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Woodland recovery following drought-induced tree mortality across an environmental stress gradient

MIRANDA D. REDMOND[1], NEIL S. COBB[2], MICHAEL J. CLIFFORD[3] and NICHOLE N. BARGER[1]

[1]*Ecology and Evolutionary Biology Department, University of Colorado, Boulder, CO 80302, USA,* [2]*Merriam Powel Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011, USA,* [3]*Division of Earth and Ecosystem Sciences, Desert Research Institute, Las Vegas, NV 89119, USA*

Abstract

Recent droughts and increasing temperatures have resulted in extensive tree mortality across the globe. Understanding the environmental controls on tree regeneration following these drought events will allow for better predictions of how these ecosystems may shift under a warmer, drier climate. Within the widely distributed piñon–juniper woodlands of the southwestern USA, a multiyear drought in 2002–2004 resulted in extensive adult piñon mortality and shifted adult woodland composition to a juniper-dominated, more savannah-type ecosystem. Here, we used pre- (1998–2001) and 10-year post- (2014) drought stand structure data of individually mapped trees at 42 sites to assess the effects of this drought on tree regeneration across a gradient of environmental stress. We found declines in piñon juvenile densities since the multiyear drought due to limited new recruitment and high (>50%) juvenile mortality. This is in contrast to juniper juvenile densities, which increased over this time period. Across the landscape, piñon recruitment was positively associated with live adult piñon densities and soil available water capacity, likely due to their respective effects on seed and water availability. Juvenile piñon survival was strongly facilitated by certain types of nurse trees and shrubs. These nurse plants also moderated the effects of environmental stress on piñon survival: Survival of interspace piñon juveniles was positively associated with soil available water capacity, whereas survival of nursed piñon juveniles was negatively associated with perennial grass cover. Thus, nurse plants had a greater facilitative effect on survival at sites with higher soil available water capacity and perennial grass cover. Notably, mean annual climatic water deficit and elevation were not associated with piñon recruitment or survival across the landscape. Our findings reveal a clear shift in successional trajectories toward a more juniper-dominated woodland and highlight the importance of incorporating biotic interactions and soil properties into species distribution modeling approaches.

Keywords: climate change, Colorado Plateau, competition, *Juniperus monosperma*, nurse plant facilitation, *Pinus edulis*, pinyon pine, stress-gradient hypothesis

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Introduction

Increasing temperatures associated with global climate change have resulted in significant shifts in vegetation distribution over the past several decades (Parmesan & Yohe, 2003; Kelly & Goulden, 2008; Chen *et al.*, 2011), and these shifts are likely to continue over the next century (Pearson *et al.*, 2002; Williams *et al.*, 2013). Regional warming and associated increasing water deficits have resulted in recent increases in tree mortality (van Mantgem *et al.*, 2009; Allen *et al.*, 2010; Williams *et al.*, 2013) and insect outbreaks (Raffa *et al.*, 2008; Mitton & Ferrenberg, 2012). These mortality events have dramatically changed forest and woodland structure and composition, altering water and energy fluxes (Guardiola-Claramonte *et al.*, 2011; Royer *et al.*, 2011; Adams *et al.*, 2012), carbon cycling (Kurz *et al.*, 2008; Brown *et al.*, 2010; Pfeifer *et al.*, 2011; Hicke *et al.*, 2012), and ecosystem services (Anderegg *et al.*, 2013). However, long-term changes in these forest and woodland ecosystems will depend on the ecosystems' ability to recover following disturbances under a warmer, drier climate.

Increasing temperatures and associated increases in water deficits are likely affecting tree regeneration dynamics, even in areas without elevated tree mortality. In arid and semi-arid forests and woodlands, cool, wet climatic conditions have historically been optimal for regional tree recruitment events (League & Veblen, 2006; Barger *et al.*, 2009; Shinneman & Baker, 2009). Experimental temperature and water manipulations further confirm the negative effects of increasing water deficits on tree recruitment (McCallum, 2011; Dulamsuren *et al.*, 2013). While these previous studies suggest

Correspondence: Miranda D. Redmond, tel. +1 (415) 300-6901, fax +1 (303) 492-8699, e-mail: mirandaredmond@gmail.com

that regional warming may alter forest and woodland composition and structure in many semi-arid ecosystems, warming effects may vary depending on differences in local climate, soil properties, and vegetation structure.

Understanding the effects of these local site factors on tree regeneration is of particular importance given the need to better assess which species and populations will be most vulnerable to increased warming. In arid and semi-arid ecosystems, populations experiencing hotter, drier local climates are generally considered more vulnerable to increasing water deficits compared to populations at cooler, wetter local climates of a species range (Allen & Breshears, 1998). However, the effects of these local climatic differences on tree establishment and survival may be moderated by nurse plant facilitation (Bertness & Callaway, 1994). For example, microclimatic conditions beneath tree and shrub canopies often favor juvenile tree survival during drought (Mueller *et al.*, 2005; Sthultz *et al.*, 2007). Conversely, perennial grasses have shallow roots and may compete with tree juveniles for water and nutrients (Scholes & Archer, 1997; Chambers *et al.*, 1999).

The facilitative effects of tree and shrub nurse plants on juvenile tree survival can vary across stress gradients (Bertness & Callaway, 1994; Gómez-Aparicio *et al.*, 2004; Sthultz *et al.*, 2007; Maestre *et al.*, 2009), with facilitative effects often becoming increasingly prevalent in areas or time periods with higher environmental stress (i.e., stress-gradient hypothesis; Bertness & Callaway, 1994). This suggests that the importance of nurse plant facilitation may be higher in areas with greater environmental stress, such as areas with higher climatic water deficits. However, the strength of these facilitative interactions across environmental stress gradients can also vary depending on the ecophysiological traits of the species and the type of stress (Maestre *et al.*, 2009; Holmgren & Scheffer, 2010).

We focused our study on the widely distributed piñon–juniper woodlands of the southwestern USA, where there was extensive piñon mortality between 2002 and 2004 due to a multiyear drought accompanied by warm temperatures and bark beetle (*Ips confusus*) infestations (Breshears *et al.*, 2005; Floyd *et al.*, 2009; Clifford *et al.*, 2011, 2013). Piñon mortality was highest among reproductively mature piñon trees (Floyd *et al.*, 2009), with mortality reaching upwards of 90% in some areas, resulting in a large increase in adult juniper dominance relative to piñon (Mueller *et al.*, 2005; Koepke *et al.*, 2010). Future woodland composition and structure will be largely determined by the effects of this drought event on tree regeneration. Previous research suggests that juniper is less strongly facilitated by overstory trees and shrubs compared to piñon (Redmond & Barger, 2013), likely due to its greater drought tolerance (West *et al.*, 2007; Breshears *et al.*, 2008; McDowell *et al.*, 2008). As a result, juniper has higher rates of establishment following disturbances compared to piñon (Tausch & Tueller, 1977; Everett & Ward, 1984; Redmond *et al.*, 2013), which may also be due to the greater seed longevity of juniper (Chambers *et al.*, 1999). Taken together, this suggests that recent piñon mortality and increasing water deficits may negatively affect piñon juveniles and shift juvenile composition to a more juniper-dominated community.

Our objective was to determine how tree mortality and recent increases in water deficits have affected tree regeneration dynamics in piñon–juniper woodlands of the southwestern USA and how these affects vary across the landscape due to differences in vegetation structure, soil properties, and local climatic conditions. Uniquely, we have detailed stand structure data from 42 sites across the San Francisco Peaks mountain range in northern Arizona with individually mapped trees of all size classes from 2 to 4 years prior to the mortality event (1998–2001) as well as 10 years after the mortality event (2014). This detailed dataset allowed us to distinguish how increasing water deficits and overstory tree mortality have affected the two pathways of tree regeneration, advanced regeneration (i.e., the survival of juveniles that established prior to the drought) and new recruitment (i.e., seedling establishment after the drought) across the landscape. Further, the study area spans a climatic, soil, and vegetation structure gradient, which allowed us to determine how tree regeneration varies across a gradient of environmental stress. The specific hypotheses we addressed were as follows: (1) Increased water deficits and overstory piñon mortality would result in a decline of piñon juvenile densities due to high juvenile mortality and limited new recruitment, but would not affect juniper juvenile densities; (2) overstory trees and shrubs would facilitate piñon juvenile survival and, to a lesser degree, juniper juvenile survival; (3) juvenile piñon survival would be lower in areas with greater environmental stress, although this relationship would be moderated by nurse plant facilitation; and (4) new piñon recruitment would be higher in areas with greater seed availability, lower environmental stress, and a greater density of nurse trees and shrubs.

Materials and Methods

Study area and sampling design

The study area was located approximately 27 km north of Flagstaff, Arizona, USA, on the north side of the San Francisco Peaks mountain range (see Fig. 1). Forty-two sites were

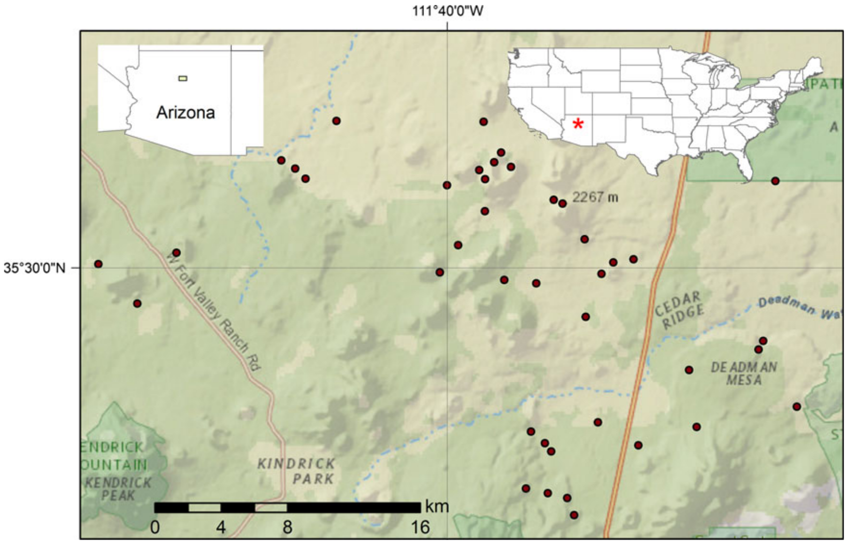

Fig. 1 Map of the 42 sites sampled in northern Arizona, USA. Map was created using ESRI software (ArcMap version 10.1), and the base map used is the National Geographic World Map, which includes data from National Geographic, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, and increment P Corp.

selected using US Forest Service maps and aerial photography to ensure sites encompassed the elevational range (1680 m–2300 m) of piñon (*Pinus edulis*)–juniper (*Juniperus monosperma*) woodlands and were <1 km from a road for accessibility. This study area averages 9 °C in mean annual temperature and 380 mm in total annual precipitation, with approximately half falling as rain and snow over winter and the rest as rain over summer (PRISM Climate Group, 2014). Soils in the study area were derived from basalt, basalt cinder, or mixed igneous parent material and include Typic Argiborolls, Typic Argiustolls, Typic Durustands, Typic Ustorthents, Typic Haplustalfs, Typic Ustochrepts, Mollic Eutroboralfs, and Vitandric Ustochrepts (USDA ESC, 1995). While the dominant species are piñon and juniper, ponderosa pine (*Pinus ponderosa*) and alligator juniper (*J. deppeana*) are also present at some of the sites (see Table S1 for stand structure data). Dominant shrub species include apache plume (*Fallugia paradoxa*), rubber rabbitbrush (*Ericameria nauseosa*), and Fremont's mahonia (*Mahonia fremontii*).

Similar to much of the southwestern USA, this study area experienced extensive adult piñon mortality between 2002 and 2004 (Table S1; Clifford *et al.*, 2011) due to a multiyear drought accompanied by abnormally high vapor pressure deficits (Floyd *et al.*, 2009; Williams *et al.*, 2013; Fig. 2). In these semi-arid woodlands, precipitation and vapor pressure deficit have been shown to strongly affect tree growth and mortality through their influence on plant water stress (Breshears *et al.*, 2013; Clifford *et al.*, 2013; Williams *et al.*, 2013). Our study area has continued to experience water stress over the past decade due to higher mean annual vapor pressure deficits and lower annual precipitation than the 1900–2014 average (Fig. 2), with the exception of 1 year (2005).

All sites were established and sampled between 1998 and 2001 (hereafter referred to as the 2000 sampling) and then re-sampled again in 2014 using the same methods as in the 2000 sampling. At each site, we established a 10 m × 200 m transect and divided that transect into twenty 10 m × 10 m plots. We then sampled alternating plots along each transect (i.e., 10 plots total per transect). At a subset of sites ($n = 7$) with lower tree densities, longer transects were established (up to 300 m) resulting in a larger number of plots sampled at those sites (up to 15 plots per transect).

In both the 2000 and 2014 sampling, for each tree located within each of these plots, we recorded their basal trunk diameter (BTD) and status (dead or alive). For all juvenile trees, which included seedlings (BTD < 2.5 cm) and saplings (BTD ≥ 2.5 to <5 cm), we also recorded whether the juvenile was beneath the canopy of a tree or shrub (hereafter referred to as 'nursed') or in the interspace (i.e., not directly beneath the canopy of a tree or shrub). If the juvenile was nursed, we recorded the nurse species and status (dead or alive). In the 2000 sampling, we installed stakes at the four corners of each plot, mapped every tree to the nearest meter, and tagged a subset of trees at each site.

For the 2014 sampling, we also quantified surface soil texture, slope, aspect, and shrub and herbaceous cover. To quantify shrub and herbaceous cover, we established a 14-m transect diagonally across each plot and used the line point intercept method. Specifically, we dropped a pin flag every 0.5 meters along each transect and recorded all shrub species and herbaceous functional groups (perennial grass, annual grass, perennial forb, annual forb) that made contact with the pin flag (Herrick *et al.*, 2005). To quantify surface soil texture, we collected one soil sample (2.5 cm in diameter and 10 cm in depth) 1 m out from the canopy dripline of a tree or shrub closest to the center of each plot. Soils were then sieved through a 2-mm sieve. The >2 mm fraction was weighed as gravel, and the <2 mm fraction was used to estimate percent sand, silt, and clay using the hydrometer method (Gee & Or, 2002) at the Colorado State University Soil Laboratory.

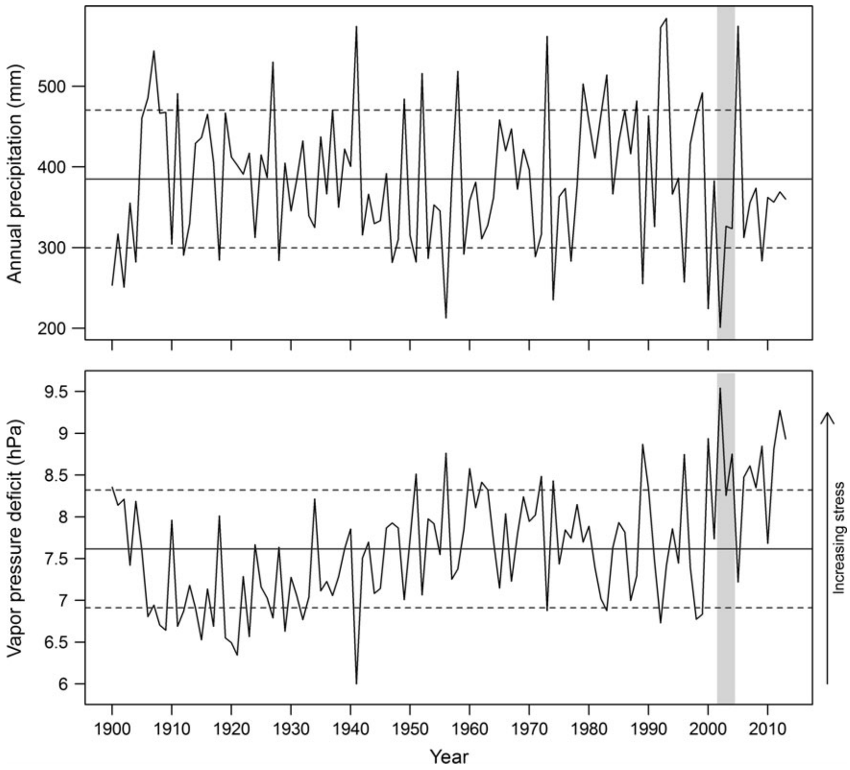

Fig. 2 Total annual precipitation (top) and mean annual vapor pressure deficit (bottom) from 1900 to 2013 averaged across our study sites. Solid horizontal line indicates the 1900–2013 mean, whereas dashed lines indicate the mean ± 1 standard deviation. Vapor pressure deficit was calculated following the equation in Williams *et al.* (2013). Climate data were from the PRISM Climate Group (PRISM Climate Group, 2014) and were averaged across all sites in our study area.

Statistical analyses: woodland regeneration dynamics

We examined whether there has been an overall shift in juvenile tree densities from 1998 to 2001 (predrought) to 2014 (10 years postdrought) across our study area. To do this, we performed paired *t*-tests to examine whether juvenile tree densities changed between the two time periods across our study sites ($n = 42$). We performed separate paired *t*-tests for the two species (piñon and juniper) and the two juvenile size classes (seedlings and saplings). There were high levels (3400 stems ha^{-1} at some sites) of newly recruited juniper seedlings that were <1 year old in 2014 at many of the sites. We performed the analysis with and without the inclusion of these newly recruited seedlings, because many of these <1-year-old seedlings will likely die by 2015.

Modeling the effects of overstory trees and shrubs on juvenile tree survival

To understand whether overstory trees and shrubs facilitate juvenile survival, we examined whether survival from 2000 to 2014 differed between tree juveniles (i.e., seedlings and saplings) that were beneath the canopy of a tree or shrub and juveniles that were in the interspace. To model juvenile survival, we used generalized linear mixed-effects models (GLMMs) with a binomial distribution and a logit link function (Zuur *et al.*, 2007; Bolker *et al.*, 2009). GLMMs were fit using the Laplace approximation method using the *glmer* function in the R package *lme4* (Bates *et al.*, 2014a,b). We performed separate analyses for each tree species (piñon [$n = 1106$] and juniper [$n = 318$]). The fixed-effect predictor variables in our models were canopy microsite (nursed vs. canopy interspace) and basal trunk diameter. We included basal trunk diameter because tree size can also affect survival (Mueller *et al.*, 2005; Floyd *et al.*, 2009). To account for variability in survival across sites, the intercept for site was included as a random effect.

We also examined the effect of different nurse plants on juvenile piñon survival. We used the same GLMM approach as above but with nurse type and basal trunk diameter as fixed effects and the intercept for site as a random effect. However, we restricted this analysis to only piñon juveniles that were nursed by a tree or shrub, because there were too few juniper juveniles that were nursed by different types of trees and shrubs (<30 juniper juveniles were nursed by live ponderosa pine, live shrubs, and live piñon). We also excluded juveniles that were nursed by multiple different types of nurse plants, such as juveniles that were nursed by both a shrub and a juniper tree. This resulted in a total of 682 piñon juveniles that were included in the analysis, of which 416 were nursed by a live juniper, 53 were nursed by a live ponderosa pine, 32 were nursed by a live piñon, 82 were nursed by a live shrub, and 99 were nursed by a recently dead piñon (i.e., a piñon that was live during the 2000 sampling but had died by the 2014 sampling). To compare the differences among nurse types, we

Table 1 Predictor variables and their hypothesized ecological function that were used to model new piñon recruitment

Predictor variable	Ecological function	Range
Climatic water deficit	Water availability	188–839 mm
Soil available water capacity	Water availability	2.0–15.0%
Live piñon basal area	Microsite and seed availability	0–7.2 m^2 ha^{-1}
Grass cover	Microsite (competition)	0–74%
Live shrub and tree cover (not including piñon)	Microsite (facilitation)	1–42%

performed *post hoc* pairwise comparisons using the Tukey HSD method to adjust *P*-values in the *lsmeans* function in the R package *lsmeans* (Lenth, 2014).

Modeling the spatial variability in juvenile piñon survival and new recruitment

To test our hypothesis that new piñon recruitment is higher in areas with greater seed availability, lower environmental stress, and a greater density of nurse trees and shrubs, we used a generalized linear modeling approach with a negative binomial type 1 distribution (family 'nbinom1' in the *glmmADMB* package; Fournier *et al.*, 2012; Skaug *et al.*, 2014) and a log link function due to over dispersion. In our model, new piñon recruitment, which we defined as the number of juveniles that established following the 2000 sampling, was our response variable and a variety of abiotic and biotic variables that we hypothesized *a priori* would influence new piñon recruitment (see Table 1) were our predictor variables.

We included two abiotic predictor variables in our model that we hypothesized would influence environmental stress: climatic water deficit and surface soil available water capacity, both of which provide an estimate of water stress in these semi-arid ecosystems. We used our estimates of percentage sand, silt, clay, and gravel from each site to calculate surface soil available water capacity by subtracting the wilting point (θ_{1500}) from field capacity (θ_{33}), which we calculated following the equations in Table 1 of Saxton & Rawls (2006). We used surface (top 10 cm) soil available water capacity because our study is focused on piñon juveniles, which have shallow rooting depths compared to adults. In addition to providing an estimate of water stress, surface soil available water capacity is also highly correlated with nutrient availability in our study area (Cobb *et al.*, 1997). Climatic water deficit is the amount of water by which potential evapotranspiration exceeds actual evapotranspiration and is a biologically meaningful measure of climate that is strongly correlated with vegetation distribution (Stephenson, 1990, 1998). Climatic water deficit was estimated using a Thornthwaite-type water balance model (Thornthwaite, 1948; Dingman, 2002) following the equations provided in Lutz *et al.* (2010). Climatic water deficit incorporates 30-year averages of monthly precipitation and temperature (800 km resolution, obtained from PRISM Climate Group, 2014), heat load (calculated based off of slope, aspect, and latitude), and day length (see Appendix S1 for more details on climatic water deficit calculations) and was highly negatively correlated with elevation (Pearson's $r = -0.94$; Fig. S1).

We also included perennial grass cover as a predictor variable in our model, because perennial grasses have been hypothesized to compete with piñon juveniles (Chambers *et al.*, 1999) and may therefore be an important type of biotic environmental stress. As an estimate of seed availability and live piñon microsite availability, we used live piñon basal area as a predictor variable in our model, which was highly correlated with surface piñon cone density (see Appendix S1 for methodology; Fig. S2a; Pearson's $r = 0.88$) and piñon canopy area (Fig. S2b; Pearson's $r = 0.99$) at our study sites. For our analyses, we log-transformed live piñon basal area to linearize the relationship between piñon basal area and new piñon recruitment. Lastly, we included total live shrub, juniper, and ponderosa pine cover as a predictor variable in our model as an estimate of nurse plant microsite availability. Predictor variables were not strongly correlated with one another (Pearson's $r \leq 0.47$), and the variance inflation factor for each predictor variable using an ordinary least-squares regression was <2. The complete model was simplified using stepwise backwards selection following the procedure in Zuur *et al.* (2007). In this procedure, we examined all predictor variables using backward selection to produce a final model based on minimizing Akaike information criterion (AIC, Akaike, 1973).

To test our hypothesis that environmental stress negatively affects juvenile piñon survival and that this effect is moderated by nurse plant facilitation, we examined the association between piñon juvenile survival and climatic water deficit, soil available water capacity, and perennial grass cover, among both nursed and interspace juveniles. To do this, we used a GLMM approach with a binomial distribution and a logit link function. Site was included as a random effect, and climatic water deficit, soil available water capacity, perennial grass cover, and nursed (nursed vs. interspace) were included as fixed effects in our model. We also included interactions between nursed and our abiotic and biotic factors, because we hypothesized that nurse plants could moderate environmental stress. Lastly, we included basal trunk diameter as a fixed effect in our model to account for variability in survival with tree size. Similar to above, we used a backwards selection approach to reduce our model by sequentially removing the three fixed-effect predictor variables of interest (climatic water deficit, soil available water capacity, and perennial grass cover) and their interactions with nursing based on minimizing AIC. For all analyses, continuous predictor variables were z-scaled using the function *scale* in R and, thus, standardized regression coefficients (β_{std}) are reported. All analyses were performed in R version 3.1.1 (R Core Team, 2014).

Results

Woodland regeneration dynamics

Juvenile (seedling + sapling) piñon densities declined by over 55% on average across the study area from

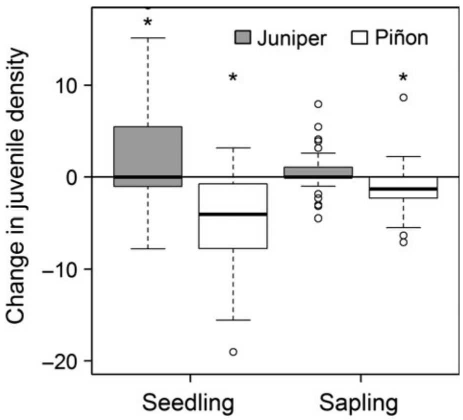

Fig. 3 Changes in juniper (gray) and piñon (white) seedling (basal trunk diameter <2.5 cm) and sapling (basal trunk diameter ≥2.5 cm and <5 cm) densities (stems ha^{-1}, square root transformed) from 2000 to 2014. Bolded middle lines represent median values, boxes represent interquartile ranges, and whiskers equal 1.5 times the interquartile range. Asterisks denote significant changes in juvenile densities, with $\alpha = 0.05$.

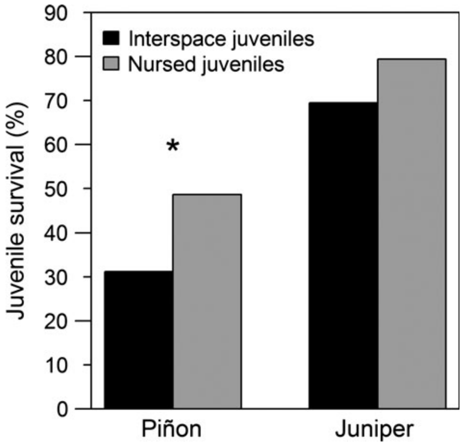

Fig. 4 Percent piñon and juniper juvenile survival among interspace (black) and nursed (gray) juveniles. Asterisks denote significant ($P < 0.05$) differences in survival between nursed and interspace juveniles within a species from the generalized linear mixed-effect modeling. The data shown do not include the random effects of site or juvenile size, which were included in the model.

2000 to 2014. Due to limited new recruitment since 2000 (mean ± SE: 21 ± 6 stems per ha^{-1}) and high juvenile mortality (61 ± 5% mortality) between 2000 and 2014, piñon seedling (basal trunk diameter ≥ 2.5 cm and <5 cm) densities declined by 57% (from 220 stems ha^{-1} in 2000 to 95 stems ha^{-1} in 2014; $P < 0.0001$; Fig. 3). Piñon sapling (basal trunk diameter ≥2.5 cm and <5 cm) densities declined by 19% during that time period (from 42 stems ha^{-1} in 2000 to 34 stems ha^{-1} in 2014; $P = 0.004$; Fig. 3).

Unlike piñon, juniper juvenile densities showed no declines from 2000 to 2014. There was over a threefold increase in juniper seedling densities from 2000 (62 ± 14 stems ha^{-1}) to 2014 (226 ± 102 stems ha^{-1}) when newly recruited (<1 year old) seedlings in 2014 were included in the analysis ($P < 0.0001$; Fig. 3). With newly recruited seedlings in 2014 excluded from the analysis, there was no change in juniper seedling densities from 2000 (62 ± 14 stems ha^{-1}) to 2014 (54 ± 11 stems ha^{-1}, $P = 0.59$). Juniper saplings showed marginally significant increases in density from 2000 (10 stems ha^{-1}) to 2014 (18 stems ha^{-1}, $P = 0.07$; Fig. 3).

Effects of overstory trees and shrubs on juvenile tree survival

Supporting our hypothesis that overstory trees and shrubs facilitate juvenile survival, piñon juveniles beneath the canopy of an overstory tree or shrub were 2.5 times more likely to survive than those in the canopy interspace (GLMM $\beta_{\text{nursed}} = 0.95 \pm 0.20$ [1 SE], $z = 0.93$, $P < 0.0001$; Fig. 4). The type of nurse plant also affected juvenile survival (Fig. 5; Table S2). Piñon juveniles beneath juniper and ponderosa pine trees were over 3.5 times more likely to survive than those beneath piñon trees that had recently (post 1998) died ($P < 0.009$; Fig. 5; Table S2). Piñon juveniles beneath juniper trees were also 2.4 times more likely to survive than those beneath shrubs ($P = 0.01$; Fig. 5; Table S2). In addition, basal trunk diameter of the juvenile was positively associated with juvenile survival (GLMM $\beta = 0.23 \pm 0.07$, $z = 3.0$, $P = 0.002$). However, unlike piñon juveniles, overstory trees and shrubs did not strongly influence juniper juvenile survival (GLMM $\beta_{\text{nursed}} = 0.78 \pm 0.42$, $z = 1.85$, $P = 0.06$; Fig. 4), although the marginally significant effect may be due to the smaller sample size of juniper juveniles ($n = 318$) compared to piñon ($n = 1106$). Basal trunk diameter was also only marginally positively associated with juniper juvenile survival (GLMM $\beta = 0.31 \pm 0.15$, $z = 1.75$, $P = 0.08$).

Spatial variability in juvenile piñon survival and new recruitment

While there were significant declines in piñon juvenile densities from 2000 to 2014 in our study area (Fig. 3), juvenile piñon survival and new piñon recruitment varied considerably across our sites, with juvenile survival ranging from 0 to 100% and new piñon recruitment (i.e., juveniles that established since 2000) ranging from 0 to 190 stems ha^{-1}. New piñon recruitment was strongly positively associated with soil available water capacity (GLM $\beta_{\text{std}} = 0.92$, GLM $z = 4.76$, $P < 0.0001$;

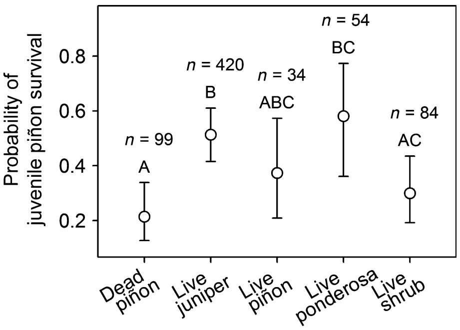

Fig. 5 The predicted mean effect and 95% confidence interval of the different types of nurse trees and shrubs on the probability of piñon juvenile survival. Different letters denote significant ($P < 0.05$) differences in parameter estimates between the different nurse plants, which was calculated using least-square means. Numbers above each letter denote the sample size. P-values were adjusted using the Tukey HSD method.

Table 2 Results of the final model resulting from our backwards stepwise selection procedure to predict new piñon recruitment. All continuous predictor variables were z-scored prior to analysis and, thus, the regression coefficients reported are standardized

Fixed-effect variable	β log(odds)	SE	z value	P-value
Intercept	0.155	0.29	0.54	0.59
Live piñon basal area (log scaled)	0.576	0.16	3.59	0.0003
Soil available water capacity (AWC)	0.92	0.19	4.76	<0.0001

Table 2; Fig. 6) and live piñon basal area (GLM $\beta_{\text{std}} = 0.58$, GLM $z = 3.59$, $P = 0.0003$; Table 2; Fig. 6). Interestingly, climatic water deficit, perennial grass cover, and tree and shrub cover were not included in the final model, suggesting those predictor variables did not strongly influence new piñon recruitment in our study area (see Fig. S3 for a plot showing the relationship between these predictor variables and new piñon recruitment). Even though our model results suggest that variability in climatic water deficit across our study area did not strongly affect new piñon recruitment, all sites with mean annual climatic water deficit >34 mm had limited (≤10 stems ha^{-1}) new recruitment (Fig. S3), suggesting there may be a threshold response.

The resulting model from our backwards stepwise selection procedure to predict juvenile piñon survival included both perennial grass cover and soil available water capacity, but not climatic water deficit (Table 3). Unlike the model for new piñon recruitment, we had survival and nursing data for each individual juvenile that had established prior to the 2000 sampling, which allowed us to model whether the effects of these predictor variables on juvenile survival depended upon nursing status. The effects of both perennial grass cover and soil available water capacity on juvenile piñon survival depended on whether the juvenile was nursed by an overstory tree or shrub. Perennial grass cover was negatively associated with juvenile piñon survival only among juveniles in the canopy interspace (Fig. 7; Table 3). Whereas survival of nursed piñon juveniles was not associated with perennial grass cover (Fig. 7; Table 3), survival of these nursed juveniles was positively associated with soil available water capacity (Fig. 7; Table 3). Unlike nursed piñon juveniles, soil available water capacity was not associated with survival of interspace piñon juveniles. Similar to new piñon recruitment, climatic water deficit was not associated with juvenile survival (Fig. S4).

Discussion

Drought-induced tree mortality is an emerging global phenomenon and is predicted to increase with climate change (Allen *et al.*, 2010; Williams *et al.*, 2013). Our study highlights how these drought events may affect woodland structure and composition over longer time scales due to changes in regeneration dynamics, which has important implications for water and energy fluxes (Guardiola-Claramonte *et al.*, 2011; Royer *et al.*, 2011), carbon cycling (Kurz *et al.*, 2008; Hicke *et al.*, 2012), and ecosystem services (Anderegg *et al.*, 2013). Further, our findings suggest that biotic interactions and soil properties strongly influence tree regeneration patterns across the landscape and will likely play an important role in species range shifts under a warmer, drier climate.

Woodland regeneration dynamics

Our findings reveal a clear shift in successional trajectories since the 2002–2004 drought due to a decline in piñon juvenile densities and marginal increases in juniper juvenile densities. Through limited new piñon recruitment and high juvenile piñon mortality, piñon–juniper woodlands will likely continue to become more juniper-dominated following recent drought-induced mortality events. The limited new piñon recruitment is consistent with previous studies (Redmond & Barger, 2013) and is likely a consequence of decreased seed availability and the sustained hotter, drier climatic conditions over the past decade. Seed availability is often a limiting factor to conifer regeneration following stand replacing or partial stand replacing disturbances (LePage *et al.*, 2000), and this may be especially the case with piñon because piñon seed viability declines rapidly after the first year (Meeuwig & Bassett, 1983).

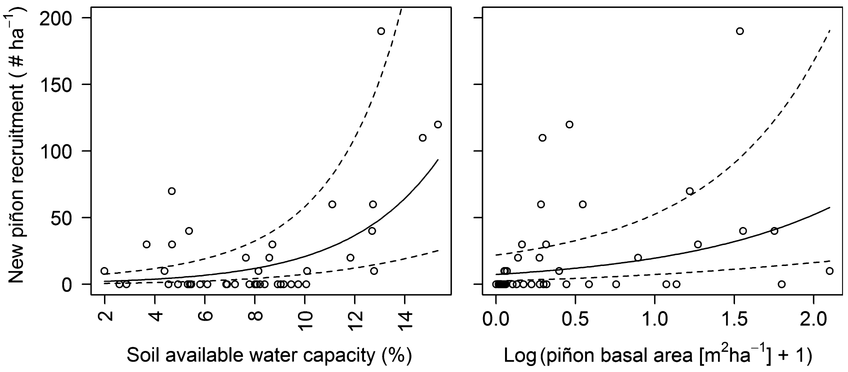

Fig. 6 The predicted mean effect (dashed lines show 95% CI) of live piñon basal area (left) and soil available water capacity (right) on new piñon recruitment. Open circles show each data point rather than the partial residuals.

Table 3 Results of the final model resulting from our backwards stepwise selection procedure to predict juvenile piñon survival among nursed and canopy interspace juveniles across an environmental stress gradient. All continuous predictor variables were z-scored prior to analysis and, thus, the regression coefficients reported are standardized

Fixed-effect variable	β log(odds)	SE	*z* value	*P*-value
Intercept (interspace juveniles)	−1.22	0.23	−5.15	0.94
Nursed	−1.70	0.60	4.71	0.005
Grass cover	−0.94	0.27	−3.47	0.0005
Soil available water capacity (AWC)	0.08	0.23	0.37	0.72
Basal trunk diameter	0.25	0.08	3.37	0.0007
Nursed X Grass Cover	0.71	0.23	3.04	0.002
Nursed X soil AWC	0.49	0.19	2.58	0.01

Consistent with the seed limitation hypothesis, we found a strong positive association between new piñon recruitment and adult live piñon densities across the landscape. Furthermore, the low levels of new piñon recruitment and juvenile piñon survival throughout our study area may have been due to the abnormally hot, dry conditions over the past decade. Cool, wet climatic conditions have historically been optimal for regional tree recruitment events in semi-arid regions (League & Veblen, 2006; Barger *et al.*, 2009; Shinneman & Baker, 2009), and the more arid conditions of the past decade may result in declines in cone production (Redmond *et al.*, 2012) and reduced seedling establishment and survival (McCallum, 2011; Dulamsuren *et al.*, 2013).

Abiotic and biotic controls on tree regeneration

Our results highlight the importance of biotic interactions and soil properties in influencing tree regeneration across the landscape. As hypothesized, nurse trees and shrubs strongly facilitated juvenile piñon survival. The facilitative effects of these nurse plants are consistent with previous studies (Sthultz *et al.*, 2007; Redmond & Barger, 2013) and may partially explain why piñon has less establishment relative to juniper following canopy disturbances such as chaining (Redmond *et al.*, 2013) and drought-induced tree mortality reported here. Our findings also show that specific types of nurse plants better facilitate juvenile piñon survival than others. In particular, juvenile piñon survival was higher beneath ponderosa pine and juniper trees compared to piñon trees that died, likely due to the loss in canopy cover following mortality. Survival was also higher among juveniles beneath juniper trees compared to those beneath shrubs. While shrubs have been hypothesized to strongly facilitate piñon recruitment (Redmond & Barger, 2013), our findings suggest that they do not facilitate juvenile piñon survival as strongly as trees and this may be due to higher temperatures beneath shrub canopies (Chambers, 2001). Our findings may be only applicable to the shrub community in our study area, which was dominated by apache plume, Fremont’s mahonia, and rubber rabbitbrush. In addition, competition may be greater beneath trees compared to shrubs once the juveniles become larger due to the above-ground competitive release that occurs once the juvenile grows taller than the shrub. Overall, the strong facilitative effects of nurse plants on juvenile piñon survival highlight how drought-induced tree mortality may continue to alter woodland regeneration dynamics and result in a more juniper-dominated woodland.

Nurse plants also moderated the effects of environmental stress on juvenile piñon survival. Consistent with our hypothesis, survival of interspace juveniles was more negatively associated with perennial grass cover compared to nursed juveniles. Perennial grasses have been hypothesized to compete with piñon

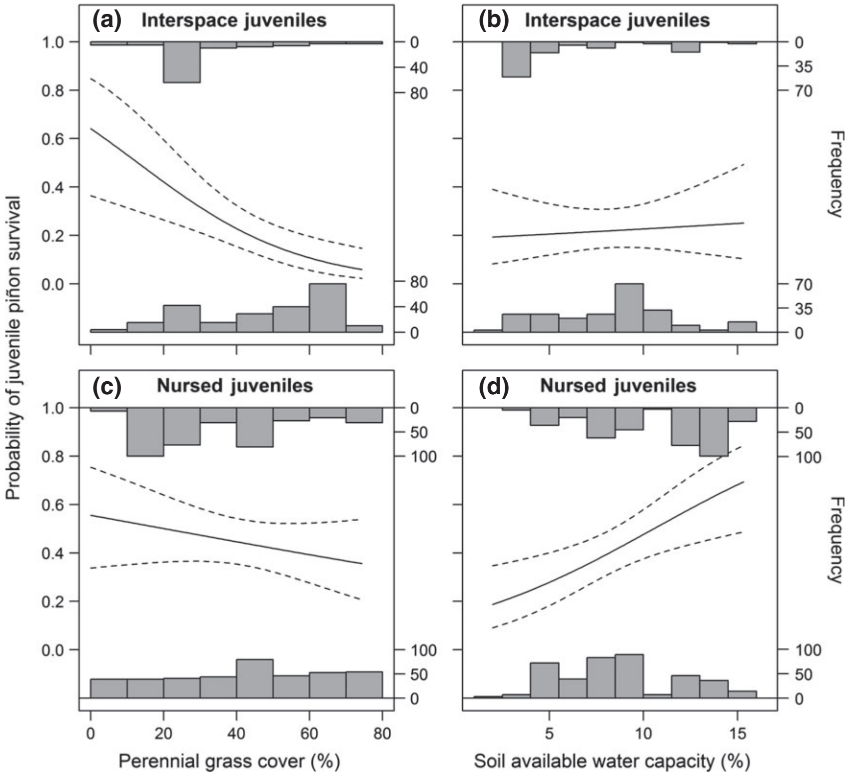

Fig. 7 The predicted mean effect (dashed lines show 95% CI) of perennial grass cover (A and C) and soil available water capacity (B and D), two site-level predictor variables, on the probability of juvenile piñon survival among both interspace (A and B) and nursed (C and D) juveniles. Histograms show how the frequency (secondary y axis) of juveniles that lived (top histogram) and died (bottom histogram) varies across each predictor variable.

juveniles (Chambers *et al.*, 1999), and our findings highlight how this perennial grass competition may be particularly important among interspace piñon juveniles. These perennial grasses have shallow roots and likely compete with piñon juveniles for water and nutrients while also not ameliorating stress by reducing evapotranspiration through shading, unlike trees and shrubs (Breshears *et al.*, 1998). The interactive effect of nurse plant facilitation and perennial grass competition on juvenile survival is likely because nurse plants moderate the environment in such a way that reduces perennial grass cover beneath their canopies. This interactive effect also supports the stress-gradient hypothesis (Bertness & Callaway, 1994), which hypothesizes that the facilitative effects of nurse plants will be greatest in areas with greater environmental stress. Contrary to our hypothesis, however, survival of nursed piñon juveniles was more strongly positively associated with soil available water capacity compared to interspace juveniles. The facilitative effects of nurse plants were therefore greater at sites with higher soil available water capacity (i.e., less abiotic stress), which is counter to the stress-gradient hypothesis. When soil resource availability is the predominant driver of stress, previous studies in arid and semi-arid ecosystems have also found limited evidence for the stress-gradient hypothesis (see Maestre *et al.*, 2009 for a review). In addition, shading provided by trees and shrubs reduces evaporation (Breshears *et al.*, 1998), and this reduction in evaporation may more strongly influence available water in areas with higher soil available water capacity.

Our findings suggest that soil properties strongly influence tree regeneration patterns across the landscape. Consistent with our findings, soil available water capacity was also strongly associated with piñon regeneration in southwestern Colorado (Redmond & Barger, 2013). Regionally, there was greater adult piñon mortality in areas with lower soil available water capacity (Peterman *et al.*, 2012), further highlighting the importance of soil properties in influencing tree mortality and recruitment.

Surprisingly, mean annual climatic water deficit and elevation, which are often strongly correlated with vegetation distribution (Stephenson, 1990, 1998), were not strongly associated with new piñon recruitment or juvenile survival across the landscape. These results are counter to species envelope model predictions, which predict that piñon pine and other semi-arid species will shift to areas with cooler, wetter locations that have lower climatic water deficits as the climate warms (McCallum, 2011). The lack of an association between climatic water deficit and new piñon recruitment may be partially due to the large number of zeroes (22 of our 42 study sites had no new recruitment). In addition, sites with mean annual climatic water deficit >34 mm had limited new piñon recruitment, suggesting there may be a threshold response to climatic water deficit. Overall, the relatively weak association between climatic water deficit and piñon regeneration, particularly juvenile survival, suggests that other factors, such as biotic interactions and soil properties, more strongly influence piñon regeneration across the landscape. As such, these results highlight the importance of incorporating biotic interactions and soil properties into species distribution modeling approaches.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description of climatic water deficit calculations and surface piñon cone density methodology.
Table S1. Average live tree density (tress ha^{-1}) in 2000 (predrought) and 2014 (postdrought) in each size class (based on basal trunk diameter [BTD]) across our study sites. The range is included in parentheses.
Table S2. Results of the *post-hoc* pairwise comparison of the effects of different nurse plants on juvenile piñon survival. *P*-values were adjusted using the Tukey HSD method.
Figure S1. The relationship between 30 year mean annual climatic water deficit (mm) and elevation (m) at our study sites.
Figure S2. The relationship between piñon basal area and surface piñon cone density (A) and total piñon canopy cover (B) at our study sites.
Figure S3. The relationship between the three predictor variables that were not included in our final regression model and new piñon recruitment.
Figure S4. Proportion of interspace (A) and nursed (B) juveniles that survived (grey) and died (black) across sites with varying climatic water deficits. Above each bar includes the sample size (i.e. the number of juveniles within each climatic water deficit bin).