Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality

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Running Headline: Woodland resilience to regional drought
Abstract

1. Drought events occurring under warmer temperatures (i.e., “hotter droughts”) have resulted in widespread tree mortality across the globe, and may result in biome-level vegetation shifts to alternate vegetation types if there is a failure of trees to regenerate. We investigated how overstorey trees, understorey vegetation, and local climatic and edaphic conditions interact to influence tree regeneration, a key prerequisite for resilience, in a region that has experienced severe overstorey tree mortality due to hotter droughts and beetle infestations.

2. We used detailed field observations from 142 sites that spanned a broad range of environmental conditions to evaluate the effects of climate and recent tree mortality on tree regeneration dynamics in the spatially extensive piñon (Pinus edulis)-juniper (Juniperus osteosperma, J. monosperma) woodland vegetation type of the southwestern USA. We used a structural equation modeling framework to identify how tree mortality and local climatic and edaphic conditions affect piñon and juniper regeneration and electivity analyses to quantify the species-specific associations of tree juveniles with overstorey trees and understorey shrubs.

3. Piñon regeneration appears to be strongly dependent upon advanced regeneration, (i.e., the survival of juvenile trees that established prior to the mortality event), the survival of adult seed-bearing trees (inferred from basal area of surviving trees), and the facilitative effects of overstorey trees for providing favourable microsites for seedling establishment. Model results suggest that local edaphoclimatic conditions directly affected piñon and juniper regeneration, such that stands with hotter, drier local climatic conditions and lower soil available water capacity had limited tree regeneration following large-scale dieback.

4. Synthesis. We identify four indicators of resilience to hotter drought conditions: (1) abundant advance regeneration of tree seedlings; (2) sufficient canopy cover for survival of emergent
seedlings and existing regeneration; (3) sufficient seed source from surviving trees with high
reproductive output; (4) areas with cooler and wetter local climates and greater soil available
water capacity. In the absence of these conditions, there is greater likelihood of woodlands
transitioning to more xeric vegetation types following die-back.

**Introduction**

Droughts occurring under warmer temperatures associated with global climate change
have resulted in widespread tree mortality in forests and woodlands globally (Allen *et al.* 2010;
Carnicer *et al.* 2011). These large-scale forest die-off events can strongly affect water and energy
fluxes (Royer *et al.* 2011; Guardiola-Claramonte *et al.* 2011), and carbon cycling (Kurz *et al.*
2008; Brown *et al.* 2010), and lead to cascading effects on ecosystems globally (Bonan 2008;
Stark *et al.* 2016). As a result, there is concern that these forests and woodlands lack resilience to
climate change, where resilience is defined as the capacity of an ecosystem to absorb disturbance
without shifting to a qualitatively different state with altered function, or that is controlled by a
different set of ecological processes (Holling 1973; Standish *et al.* 2014). This concern is
predicated on the assumption that mortality of overstorey trees due to drought will result in
biome-level vegetation shifts to alternate vegetation types that are better adapted to the hotter and
drier climate conditions (Gonzalez *et al.* 2010; Allen, Breshears & McDowell 2015).

Forest resilience to climate change depends not only on overstorey mortality processes
(i.e. resistance component of resilience; Hodgson, McDonald & Hosken 2015), but also on the
ability of dominant tree species to regenerate following drought-related mortality of the canopy
vegetation (i.e. recovery component of resilience). Yet despite the intense level of scientific
focus on forest mortality, relatively little is known concerning the response of tree regeneration to the co-occurrence of drought and associated overstorey mortality events (Martínez-Vilalta & Lloret 2016). This disparity in research interest may be due to the dramatic, visual nature of forest mortality, which is more readily observed than forest regeneration and can be detected across large areas using remote sensing approaches (e.g., Huang et al. 2010; Van Gunst et al. 2016). As a result, fundamental population-level processes such as tree seedling establishment and juvenile survivorship are not well understood and yet necessary to determine vegetation shifts following drought-related dieoff (Lloret et al. 2012).

The climatic extremes that result in overstorey tree mortality may also strongly affect tree regeneration dynamics. In arid and semi-arid forests and woodlands, regionally synchronous tree recruitment events have been associated with cooler and wetter climatic conditions (League & Veblen 2006; Barger et al. 2009). Experimental water manipulations also show negative effects of drought on tree establishment and survival (McCallum 2011; Dulamsuren, Hauck & Leuschner 2013). However, it is unclear that the same drought conditions that result in large-scale overstorey tree mortality will consistently lead to negative effects on tree regeneration.

The microclimate conditions a juvenile tree experiences are strongly controlled by availability of ‘safe sites’ that have the potential to ameliorate water stress during hot and dry periods, decoupling regeneration from regional climate (Bertness & Callaway 1994; von Arx et al. 2013). For instance, the shading provided by overstorey vegetation can result in over two-fold reductions in summer potential soil evaporation in arid and semi-arid ecosystems (Franco & Nobel 1988; Breshears et al. 1997), which may explain why juvenile tree establishment and survival during drought is generally higher beneath the canopy of overstorey trees and shrubs (Kitzberger, Steinaker & Veblen 2000; Gómez-Aparicio et al. 2004; Redmond et al. 2015). The
loss in overstorey tree microsites due to recent mortality events may therefore adversely affect new recruitment and juvenile survival. Alternatively, dead logs and snags generated by overstorey mortality may provide sufficient microclimatic conditions to facilitate tree recruitment and thus forest and woodland resilience ( Flake 2016). Tree recruitment may also be strongly limited by competition for water and nutrients from perennial grasses (Scholes & Archer 1997; Chambers, Vander Wall & Schupp 1999), and overstorey tree mortality may indirectly affect tree recruitment by affecting understorey vegetation ( Kane et al. 2010).

Forest and woodland resilience to drought may strongly vary among populations due to physiographic and edaphic characteristics that affect the local climatic conditions experienced by juvenile trees. Populations experiencing hotter, drier local climates, such as those at lower elevations or in soil with poor water holding capacity, have generally been more vulnerable to increasing temperatures and drought ( Carnicer et al. 2011; Peterman et al. 2012). Yet because vegetation strongly controls the microclimate conditions a juvenile tree experiences, the effects of these local climatic conditions and soil properties on juvenile tree recruitment may be largely due to the indirect effects on tree cover and composition and the understorey plant community.

There are two different pathways to obtain tree regeneration following drought that may be differentially affected by overstorey tree mortality: advanced regeneration (i.e. the survival of juvenile trees that established prior to the drought) and new recruitment (i.e. seedling establishment and survival after the drought). New recruitment may be more strongly affected by recent overstorey mortality compared to advanced regeneration due to limited seed availability. Overstorey vegetation that facilitates seedling establishment and survival can shift to becoming competitive as seedlings age ( Miriti 2006; Soliveres et al. 2010), suggesting that older, advanced regeneration juveniles may not be as strongly affected by microsite changes following dieoff.
The surviving advanced regeneration juveniles had to survive the multi-year drought, however, and thus may be more strongly affected by local climatic conditions and soil properties. We focused our study on the widely distributed piñon (*Pinus edulis*) -juniper (*Juniperus monosperma, J. osteosperma*) woodlands of the southwestern USA, which have been particularly susceptible to large-scale tree mortality events associated with hotter drought conditions resulting from climate change processes (Breshears *et al.* 2005; Gaylord *et al.* 2013). Extreme drought in combination with warmer temperatures and bark beetle infestations resulted in woodland decline over at least 12,000 km² in the southwestern USA, with upwards of 90% piñon mortality in some stands between 2002-2004 (Breshears *et al.* 2005; Shaw, Steed & DeBlander 2005). Most dead piñon trees were infested by the pinyon ips (*Ips confusus*) bark beetle, which specifically targets adult piñon trees, leading to particularly high levels of adult piñon mortality at regional scales (Floyd *et al.* 2009). Juniper, the other co-dominant species, had low mortality rates and no evidence of insect infestations (Floyd *et al.*, 2009), and, as a result, woodland composition shifted to becoming much more juniper-dominated (Mueller *et al.*, 2005). However, piñon-juniper woodlands experiencing widespread drought mortality could still be considered resilient to climate change if woodland cover was ultimately maintained through tree seedling regeneration and subsequent stand development.

Through an observational field survey across a gradient of environmental conditions in Colorado, Arizona, and New Mexico, this study assesses the effects of recent drought- and concomitant beetle-induced tree mortality, local climate, soil properties and vegetation structure on piñon and juniper recruitment dynamics. Using a structural equation modeling approach, we explore the following hypotheses: 1.) Overstorey trees affect piñon and juniper recruitment by providing favourable microsites (*Hypothesis 1A; Fig. 1*) or indirectly by altering understorey
vegetation cover (*Hypothesis 1B*; Fig. 1); 2.) Overstorey piñon mortality indirectly affects new piñon recruitment by reducing seed availability (*Hypothesis 2A*; Fig. 1) or by reducing overstorey microsites (*Hypothesis 2B*; Fig. 1); 3.) Variability in local climate and soil properties affects piñon and juniper recruitment directly (*Hypothesis 3A*; Fig. 1) or indirectly through changes in overstorey and understorey vegetation (*Hypothesis 3B*; Fig. 1). To more directly explore the relationship between tree regeneration and tree versus shrub microsites, we performed electivity analyses to quantify the species-specific associations of piñon and juniper juveniles with overstorey trees and understorey shrubs.

**Materials and Methods**

**Study Areas**

We focused our study on three areas within the Colorado Plateau ecoregion: southwestern Colorado, northern Arizona, and central New Mexico (Fig. 2). Data collected from the three study areas were sampled between 2012 and 2014 using comparable methods. The three study areas differed slightly in the sampling design and the placement of sample plots, with the New Mexico and Colorado study areas spanning a much larger area (7,500 and 22,000 km$^2$, respectively) than the Arizona study area (1,100 km$^2$). In all study areas, the sampling methods followed the same protocol except for differences in the plot layout and the sampling area, outlined below.
Colorado Study Area- Fifty two study sites were established and sampled between 2012 (28 sites) and 2013 (24 sites) across southwestern Colorado that spanned an elevational (1827 – 2317 m), soil available water capacity (7 – 18%), and latitudinal gradient (Fig. 2). Sites were selected using Geographic Information Systems (ArcMap 10.1, Redlands, California, USA), digital elevation models (USGS 2013), and NRCS soils maps (NRCS 2004) to ensure sites varied in elevation, soil type, and were within 1 km of a road (Fig. 2; and see Redmond & Barger 2013; Redmond et al. 2017a for site selection details). In the 2013 field survey only, sites also had to have live adult piñon trees present, and thus, mortality could not reach 100% (maximum piñon mortality was 99.6%). Mean annual precipitation was 368 mm across the Colorado study area from 1900 to 2012, with 25% of annual precipitation occurring during the summer months. Mean monthly temperatures averaged 8.8°C, with July having the warmest temperatures (21.5°C) and January having the coolest temperatures (−3.1°C) on average (PRISM Climate Group 2014). The dominant tree species in the Colorado study area were piñon pine and Utah juniper (J. osteosperma), with ponderosa pine (Pinus ponderosa) present at a small subset of the higher elevation sites. The common shrub species were antelope bitterbrush (Purshia tridentata), mountain mahogany (Cercocarpus montanus) and sagebrush (Artemisia spp.).

At each site, we established three 50 m long transects, spaced 25 m apart, to quantify vegetation cover using the line intercept methods (see Field Methods for sampling protocol). Tree juveniles (< 5 cm in basal trunk diameter) were sampled within a 10 m belt of each transect whereas adult trees (≥ 5 cm in basal trunk diameter) were sampled within five circular plots of 7 m in radius (see Field Methods for juvenile and adult tree sampling protocol). One soil core was
taken from 0 to 10 cm soil depth at each transect end (six per site) to estimate soil available
water capacity in surface soils.

Arizona Study Area - Forty two study sites were sampled in 2014 in the northern Arizona study
area, approximately 27 km north of Flagstaff, Arizona, USA on the north side of the San
Francisco Peaks mountain range (Fig. 2). Sites were selected in a stratified random approach to
ensure the sites spanned an elevational (1680 - 2300 m) and soil available water capacity (4 –
16%) gradient, with the one requirement that they need to be < 1 km from a road for accessibility
(see Redmond et al. 2015 for site selection details). This study area averages 9°C in mean annual
temperature and 380 mm in total annual precipitation, with approximately 65% falling as rain
and snow over winter and the rest as rain over summer (PRISM Climate Group, 2014). The
dominant tree species in the Arizona study area are piñon pine and one seed juniper (Juniperus
monosperma), although ponderosa pine and alligator juniper (J. deppeana) are also present at
some of the sites. Dominant shrub species include apache plume (Fallugia paradoxa), rubber
rabbitbrush (Ericameria nauseosa), and Fremont’s mahonia (Mahonia fremontii).

At each site, we established a 10 m x 200 m transect and divided that transect into twenty
10 m x 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). We established a 14-m transect diagonally across each plot to quantify vegetation
cover using the line intercept methods (see Field Methods for sampling protocol). Within each
plot, all trees (including both adult and juvenile trees) were sampled (see Field Methods for
sampling protocol). One soil core was taken from 0 to 10 cm soil depth at the center of each plot (ten per site) to estimate soil available water capacity in surface soils.

**New Mexico Study Area**

Forty five study sites were surveyed in the central New Mexico study area in 2014 (Fig. 2). Site locations were selected following a stratified random protocol (see Clifford et al., 2013 for details), such that locations were chosen by the proximity to a road (> 50 m and < 1 km), and the proximity to other sites (c. 5 km from another site). The sites ranged in elevation from 1670 m to 2300 m, and extended approximately 150 km latitudinally. Available soil moisture was between 4% and 15% on the sites. This study area averages 414 mm in mean annual precipitation, with approximately 42% of annual precipitation occurring during the summer months, although sites varied considerably in the amount of annual precipitation (mean annual precipitation ranged from 294 mm to 538 mm across the 45 study sites). Mean monthly temperatures averaged 10.4°C, although there was also considerable variability in mean annual temperature across the study area, ranging from 8.6 to 12.7°C across the 45 study sites (PRISM Climate Group 2014). Sites were generally co-dominated by piñon pine and one-seed juniper, however alligator juniper and ponderosa pine were also present on sites at higher elevations. The common shrub species included broom snakeweed (*Gutierrezia sarothrae*), sagebrush, and Apache plume.

Sites were comprised of three, 100 m² square plots aligned in a triangular shape 75 m apart (Clifford et al. 2013). A 14 m long transect was established diagonally across each plot to measure understorey plant cover using line point intercept. All trees found within each plot were
sampled, and a soil core was taken from 0 to 10 cm depth in each plot (3 cores per site) to
estimate soil available water capacity in surface soils.

Field and Laboratory Methods

Vegetation Sampling- For each juvenile (basal trunk diameter < 5 cm.) and adult (basal trunk
diameter ≥ 5 cm) tree encountered within each sampling area, we recorded the species, status
(live or dead), and basal trunk diameter. For all juveniles, we also recorded whether the base of
the juvenile stem was located beneath the canopy of a tree or shrub (hereafter referred to as a
‘nursed’ juvenile) or in the interspace (i.e. not directly beneath the canopy of a tree or shrub). If
the juvenile was nursed, we also recorded the nurse tree or shrub species. For dead adult trees
encountered, we noted whether the tree mortality was recent (≤ 10 yr) by following the
guidelines in Kearns et al. (2005), which were established for piñon pine in southwestern
Colorado. Trees were considered recently dead if 33% or less of the branches were broken, some
small limbs were present, and at least 50% of the bark was attached and not > 2 mm from the
tree. We used these same guidelines consistently across our study areas. There is the potential for
snag decay to differ across our study sites due to different abiotic conditions, although these
guidelines accurately worked for the sites sampled by Kearns et al. (2005) in southwestern
Colorado that spanned a range of climatic conditions, suggesting that snag decay after 10 years
would be similar across our study sites in these semi-arid ecosystems. We quantified tree, shrub,
and perennial grass cover using the line point intercept method every 50 cm along the transect in
each site (Herrick et al. 2005).
Soil Laboratory Methods- We quantified surface soil available water capacity by using estimates of percent sand, silt, and clay from the soil samples collected from each site. To do this, soils were first sieved through a 2-mm sieve and 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. We then used the estimates of percentage sand, silt, clay, and gravel from each site to calculate surface soil available water capacity by subtracting the wilting point from field capacity, which we calculated following the equations in Table 1 of Saxton & Rawls (2006).

Analyses of Regional Patterns of Tree Regeneration

We assessed the effects of abiotic conditions, understorey vegetation, overstorey vegetation, and recent adult piñon mortality on piñon and juniper recruitment across our study area using piecewise structural equation modeling (SEM; see Table 1 for a list of all predictor variables). This approach allowed us to assess whether overstorey tree cover directly affects tree recruitment by providing facilitative microsites or whether overstorey tree cover indirectly affects tree recruitment by altering understorey vegetation cover (H1; Fig. 1). This approach also allowed us to assess more mechanistically how overstorey piñon mortality affects tree recruitment through changes in microsites and/or seed availability (H2; Fig. 1). Using this approach, we were also able to assess the direct and indirect effects of abiotic conditions on juvenile recruitment (H3; Fig. 1).

We examined the effects of three abiotic variables that we hypothesised would influence environmental stress: surface soil available water capacity, mean 30 year cumulative climatic
water deficit, and mean 30 year cumulative actual evapotranspiration (Table 1; see Appendix S1 for details on how these were calculated). Both actual evapotranspiration and climatic water deficit are biologically meaningful measures of plant water balance and collectively are strongly correlated with vegetation distribution (Stephenson 1990), and surface soil available water capacity provides an estimate of water stress and is also highly correlated with nutrient availability in the northern Arizona study area (Cobb et al. 1997).

In order to assess whether overstorey piñon mortality more strongly affects tree recruitment through changes in microsite or seed availability, we used live piñon basal area as an estimate of current seed availability and total live tree cover as an estimate of current microsite availability in our structural equation model. Previous research in our study area found live piñon basal area to be strongly correlated with surface piñon cone density (Pearson’s r = 0.88; Redmond et al. 2015), suggesting that piñon basal area is a good proxy for seed availability. Further, live piñon basal area was only moderately correlated with live tree cover (Pearson’s r = 0.56), and the variance inflation factors of all models were always less than 2.5.

We performed separate SEMs for piñon (P. edulis) and juniper (J. monosperma and J. osteosperma combined) as we were interested in how recruitment patterns of piñon and juniper may be differentially affected by abiotic and biotic conditions. We also performed separate analyses for piñon juveniles that likely established after the recent (2002-2004) piñon mortality event (defined as juveniles with a basal diameter ≤ 0.5 cm; hereafter referred to as new piñon juveniles) and for piñon juveniles that likely established before the mortality event (defined as juveniles with a basal diameter > 0.5 and < 5 cm; advanced piñon juveniles). These size classes were chosen using size-age relationships established by Redmond and Barger (2013) in our southwestern Colorado study area, who found that piñon juveniles with a basal diameter ≤ 0.5
cm were 3.4 times as likely to have established after the mortality event (i.e. were \( \leq 10 \) years old) whereas piñon juveniles with a basal diameter > 0.5 cm were more likely to have established before the mortality event.

The piecewise structural equation modeling used here combines information from multiple separate linear models into a single causal network and allows for non-normal distributions, random effects, and correlated error structures (Shipley, 2009). For the three SEMs, juvenile density response was modeled using generalized linear mixed effect models with a negative binomial distribution (\texttt{glmer.nb} function in R package \texttt{lme4}; Bates et al., 2015) whereas all other model components were modeled with a normal distribution using the \texttt{lmer} function in the R package \texttt{lme4} (Bates \textit{et al.} 2015). All models included a random intercept for study area. Prior to SEM modelling, we performed model selection for each model component by fitting all possible model subsets of our overall model (\texttt{dredge} function in the R package \texttt{MuMIn}; Barton 2016) and selecting the model that minimized Akaike Information Criterion modified for small sample sizes (AICc; see Tables S1-S3 for piñon and juniper recruitment model selection results). We also assessed whether the environmental drivers of tree recruitment differed within each of the three study areas by comparing AICc values of models that also included a random slope for study area for each predictor variable to the full model (prior to model selection) used to predict new and advanced pinon recruitment (see Table S4 for a description of each model). We did not perform this analysis for juniper recruitment due to a lack of model convergence once a random slope for study area was added to the model. In all instances, the models that included a random slope had higher AICc values than the full model that only included the random intercept for study area (Table S4). All full models (prior to model selection) had variance inflation factors < 2.5 and all final models had variance inflation factors
The SEMs were fit using the R package `piecewiseSEM` following Lefcheck (2016). Following the method described by Shipley (2009), we assessed overall model fit using direct separation tests (d-sep) of conditional independence based on Fisher’s C statistic that follows a $\chi^2$ distribution. If the model was considered to have inadequate fit to the data ($P < 0.05$), then we revised our model to include the additional pathways until the resulting model had a Fisher’s C statistic with $P > 0.05$.

To quantify the facilitative and competitive effects of overstorey trees and shrubs on juvenile tree recruitment and how these effects vary by species and juvenile life stage, we used relative interaction indices, also referred to as electivity indices, proposed by Armas et al. (2004). The interaction index represents the relative difference in seedling density occurring beneath tree and shrub canopies and the interspace, and is calculated as:

$$ I = \frac{(\text{Density}_{\text{Beneath Canopy}} - \text{Density}_{\text{Interspace}})}{(\text{Density}_{\text{Beneath Canopy}} + \text{Density}_{\text{Interspace}})} $$

The interaction index thus ranges from -1 to 1, with positive values indicating a facilitative effect (i.e. juvenile trees are more likely to be found beneath tree and shrub canopies than in the adjacent interspaces) and negative values indicating a competitive effect. At each site, we calculated the interaction index for each species (piñon and juniper), juvenile life stage (new seedling [BTD < 0.5], advanced seedling [BTD > 0.5 and < 2.5], sapling [BTD ≥ 2.5 and < 5 cm]), and nurse type (overstorey trees and shrubs). For calculating the interaction index between overstorey trees and tree juveniles, we excluded trees of the same species to reduce inflated interaction indices due to higher abundances of seeds beneath conspecific tree species. As such, this analytical approach takes into account the relative proportion of overstorey tree cover.
compared to shrub cover and omitted conspecific trees to reduce the potential confounding effect of differences in seed abundance. However, the higher interaction indices between overstorey trees compared to shrubs may still be partly due to confounding effects of differences in seed abundance due to the caching of seeds underneath heterospecific trees by birds and small mammals (Vander Wall & Balda 1977; Vander Wall 1997). We only calculated the interaction index for each combination of life stage, nurse type, and species, for which there was the statistical expectation of at least one individual assuming a uniform distribution (i.e. total # of individuals_{species X, life stage Y} \times \text{proportion canopy cover}_{nurse type} \geq 1).

We used the interaction index as a response variable in a mixed-effect multiple linear regression model to assess how the interaction index varies among the two species (piñon and juniper), juvenile life stage (new seedling, advanced seedling, and sapling), and nurse type (overstorey trees and shrubs). We did not perform any transformations prior to analysis as the data were approximately normal and any transformations increased heteroscedasticity. Study area and site (nested within study area) were included as random effects. Analyses were done in R (R Core Team 2014) using the \textit{lme} function in the R package \textit{nlme} (Pinheiro \textit{et al.} 2015).

\textbf{Results}

As intended by the sampling design, there was high variability in woodland structural and abiotic conditions across our study sites within each of the three study areas: Arizona, Colorado, and New Mexico (Table 2). Adult piñon mortality following the 2002 drought averaged 53\% (interquartile range = 20\% to 91\%) with the Arizona study area having the highest mortality rates and Colorado having the lowest (Table 2). Tree recruitment also varied
considerably across our study sites (Table 2), ranging from no juveniles present to upwards of 5000 stems ha\(^{-1}\).

**Effects of recent piñon mortality on tree recruitment**

New piñon recruitment (i.e. piñon establishment following the 2002-2004 mortality event) was strongly associated with live piñon basal area (our proxy for seed availability) and live tree canopy cover (Fig. 3a), both of which were negatively associated with piñon mortality (Fig. 3a). These findings suggest that new piñon recruitment was negatively affected by recent piñon mortality through both hypothesised mechanisms: reduced seed availability and reduced overstorey tree cover. However, piñon mortality appears to most strongly affect new piñon recruitment by reducing seed availability: live piñon basal area, rather than live tree cover, was most strongly associated with new piñon recruitment (Fig. 3a). SEM model results also suggest that the reduction in overstorey tree cover following recent piñon mortality had no direct effect on new piñon recruitment but instead negatively affected new recruitment indirectly by increasing grass cover: new recruitment was strongly associated with grass cover ($\beta_{\text{std}} = -0.65; P < 0.001$; Fig. 4), but not tree cover (Fig. 3a). Unlike new piñon recruitment, SEM model results suggest juniper juvenile density and advanced piñon juvenile density (i.e. piñon juveniles that established prior to the 2002-2004 mortality event) were only moderately affected by recent adult piñon mortality through reductions in overstorey tree cover (Figs. 3b, 3c). Advanced piñon juvenile density was also strongly associated with live and dead piñon basal area (Fig. 4), which represents seed availability at the time of establishment and is also strongly correlated with piñon canopy cover.
Effects of overstorey trees on tree recruitment

Our piecewise SEM model results suggest overstorey trees had both direct and indirect effects on tree recruitment. Whereas overstorey tree cover was indirectly and positively associated with new piñon recruitment by reducing perennial grass cover (Figs. 3a, 4, 5), overstorey tree cover was directly and positively associated with advanced piñon juveniles (Figs. 3b, 4). Interestingly, our model results suggest overstorey tree cover directly and positively affects juniper juveniles but also has a weak, indirect, negative effect on juniper juveniles by reducing perennial grass cover (Figs. 3c, 4, 5). As a result, juniper juvenile density was only moderately correlated with overstorey tree cover (Pearson’s $r = 0.28$) compared to both new and advanced piñon juveniles (Pearson’s $r = 0.42$ and 0.43, respectively). There was both greater variability and higher levels of perennial grass cover on average in the Arizona study area (Table 2; Fig. 3), suggesting that perennial grass cover may most strongly influence tree regeneration in the Arizona study area compared to the Colorado and New Mexico study areas.

Consistent with the piecewise SEM model results, piñon and juniper juveniles were more likely to be found beneath canopies of heterospecific tree species than in the interspaces, as evidenced by the high positive interaction indices (indicating facilitation) between tree cover and juvenile trees (Fig. 6a). Interaction indices were significantly higher between overstorey trees and piñon and juniper juveniles compared to shrubs ($P < 0.0001$; Fig. 6), suggesting that overstorey trees more strongly facilitate juvenile tree recruitment of heterospecific tree species. Our results suggest that piñon juveniles are much more strongly facilitated by overstorey trees than junipers, as evidenced by the significantly higher interaction indices of piñon compared to
juniper ($P < 0.0001$; Fig. 6). Facilitation by overstorey trees and shrubs appeared to decrease with tree size of both piñon and juniper (Fig. 6), with juvenile saplings having lower interaction indices ($P = 0.04$).

Effects of abiotic conditions on tree recruitment

Surface soil available water capacity (soil AWC) was directly positively associated with tree recruitment across both species and piñon size classes (Fig. 3; Fig. 4), and 30 year normal annual evapotranspiration (AET) was also directly positively associated with new piñon recruitment (Fig. 3a; Fig. 4) and weakly with juniper (Fig. 3c; Fig. 4). Our model results suggest there was no direct association between AET and advanced piñon recruitment (Fig 3b), although there was a significant positive correlation between AET and advanced piñon recruitment when the clustering of sites within a study area is not explicitly incorporated into the analyses (Pearson’s $r = 0.22$, $P = 0.01$). This is because both AET and advanced piñon recruitment were generally higher at the sites in the New Mexico study area compared to the Arizona study area (Table 2). There was no strong direct association between 30-year normal climatic water deficit (CWD) and tree recruitment (Fig. 3), but there was an indirect negative association of CWD and tree recruitment through reducing overstorey tree cover and piñon basal area (Fig. 3). Soil AWC and AET were also indirectly positively associated with tree recruitment through increasing grass cover and reducing piñon mortality, respectively (Fig. 3).

Discussion
Drought-induced tree mortality events are occurring globally and are predicted to continue with global climate change (Carnicer et al. 2011; Allen et al. 2015). Our study highlights how woodland resilience to these tree mortality events varies across the landscape in relation to physiographic conditions and is partially dependent upon the herbaceous vegetation response to overstorey mortality. Further, we show that woodland resilience is strongly dependent upon advanced regeneration, (i.e., the survival of juvenile trees that established prior to the mortality event), the survival of adult seed-bearing trees, and the facilitative effects of surviving tree crowns and nurse shrubs for providing favourable microsites for seedling establishment.

Recent widespread adult piñon mortality was strongly negatively associated with piñon regeneration through both hypothesised mechanisms: reducing seed availability and altering available microsites. New piñon recruitment appears to be most strongly negatively affected by recent adult piñon mortality due to limited seed availability (Fig. 3a), but was also associated with microsite availability. Piñon pine has large animal-dispersed seeds and short seed longevity (Chambers et al. 1999), two factors that make seed limitation more likely following a disturbance (Clark et al. 2007). These results suggest that areas with low densities of older juveniles, such as areas that recently experienced prescribed burning or wildfire, will transition to other vegetation types following overstorey piñon mortality either permanently (i.e. lack resilience) or for an extended time period due to slow recovery.

Our results suggest that the effects of overstorey tree mortality on tree regeneration can be mediated by the loss in overstorey tree microsites and subsequent changes in understorey vegetation. Consistent with previous research (Mueller et al. 2005; Kane, Dugi & Kolb 2015), juvenile piñon and juniper trees were much more likely to be located beneath the canopies of live overstorey trees and, to a lesser degree, shrubs, highlighting the importance of trees as nurse
plants in facilitating juvenile tree recruitment. Similar to other semi-arid ecosystems (von Arx et al. 2013), woodland tree canopies reduce soil temperatures and increase soil moisture relative to intercanopy patches by reducing evaporation rates during the summer months (Breshears et al. 1998), which likely explains why there is a strong facilitative effect of overstorey trees on juvenile tree recruitment. This facilitative effect may be particularly evident because of the general warm and dry conditions that have occurred over the past two decades across the study region (Williams et al. 2013), which can increase the facilitative effects of nurse plants in semi-arid ecosystems (e.g. stress gradient hypothesis – Bertness & Callaway 1994). Unlike in light (or energy)-limited forests where overstorey tree mortality creates canopy gaps to allow for the recruitment of new trees (Veblen et al., 1991), our findings suggest that the recent, rapid large-scale tree mortality events in water-limited semi-arid woodlands may actually reduce tree recruitment due to limited microsite availability.

Drought-induced mortality of overstorey trees can strongly affect the microclimatic conditions that juvenile trees experience and thereby alter recruitment dynamics (Suarez & Kitzberger 2008; Vilà-Cabrera et al. 2013), and our results suggest these effects may be partially mediated by understorey vegetation responses. In particular, overstorey trees appeared to affect tree recruitment through changes in understorey vegetation, specifically by reducing the abundance of perennial grasses, which differentially affected piñon and juniper recruitment. Juniper seedlings can better compete with the shallow root system of perennial grasses (Scholes & Archer 1997; Chambers et al. 1999), and, unlike piñon, were positively associated with perennial grasses across our study areas. The inability to compete with perennial grasses explains why piñon juveniles are much more likely to establish beneath the canopies of overstorey trees in our study and others (Kane et al. 2015). Indeed, piñon juveniles were
negatively associated with perennial grass cover across our study areas and survival of juveniles located in the canopy interspaces was much lower in areas with high perennial grass cover in northern Arizona (Redmond et al. 2015).

The differential effects of perennial grasses on piñon and juniper are likely due to the ecophysiological differences between these two species and have important implications for how these woodlands may respond to overstorey mortality events over longer time-scales. Juniper juveniles have greater water use efficiency and can handle more negative water potentials during drought than piñon (Nowak, Moore & Tausch 1999; West et al. 2007). This is likely why juniper is more often found in the tree canopy interspaces, which are both hotter and drier during the summer months (Breshears et al. 1997). This is also consistent with previous research that has found juniper to have higher rates of establishment following large canopy disturbances (Redmond et al. 2013; Bristow, Weisberg & Tausch 2014). Taken together, this suggests the canopy gaps created by recent drought-induced tree mortality events may favour juniper recruitment over piñon recruitment. In addition, the understorey response to overstorey mortality events (increased establishment of perennial grasses versus shrubs) will likely have a strong influence on tree recruitment dynamics and needs to be further studied.

Consistent with studies in other wooded ecosystems (Galiano, Martínez-Vilalta & Lloret 2010; Sanger et al. 2011), our findings suggest that woodland resilience across the Colorado Plateau region of the southwestern USA to drought will vary spatially due to differences in local physiographic conditions. Surface soil available water capacity and local climatic conditions defining resource availability were directly associated with tree recruitment of both piñon and juniper. Past tree recruitment in piñon-juniper woodlands has generally occurred during cool and wet climate periods (Shinneman & Baker 2009; Barger et al. 2009), so it would make sense that
recruitment during the warmer and drier conditions over the past decade is more prevalent in areas with more water availability. Similarly, variability in landscape physiography also affects piñon growth responses to climate (Barger & Woodhouse 2015; Redmond et al. 2017) and adult piñon mortality rates (Peterman et al. 2012). This effect of landscape physiography on tree juvenile densities may explain why there was a limited effect of tree mortality on juvenile tree composition in the generally cooler, wetter sites in southwestern Colorado (Redmond & Barger 2013) but a strong effect in northern Arizona (Redmond et al. 2015). Overall, these results suggest that under future warmer and drier conditions, recruitment of both piñon and juniper trees may be a bottleneck to woodland recovery in areas with coarse textured soils or dry climatic conditions, and permanent woodland conversion to other more xeric vegetation types may occur.

\textbf{Conclusions}

The frequency and severity of drought events occurring under warmer temperatures are predicted to increase with global climate change (IPCC 2014). Widespread tree mortality events have already occurred across the globe due to recent hotter droughts (Allen et al. 2010; Carnicer et al. 2011), which have the potential to result in long-term changes in ecosystem structure and function if there is limited tree regeneration (Lloret et al. 2012). Our findings suggest that tree resilience to drought among the widespread piñon-juniper woodlands of the southwestern USA is highly variable and dependent upon several key conditions. In the absence of live seed-producing trees, our results demonstrate that the recovery of piñon pine populations following overstorey piñon mortality is dependent upon advance regeneration. Thus, due to the importance of seed
limitation, the timing of drought events (i.e. the drought-free interval) can have a strong impact on woodland resilience to climate change. Overstorey trees often facilitate tree seedling establishment and survival in semi-arid woodlands (Kitzberger, Steinaker & Veblen 2000; Gómez-Aparicio et al. 2004), and therefore widespread overstorey mortality caused by droughts could reduce tree regeneration (Vilà-Cabrera et al. 2013). Since piñon pine regeneration depends more strongly on facilitation by overstorey trees than juniper, tree mortality caused by droughts could result in a shift to juniper dominance in the semi-arid woodlands of the southwestern USA. Finally, tree regeneration varied among sites due to differences in soil water-holding capacity and site productivity, such that stands with hotter, drier local climatic conditions will have limited piñon and juniper regeneration following large-scale dieback.

Based on our results we identify four indicators of resilience to woodland die-back associated with hotter drought conditions: (1) abundant advance regeneration of tree seedlings; (2) sufficient canopy cover for survival of emergent seedlings and existing regeneration; (3) sufficient seed source from surviving trees with high reproductive output; (4) areas with cooler and wetter local climate conditions and high soil available water capacity. In the absence of these conditions, there is greater likelihood of woodlands transitioning to other, more xeric vegetation types following die-back.

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Authors’ Contributions

MDR formulated the idea with critical input from all authors. MDR and MJC conducted the field work and MDR analyzed the data. MDR and PJW wrote the paper with substantial contributions from NSC and MJC.

Data Accessibility

All data are available on the Dryad data repository: doi:10.5061/dryad.31887 (Redmond et al. 2017b).

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**Supporting Information**

**Appendix S1.** Description of the calculations of abiotic variables used in SEM analyses.

**Table S1.** A list of parameters and their standardized regression coefficients for all models of new piñon juvenile density with $\Delta AIC_c \leq 2$. Dashes (-) indicate parameters that were not included in a given model. The top model (lowest AICc value) was used in the structural equation modeling. See Table 1 for a detailed description of each parameter.

**Table S2.** A list of parameters and their standardized regression coefficients for all models of advanced piñon juvenile density with $\Delta AIC_c \leq 2$. Dashes (-) indicate parameters that were not included in a given model. The top model (lowest AICc value) was used in the structural equation modeling. See Table 1 for a detailed description of each parameter.

**Table S3.** A list of parameters and their standardized regression coefficients for all models of juniper juvenile density with $\Delta AIC_c \leq 2$. Dashes (-) indicate parameters that were not included in
a given model. The top model (lowest AICc value) was used in the structural equation modeling. See Table 1 for a detailed description of each parameter.

**Table S4.** List of models and their AICc values used to assess whether the environmental drivers of new (middle column) and advanced (right column) pinon pine recruitment differed within each of the three study areas. See Table 1 for a list of all parameters used to predict new and advanced pinon pine recruitment. AET = mean 30 year cumulative actual evapotranspiration; CWD = mean 30 year cumulative climatic water deficit; soil AWC = surface soil available water capacity.
Table 1. Predictor variables included in piecewise structural equation models of juvenile tree density.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Abiotic Conditions</strong></td>
<td></td>
</tr>
<tr>
<td>Actual Evapotranspiration (AET)</td>
<td>Mean 30 year cumulative actual evapotranspiration (see Appendix S1 for details). Represents the simultaneous availability of water and energy and ranges from 258 mm (driest sites) to 504 mm (wettest sites) across our study area.</td>
</tr>
<tr>
<td>Climatic Water Deficit (CWD)</td>
<td>Mean 30 year cumulative climatic water deficit (see Appendix S1 for details), which represents the amount of water by which potential evapotranspiration exceeds actual evapotranspiration. Ranges from 71 mm (cool, wet sites) to 894 mm (hot, dry sites) across our study area.</td>
</tr>
<tr>
<td>Soil Available Water Capacity (soil AWC)</td>
<td>Surface (top 10 cm.) soil available water capacity calculated based off soil texture (see Appendix S1 for details).</td>
</tr>
<tr>
<td><strong>Overstorey Vegetation</strong></td>
<td></td>
</tr>
<tr>
<td>Tree Cover</td>
<td>Live tree cover. Represents available tree microsites and was calculated using the line point intercept data. *The majority of dead piñon trees had fallen over across our study area, thus live + dead tree cover was highly correlated with live tree cover (r = 0.98).</td>
</tr>
<tr>
<td>Piñon/Juniper Basal Area at the time of juvenile establishment</td>
<td>Represents seed availability at the time of juvenile establishment. For the SEM model of juniper juvenile density, total live juniper basal area was used due to low juniper mortality across our study area (8% on average). For the SEM model of new piñon juvenile density, total live piñon basal area was used whereas total live + recently dead piñon basal area was used for the SEM model of advanced piñon juvenile density.</td>
</tr>
<tr>
<td>% Piñon Mortality</td>
<td>Percent adult piñon mortality over the past decade, calculated from basal area as: dead piñon basal area /(live + dead piñon basal area)*100%.</td>
</tr>
<tr>
<td><strong>Understorey Vegetation</strong></td>
<td></td>
</tr>
<tr>
<td>Perennial grass cover</td>
<td>Perennial grass cover. Represents available grass microsites and was calculated using the line point intercept data.</td>
</tr>
<tr>
<td>Shrub Cover</td>
<td>Live shrub cover. Represents available shrub microsites and was calculated using the line point intercept data.</td>
</tr>
</tbody>
</table>
### Table 2. Mean (range) of abiotic and woodland structural conditions across our study sites in Arizona, Colorado, and New Mexico.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Arizona</th>
<th>Colorado</th>
<th>New Mexico</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abiotic Conditions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Actual Evapotranspiration (mm.)</td>
<td>385 (359 - 419)</td>
<td>373 (340 - 431)</td>
<td>447 (288 - 504)</td>
</tr>
<tr>
<td>Climatic Water Deficit (mm.)</td>
<td>338 (71 - 510)</td>
<td>424 (214 - 572)</td>
<td>407 (174 - 769)</td>
</tr>
<tr>
<td>Soil Available Water Capacity (%)</td>
<td>10 (4 - 16)</td>
<td>13 (8 - 18)</td>
<td>10 (6 - 15)</td>
</tr>
<tr>
<td>Overstorey Vegetation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree Cover (%)</td>
<td>17 (0 - 49)</td>
<td>36 (17 - 64)</td>
<td>26 (0 - 65)</td>
</tr>
<tr>
<td>Piñon Mortality (%)</td>
<td>64 (0 - 100)</td>
<td>45 (0 - 100)</td>
<td>51 (0 - 100)</td>
</tr>
<tr>
<td>Live + Dead Piñon BA (m²ha⁻¹)</td>
<td>3 (0 - 20)</td>
<td>10 (2 - 29)</td>
<td>4 (0 - 14)</td>
</tr>
<tr>
<td>Juniper Basal Area (BA; m²ha⁻¹)</td>
<td>13 (0 - 44)</td>
<td>27 (2 - 49)</td>
<td>5 (0 - 17)</td>
</tr>
<tr>
<td>Understorey Vegetation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perennial grass cover (%)</td>
<td>37 (0 - 74)</td>
<td>10 (0 - 44)</td>
<td>16 (0 - 51)</td>
</tr>
<tr>
<td>Shrub Cover (%)</td>
<td>5 (0 - 25)</td>
<td>3 (0 - 13)</td>
<td>6 (0 - 40)</td>
</tr>
<tr>
<td>Tree Recruitment</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>New piñon juvenile density (stems ha⁻¹)</td>
<td>21 (0 - 220)</td>
<td>180 (0 - 2120)</td>
<td>195 (0 - 2400)</td>
</tr>
<tr>
<td>Adv. piñon juvenile density (stems ha⁻¹)</td>
<td>108 (0 - 960)</td>
<td>435 (20 - 2393)</td>
<td>425 (0 - 2767)</td>
</tr>
<tr>
<td>Juniper juvenile density (stems ha⁻¹)</td>
<td>243 (0 - 3640)</td>
<td>267 (20 - 827)</td>
<td>177 (0 - 1433)</td>
</tr>
</tbody>
</table>
Figure 1. Path diagram illustrating the structural equation modeling (SEM) conceptual framework used to understand the effects of abiotic conditions, understorey vegetation, and overstorey vegetation on juvenile tree density. Numbers correspond to each hypothesis described in the introduction. We used three different SEMs to predict new piñon juvenile density, advanced piñon juvenile density, and juniper juvenile density, which differed slightly in their predictor variables (see Table 1). Correlated errors were included between % piñon mortality and piñon or juniper basal area at the time of establishment for the two SEMs predicting juniper juvenile density and advanced piñon juvenile density, whereas a direct causal relationship between % piñon mortality and live piñon basal area were included for the SEM predicting new piñon juvenile density. Thick black lines connecting dashed boxes indicate that all possible pathways were included in the analyses.
Figure 2. Map of the sites sampled within the three study areas. Shaded green area in the top right map shows the distribution of piñon pine (Cole et al., 2006). Map was created using ESRI software (ArcMap version 10.3), and the base maps 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.
Figure 3. Final piecewise structural equation models illustrating the factors that affect (A) new piñon juvenile density (i.e. juveniles with a basal diameter ≤ 0.5 cm, which are juveniles that likely established after the 2002-2004 adult piñon mortality event), (B) advanced piñon juvenile
density (i.e. juveniles with a basal diameter > 0.5 cm and < 5 cm, which are juveniles that likely established prior to the 2002-2004 adult piñon mortality event) and (C) juniper juvenile density (i.e. trees with a basal diameter < 5 cm). Line thickness is proportional to standardised path coefficients that are shown next to the line and significance is denoted as ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. Lines are colored red for negative associations and black for positive associations. Paths where $P > 0.10$ are lighter in color.

Figure 4. Partial residual plots showing the relationship between the predictor variables that were most strongly directly associated with new piñon juvenile density (top), advanced piñon juvenile density (middle), and juniper juvenile density (bottom) across the Arizona (open circles), Colorado (cross symbols), and New Mexico (closed circles) study areas.
Figure 5. Partial residual plots showing the relationship between (A.) live tree cover and perennial grass cover, (B.) percent piñon mortality and live tree cover, and (C.) piñon mortality and live piñon basal area, which were indirectly associated with tree recruitment (Fig. 3) across the Arizona (open circles), Colorado (cross symbols), and New Mexico (closed circles) study areas.
Figure 6. Interaction indices between live trees (excluding conspecific species; A.) and shrubs (B.) and juvenile juniper (grey boxes) and piñon (white boxes) trees. Interaction indices between 0 and 1 represent a facilitative effect of trees and shrubs on piñon and juniper recruitment, with increasingly positive values representing an increasingly facilitative effect. Interaction indices were higher for piñon than juniper ($P < 0.0001$), live trees (excluding conspecifics) than shrubs ($P < 0.0001$), and new juveniles than saplings ($P = 0.04$).