanson and Weltzin 2000; Williams et al. 2010; Bell et al. 2014; Rother et al. 2015). Ponderosa pine in our study had little reproduction likely because of the combined effects of high stand density, warming climate, and drought. These conditions predispose ponderosa pine forests to another important driver of range contraction, severe wildfire (Fulé et al. 2003; Miller et al. 2009; Hurteau et al., 2014). Rapid loss of overstory trees limits seed availability and creates harsh conditions for ponderosa seedling establishment and survival (Davis et al. 2019).

The woodlands we studied appear to have a sufficient amount of pinyon pine and juniper regeneration to maintain both of these species in the near future. This could change, however, if drought severity and frequency increase in the future as temperatures warm (Seager et al. 2007; Breshears et al. 2013; Williams et al. 2013; Cook et al. 2015). Pinyon pine regeneration depends on mature pinyon trees for sheltered microsites and as a seed source, both of which were reduced during the recent drought (Chambers et al. 1999; Redmond and Barger, 2013; Redmond et al. 2012, 2015). We found that pinyon pine regeneration was most likely to grow near a nurse object or under canopy cover than in open interspace conditions in our study sites, consistent with earlier reports (Chambers et al. 1999; Redmond and Barger 2013; Floyd et al. 2015; Redmond et al. 2015). Additional pinyon pine mortality events are expected in the coming decades (Adams et al. 2009; McDowell et al. 2015), which would further reduce seed production and sheltered microsites, resulting in constrained reproduction. Our logistic regression models indicate that mean annual temperature is negatively associated with both pinyon and juniper regeneration occurrence, suggesting warming climate as an additional constraint to regeneration.

4.4. Management implications

Our results provide guidance for efforts to maintain low-elevation ponderosa pine forests. We documented little ponderosa regeneration in low-elevation forests that currently have an ample number of seed trees. This likely results from several interacting factors, including lack of disturbances that create a favorable regeneration niche, abiotic stresses caused by drought and warm temperatures, and maladaptation of current seed sources to warming climate. To enhance seed

production and seedling establishment, we recommend the consideration of silvicultural treatments such as shelterwood cuts, group selection, or thinning from below to emulate pre-settlement forest structure (Covington et al. 1997; Shepperd et al. 2006; Francis et al. 2018). By increasing the sunlight available to regeneration on the forest floor, reducing accumulated litter, and reducing competition for water, these treatments should promote regeneration (Schubert 1974; Puhlick et al. 2012). Recent studies in northern Arizona in higher elevation ponderosa forests show that cutting treatments producing intermediate stand basal areas (e.g., 7 to 28 m²/ha) enhance cone production and seedling establishment (Flathers et al. 2016). Low-intensity burning should be applied cautiously after seedling establishment until saplings develop thick heat-resistant bark. While controlled burning could be used to weed dense thickets of regeneration to reduce future fire severity, we consider the future development of such thickets in low-elevation forests to be unlikely given current constraints on regeneration. Additional benefits of forest thinning and prescribed fire include bringing ponderosa stand structure and fire regimes closer to reference conditions that are less vulnerable to severe wildfire (Roccaforte et al. 2008; Fulé et al. 2012; Roccaforte et al. 2015). More proactive management to promote ponderosa regeneration in areas that do not regenerate could include planting of seedlings with high tolerance to drought and heat. Research leading to identification of appropriate stress-tolerant seed sources is underway (Kolb et al., 2019b; Rehfeldt et al., 2014).

Maintenance of ponderosa pine in woodland-forest ecotones is problematic due to sparse current regeneration, recent and projected future mortality of seed trees (Koepke et al. 2010; McDowell et al. 2015), and an increasingly stressful abiotic environment (Williams et al. 2013; Petrie et al. 2017; Davis et al. 2019). Given limited resources for forest management, we recommend that forest managers focus on maintaining more drought tolerant woodland trees, such as pinyon pine and junipers, and shrubs on these sites rather than ponderosa pine.

Our research and others (Kane et al. 2015; Redmond et al. 2018) support management actions that maintain pinyon pine seed trees and nurse objects in order to promote pinyon pine regeneration in ecotones and woodlands. While there is little forest managers can do to prevent pinyon pine mortality on the landscape scale during drought and associated bark beetle attacks, managers can limit practices that kill pinyon pine seed trees, such as clearing to promote livestock forage and wood-cutting. Limiting fire in pinyon-juniper woodlands also should to help retain mature pinyon pines (Romme et al. 2009). It is important to preserve pinyon pine trees that survived the last severe drought. These trees provide the seeds and sheltered microsites required for pinyon regeneration and possible woodland recovery (Redmond et al. 2018). Stand treatments may be useful for stimulating the development of pinyon pine mature trees. A recent study of woodland fire-reduction treatments reported that thinning accelerated recruitment of pinyon pine regeneration to overstory trees, whereas prescribed burning with and without thinning decreased recruitment due to fire-induced mortality (Huffman et al. 2019).

Assisted migration (Ste-Marie et al. 2011) may be an appropriate management action to sustain woodlands and forests of the southwestern United States. Distributions of both ponderosa pine and pinyon pine are projected to shrink during future warming as some of their current range becomes unsuitable for regeneration (Rehfeldt et al. 2006; Bell et al. 2014). The limited seed dispersal distance of these species constrains rapid migration to keep pace with a changing climate (Chambers et al. 1999; Pearson and Theimer 2004; Lentile et al. 2005; Vander Wall and Beck 2011). Assisted migration could involve planting these species beyond their current distributions (e.g. upward in elevation), or planting highly drought-adapted genotypes from low elevation provenances at higher elevation sites within current distributions. Genetic differences in drought adaptation have been reported among southwestern United States populations of ponderosa pine (Kolb et al.

2016) and pinyon pine (Gehring et al. 2017; Whipple et al. 2019). More information is needed about the effectiveness of such management actions in maintaining woodlands and forests in the southwestern United States.

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.

Acknowledgements

We thank David Huffman (Northern Arizona University (NAU) Ecological Restoration Institute), Catherine Gehring (NAU), and two anonymous reviewers for helpful reviews of earlier versions of this manuscript; Roy St. Laurent (NAU) for help with statistical analysis; Lindsey Brown, Aalap Dixit, and James Lauder (NAU) for help with field data collection; Joe Crouse (NAU Ecological Restoration Institute) and Jose Gabriel Martinez-Fonseca (NAU) for help with maps and spatial analysis; Don Normandin (NAU Ecological Restoration Institute) for field equipment; and Dan Koepke (Desert Botanical Garden) for study site information.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117640>.

References

- Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* 106, 7063–7066.
- Allen, C.D., 2016. Chapter 4 - Forest ecosystem reorganization underway in the Southwestern US: a preview of widespread forest changes in the Anthropocene? In: Bixler, R.P., Miller, C. (Eds.), *Forest Conservation and Management in the Anthropocene: Adaptation of Science, Policy and Practice*. University Press of Colorado, Boulder, Colorado, pp. 57–79.
- Bell, D.M., Bradford, J.B., Lauenroth, W.K., 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Glob. Ecol. Biogeogr.* 23, 168–180.
- Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., Allen, C.D., McDowell, N.G., Pockman, W.T., 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Front. Ecol. Environ.* 7 (4), 185–189.
- Breshears, D.D., Adams, H.D., Eamus, D., McDowell, N.G., Law, D.J., Will, R.E., Zou, C.B., 2013. The critical amplifying role of increasing atmospheric moisture demand on tree mortality and associated regional die-off. *Front. Plant Sci.* 4, 2–5.
- Chambers, J.C., Vander Wall, S.B., Schupp, E.W., 1999. Seed and seedling ecology of piñon and juniper species in the pygmy woodlands of western North America. *Bot. Rev.* 65, 1–38.
- Chojnacki, D., 1999. Converting tree diameter measured at root collar to diameter at breast height. *West. J. Appl. For.* 14, 14–16.
- Cobb, N.S., Mopper, S., Gehring, C.A., Caouette, M., Christensen, K.M., Whitham, T.G., 1997. Increased moth herbivory associated with environmental stress of piñon pine at local and regional levels. *Oecologia* 109, 389–397.
- Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and central plains. *Sci. Adv.* 1 (1), e1400082.
- Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. *J. For.* 95 (4), 23–29.
- Crane, T.A., Surles, J.G., 2002. Model-dependent variance inflation factor cutoff values. *Qual. Eng.* 14, 391–403.
- Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M.P., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proc. Natl. Acad. Sci. U.S.A.* 116, 6193–6198.
- Dunn, P.K., Smyth, G.K., 2001. Tweedie family densities: methods of evaluation. In: *Proceedings of the 16th International Workshop on Statistical Modelling*. Odense, Denmark 2–6 July.
- Ffolliott, P.F., Baker Jr, M.B., 1977. Characteristics of Arizona ponderosa pine stands on sandstone soils. *USDA For. Serv. Gen. Tech. Rep. RM-44* 6.
- Flathers, K.N., Kolb, T.E., Bradford, J.B., Waring, K.M., Moser, W.K., 2016. Long-term thinning alters ponderosa pine reproduction in northern Arizona. *For. Ecol. Manage.* 374, 154–165.
- Floyd, M.L., Clifford, M., Cobb, N.S., Hanna, D., Delph, R., Ford, P., Turner, D., 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon-juniper woodlands. *Ecol. Appl.* 19, 1223–1230.
- Floyd, M.L., Romme, W.H., Rocca, M.E., Hanna, D.P., Hanna, D.D., 2015. Structural and regenerative changes in old-growth piñon-juniper woodlands following drought-induced mortality. *For. Ecol. Manage.* 341, 18–29.
- Francis, D., Ex, S., Hoffman, C., 2018. Stand composition and aspect are related to conifer regeneration densities following hazardous fuels treatments in Colorado, USA. *For. Ecol. Manage.* 409, 417–424.
- Fulé, P.Z., Crouse, J.E., Heinlein, T.A., Moore, M.M., Covington, W.W., Verkamp, G., 2003. Mixed-severity fire regime in a high-elevation forest: Grand Canyon Arizona. *Landscape Ecol.* 18, 465–486.
- Fulé, P.Z., Crouse, J.E., Roccaforte, J.P., Kalies, E.L., 2012. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *For. Ecol. Manage.* 269, 68–81.
- Gaylord, M.L., Kolb, T.E., Pockman, W.T., Plaut, J.A., Yepez, E.A., Macalady, A.K., Pangle, R.E., McDowell, N.G., 2013. Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytol.* 198, 567–578.
- Gehring, C.A., Stultz, C.M., Flores-Renteria, L., Whipple, A.V., 2017. Tree genetics defines fungal partner communities that may confer drought tolerance. *Proc. Natl. Acad. Sci. U.S.A.* 114, 11169–11174.
- Goodwin, K., 2004. Modeling natural regeneration of ponderosa pine on the Coconino National Forest in Arizona. PhD dissertation, Northern Arizona University, Flagstaff, AZ.
- Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. *Sci. Total Environ.* 262, 205–220.
- Heidmann, L.J., Thorud, D.B., 1976. Controlling frost heaving of ponderosa pine regeneration in Arizona. *USDA, Forest Service, Rocky Mountain Forest and Range Research Station, Research Paper RM-172*.
- Heidmann, L.J., Harrington, M.G., King, R.M., 1990. Comparison of moisture retention curves for representative basaltic and sedimentary soils in Arizona prepared by two methods. *USDA For Serv, Rocky Mountain For Range Exp Stn. Res Pap RM-500*.
- Heidmann, L.J., King, R.M., 1992. Effect of prolonged drought on water relation of ponderosa pine regeneration growing in basalt and sedimentary soils. *USDA For Serv, Rocky Mountain For Range Exp Stn. Res Pap RM-301*.
- Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E., Wheeler, I., Mantel, S., Kempen, B., 2017. SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE* 12 (2), e0169748.
- Hicke, J.A., Meddens, A.J.H., Kolden, C.A., 2015. Recent tree mortality in the western United States from bark beetles and forest fires. *For. Sci.* 62, 141–153.
- Huffman, D.W., Stoddard, M.T., Springer, J.D., Crouse, J.E., Sanchez Meador, A.J., Nepal, S., 2019. Stand dynamics of piñon-juniper woodlands after hazardous fuels reduction treatments in Arizona. *Rangeland Ecol. Manag.* <https://doi.org/10.1016/j.rama.2019.05.005>.
- Hurteau, M.D., Bradford, J.B., Fulé, P.Z., Taylor, A.H., Martin, K.L., 2014. Climate change, fire management, and ecological services in the southwestern US. *For. Ecol. Manage.* 327, 280–289.
- Kane, J.M., Dugi, F.L., Kolb, T.E., 2015. Establishment and growth of piñon pine regeneration vary by nurse type along a soil substrate age gradient in northern Arizona. *J. Arid. Env.* 115, 113–119.
- Koepke, D.F., Kolb, T.E., Adams, H.D., 2010. Variation in woody plant mortality and dieback from severe drought among soils, plant groups, and species within a northern Arizona ecotone. *Oecologia* 163, 1079–1090.
- Kolb, T.E., Keefover-Ring, K., Burr, S.J., Hofstetter, R., Gaylord, M., Raffa, K.F., 2019a. Drought-mediated changes in tree physiological processes weaken tree defenses to bark beetle attack. *J. Chem. Ecol.* <https://doi.org/10.1007/s10886-019-01105-0>.
- Kolb, P.F., Robberecht, R., 1996. High temperature and drought stress effects on survival of Pinus ponderosa regeneration. *Tree Physiol.* 16, 665–672.
- Kolb, T.E., Dixit, A., Burney, O., 2019b. Challenges and opportunities for maintaining ponderosa pine forests in the southwestern U.S. *Tree Planters. Notes* 62, 104–112.
- Kolb, T.E., Grady, K.C., McEtrick, M.P., Herrero, A., 2016. Local-scale drought adaptation of ponderosa pine seedlings at habitat ecotones. *For. Sci.* 62, 641–651.
- Krannitz, P.G., Duralia, T.E., 2004. Cone and seed production in *Pinus ponderosa*: a review. *West N. Am. Nat.* 64, 208–218.
- Laughlin, D.C., Moore, M.M., Fulé, P.Z., 2011. A century of increasing pine density and associated shifts in understory plant strategies. *Ecology* 92, 556–561.
- Lentile, L.B., Smith, F.W., Shepperd, W.D., 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. *Can. J. For. Res.* 35, 2875–2885.
- Looney, C.E., Sullivan, B.W., Kolb, T.E., Kane, J.M., Hart, S.C., 2012. Pinyon pine (*Pinus edulis*) mortality and response to water addition across a three million year substrate age gradient in northern Arizona, USA. *Plant Soil* 357, 89–102.
- McDowell, N.G., Williams, A.P., Xu, C., Pockman, W.T., Dickman, L.T., Sevanto, S., Pangle, R., Limousin, J., Plaut, J., MacKay, D.S., Ogee, J., Domec, J.C., Allen, C.D., Fisher, R.A., Jiang, X., Muss, J.D., Breshears, D.D., Rauscher, S.A., Koven, C., 2015. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nat. Clim. Change* 6, 295–300.
- Miller, J.D., Safford, H.D., Crimmins, M., Thode, A.E., 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12, 16–32.
- Mitchell, K., 2007. Quantitative analysis by the point-centered quarter method. Geneva: Department of Mathematics and Computer Science, Hobart and William Smith Colleges, <https://arxiv.org/pdf/1010.3303.pdf>.

- Mueller, R.C., Scudder, C.M., Porter, M.E., Talbot Trotter, R., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: Evidence for long-term vegetation shifts. *J. Ecol.* 93, 1085–1093.
- Nagelkerke, N.J.D., 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78, 691–692.
- Negrón, J.F., McMillin, J.D., Anhold, J.A., Coulson, D., 2009. Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. *For. Ecol. Manage.* 257, 1353–1362.
- Pearson, K.M., Theimer, T.C., 2004. Seed-caching responses to substrate and rock cover by two *Peromyscus* species: Implications for pinyon pine establishment. *Oecologia* 141, 76–83.
- Petrie, M.D., Bradford, J.B., Hubbard, R.M., Lauenroth, W.K., Andrews, C.M., Schlaepfer, D.R., 2017. Climate change may restrict dryland forest regeneration in the 21st century. *Ecology* 98, 1548–1559.
- Petrie, M.D., Wildeman, A.M., Bradford, J.B., Hubbard, R.M., Lauenroth, W.K., 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. *For. Ecol. Manage.* 361, 328–338.
- Puhlick, J.J., Laughlin, D.C., Moore, M.M., 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. *For. Ecol. Manage.* 264, 10–19.
- PRISM Climate Group (2019) PRISM Climate Group Data.
- R Core Team, 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Redmond, M.D., Barger, N.N., 2013. Tree regeneration following drought and insect-induced mortality in pinon-juniper woodlands. *New Phytol.* 200, 402–412.
- Redmond, M.D., Cobb, N.S., Clifford, M.J., Barger, N.N., 2015. Woodland recovery following drought-induced tree mortality across an environmental stress gradient. *Glob. Change Biol.* 21, 3685–3695.
- Redmond, M.D., Forcella, F., Barger, N.N., 2012. Declines in pinyon pine cone production associated with regional warming. *Ecosphere* 3 (12), 1–12. <https://doi.org/10.1890/ES12-00306.1>.
- Redmond, M.D., Weisberg, P.J., Cobb, N.S., Clifford, M.J., 2018. Woodland resilience to regional drought: dominant controls on tree regeneration following overstorey mortality. *J. Ecol.* 106, 625–639.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analyses of plant-climate relationships for the western United States. *Int. J. Plant Sci.* 6, 1123–1150.
- Rehfeldt, G.E., Jaquish, B.C., Sáenz-Romero, C., Joyce, D.G., Leites, L.P., St Clair, J.B., López-Upton, J., 2014. Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: reforestation. *For. Ecol. Manage.* 324, 147–157.
- Reynolds, R.T., Meador, A.J.S., Youtz, J.A., Nicolet, T., Matonis, M.S., Jackson, P.L., DeLorenzo, D.G., Graves, A.D., 2013. Restoring composition and structure in southwestern frequent-fire forests: a science-based framework for improving ecosystem resiliency. USDA Forest Service, RMRS-GTR-310.
- Roccaforte, J.P., Fulé, P.Z., Covington, W.W., 2008. Landscape-scale changes in canopy fuels and potential fire behaviour following ponderosa pine restoration treatments. *Int. J. Wildland Fire* 17, 293–303.
- Roccaforte, J.P., Huffman, D.W., Fulé, P.Z., Covington, W.W., Chancellor, W.W., Stoddard, M.T., Crouse, J.E., 2015. Forest structure and fuels dynamics following ponderosa pine restoration treatments, White Mountains, Arizona, USA. *For. Ecol. Manage.* 337, 174–185.
- Romme, W.H., Allen, C.D., Bailey, J.D., Baker, W.L., Bestelmeyer, B.T., Brown, P.M., Eisenhart, K.S., Floyd, M.L., Huffman, D.W., Jacobs, B.F., Miller, R.F., Muldavin, E.H., Swetnam, T.W., Tausch, R.J., Weisberg, P.J., 2009. Historical and modern disturbance regimes, stand structures, and landscape dynamics in pinon-juniper vegetation of the western United States. *Range Ecol. Manage.* 62, 203–222.
- Rother, M.T., Veblen, T.T., Furman, L.G., 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. *Can. J. For. Res.* 45, 1607–1616.
- Savage, M., Mast, J.N., Feddema, J.J., 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. *Can. J. For. Res.* 43, 570–583.
- Schubert, G.H., 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. USDA Forest Service Research Paper RM-123.
- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A., Lau, N.-C., Li, C., Velez, J., Naik, N., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316, 1181–1184.
- Sheppard, P.R., Comrie, A.C., Packin, G.D., Angersbach, K., Hughes, M.K., 2002. The climate of the US Southwest. *Clim. Res.* 21, 219–238.
- Shepperd, W.D., Edminster, C.B., Mata, S.A., 2006. Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado front range. *West. J. Appl. For.* 21, 19–26.
- Singleton, M.P., Thode, A.E., Sánchez Meador, A.J., Iniguez, J.M., 2019. Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. *For. Ecol. Manage.* 433, 709–719.
- Stein, S.J., Kimberling, D.N., 2003. Germination, establishment, and mortality of naturally seeded southwestern ponderosa pine. *West. J. Appl. For.* 18, 109–114.
- Ste-Marie, C., Nelson, E.A., Dabros, A., Bonneau, M.E., 2011. Assisted migration: Introduction to a multifaceted concept. *For. Chron.* 87, 724–730.
- Stultz, C.M., Gehring, C.A., Whitham, T.G., 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytol.* 173, 135–145.
- Vander Wall, S.B., Beck, M.J., 2011. A comparison of frugivory and scatter-hoarding seed-dispersal syndromes. *Bot. Rev.* 78, 10–31.
- Williams, A.P., Allen, C.D., Millar, C.I., Swetnam, T.W., Michaelsen, J., Still, C.J., Leavitt, S.W., 2010. Forest responses to increasing aridity and warmth in the southwestern United States. *Proc. Natl. Acad. Sci. U.S.A.* 107 (50), 21289–21294.
- Williams, A., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., McDowell, D.M., Meko, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* 34, 292–297.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943.
- Whipple, A.V., Cobb, N.S., Gehring, C.A., Mopper, S., Flores-Rentería, L., Whitham, T.G., 2019. Long-term studies reveal differential responses to climate change for trees under soil- or herbivore-related stress. *Front. Plant Sci.* 10, 132.