Tree regeneration following drought- and insect-induced mortality in piñon–juniper woodlands

Miranda D. Redmond and Nichole N. Barger

Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA

Summary

• Widespread piñon (*Pinus edulis*) mortality occurred across the southwestern USA during 2002–2003 in response to drought and bark beetle infestations. Given the recent mortality and changes in regional climate over the past several decades, there is a keen interest in post-mortality regeneration dynamics in piñon–juniper woodlands.

• Here, we examined piñon and Utah juniper (*Juniperus osteosperma*) recruitment at 30 sites across southwestern Colorado, USA that spanned a gradient of adult piñon mortality levels (10–100%) to understand current regeneration dynamics.

• Piñon and juniper recruitment was greater at sites with more tree and shrub cover. Piñon recruitment was more strongly facilitated than juniper recruitment by trees and shrubs. New (post-mortality) piñon recruitment was negatively affected by recent mortality. However, mortality had no effect on piñon advanced regeneration (juveniles established pre-mortality) and did not shift juvenile piñon dominance.

• Our results highlight the importance of shrubs and juniper trees for the facilitation of piñon establishment and survival. Regardless of adult piñon mortality levels, areas with low tree and shrub cover may become increasingly juniper dominated as a result of the few suitable micro-sites for piñon establishment and survival. In areas with high piñon mortality and high tree and shrub cover, our results suggest that piñon is regenerating via advanced regeneration.

Introduction

Global climate change has been predicted to increase the frequency and severity of drought events occurring under warmer temperatures (Meehl & Tebaldi, 2004; Seager *et al.*, 2007), which may lead to substantial shifts in vegetation distribution (Choat *et al.*, 2012). Extensive tree mortality has already occurred across the western USA (Breshears *et al.*, 2005; Van Mantgem & Stephenson, 2007; Van Mantgem *et al.*, 2009; Worrall *et al.*, 2010) and globally (Allen *et al.*, 2010; Carnicer *et al.*, 2011) over the past decade as a result of a combination of drought, insect outbreaks and warmer temperatures. These regional mortality events have altered 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 (Walton, 2012; Anderegg *et al.*, 2013). Yet, at present, we lack a clear understanding of how these regional mortality events may affect future forest and woodland composition, which is critical in understanding the long-term effects of recent tree mortality on these ecosystem processes and functions (Kurz *et al.*, 2008; Anderegg *et al.*, 2013). Thus, research examining tree regeneration patterns following recent mortality under a warmer, drier climate will help to elucidate the long-term changes in water and energy fluxes and carbon stocks.

Several abiotic and biotic factors are important drivers of successful tree regeneration under warmer, drier conditions. With increasing aridity, tree regeneration may become increasingly dependent on the availability of cooler, wetter microsites to facilitate seedling establishment and survival (Kitzberger *et al.*, 2000; Sthultz 2007). In arid and semi-arid ecosystems, tree seedling establishment and survival are greater beneath tree and shrub canopies than in the adjacent canopy interspaces (Chambers, 2001; Mueller *et al.*, 2005). Tree recruitment beneath canopies is probably a result of reduced solar radiation, resulting in less plant transpiration loss, cooler soil temperatures and less soil water loss through evaporation, as well as increased soil organic matter and nutrient availability (Callaway *et al.*, 1996; Kitzberger *et al.*, 2000; Chambers, 2001). Thus, facilitation, or the positive interaction among plants, by trees and shrubs may become increasingly important for tree regeneration by reducing water stress. However, trees and shrubs may also compete for resources, such as sunlight and water, and may negatively affect seedling growth and survival (Callaway *et al.*, 1996; Breshears *et al.*, 1997), particularly among later life stages (Callaway & Walker, 1997). Soil physical and chemical properties, such as texture and organic matter, influence soil water availability and may also be important in promoting seedling establishment and survival under a warmer, drier climate.

In this study, we examine how vegetation structure and soil properties influence piñon pine (*Pinus edulis* Engelm., hereafter referred to as piñon) and Utah juniper (*Juniperus osteosperma* (Torr.) Little, hereafter referred to as juniper) regeneration dynamics following drought- and insect-induced adult piñon mortality. We focus our research on woodlands co-dominated by piñon and juniper, because they are widely distributed across the southwestern USA and provide a range of ecosystem services to humans and critical habitat for a variety of wildlife species (Brown *et al.*, 2001). Importantly, during the most recent multiyear drought (2002–2003), piñon experienced extensive mortality across populations, with mortality reaching upwards of 90% in some stands (Breshears *et al.*, 2005; Mueller *et al.*, 2005). This widespread piñon mortality event was caused by a combination of high temperatures, low precipitation and high bark beetle (*Ips confusus*) infestation (Breshears *et al.*, 2005; McDowell *et al.*, 2008; Adams *et al.*, 2009). Mortality was highest among reproductively mature piñon trees (Mueller *et al.*, 2005; Floyd *et al.*, 2009), which resulted in large increases in relative dominance by adult juniper (Mueller *et al.*, 2005; Koepke *et al.*, 2010). Although recent piñon mortality increased adult juniper dominance, future woodland composition will be largely determined by regeneration dynamics.

With increasingly arid conditions, several authors have hypothesized that juvenile juniper dominance may increase relative to piñon, because juniper is more drought tolerant and is also more abundant in warmer, drier sites (Linton *et al.*, 1998; West *et al.*, 2007; Breshears *et al.*, 2008; McDowell *et al.*, 2008). In addition, although both piñon and juniper have greater rates of seedling establishment and survival beneath the canopy of trees and shrubs (Miller & Rose, 1995; Mueller *et al.*, 2005), juniper is better able to establish in open environments and is also better able to compete with herbaceous vegetation than piñon (Chambers *et al.*, 1999). Consequently, juniper establishment is commonly greater than piñon establishment following overstory tree and shrub removal (Tausch & Tueller, 1977; Everett & Ward, 1984; Redmond *et al.*, 2013). Following this, we predict that the high mortality of overstory piñon may lead to reduced suitable microsites for piñon establishment, and shift the juvenile tree community to become more juniper dominated.

In addition to changes in suitable microsite availability, seed availability may influence piñon and juniper recruitment. Piñon cone production has declined by over 40% in areas of New Mexico over the last several decades (Redmond *et al.*, 2012). These declines have been associated with recent increases in temperature (Redmond *et al.*, 2012) and may negatively impact recent recruitment. Piñon seed viability also declines rapidly after 1 yr of storage (Meeuwig & Bassett, 1983), unlike juniper (Johnsen, 1959). Thus, piñon recruitment following high adult mortality may be dependent on the survival of juveniles that established before the mortality (i.e. advanced regeneration) as a result of limited seed availability.

Through an observational study that examined piñon and juniper recruitment across a gradient of adult piñon mortality levels in southwestern Colorado, we addressed the following hypotheses: piñon and juniper recruitment is greater at sites with more tree and shrub cover and higher soil available water capacity; piñon recruitment is more strongly facilitated than juniper recruitment by overstory trees and shrubs; piñon recruitment following high adult mortality is dependent on advanced regeneration; juvenile piñon dominance decreases with increased adult piñon mortality.

Materials and Methods

Study area

From May to June 2012, we sampled 30 sites across southwestern Colorado that had experienced varying levels (10–100%) of adult piñon mortality during the 2002–2003 drought (Fig. 1). Sites were similar in elevation (2080 ± 70 m), climate (mean annual temperature, 9.4 ± 0.8°C; mean annual precipitation, 398 ± 28 mm; data from the PRISM Climate Database, http://www.prism.oregonstate.edu) and juniper mortality (< 12%). We selected sites that were in the mid to upper elevation limits of piñon–juniper woodlands, as these elevations had the greatest mortality (Breshears *et al.*, 2005). Sites were located on either Gladel–Pulpit complex soils (ecological sites, Pinyon–Juniper (Gladel) or Loamy Foothill (Pulpit)) or Wetherill soils (Loamy Foothill) (Natural Resources Conservation Service, 2006), which are the two most spatially extensive soil complexes in the region dominated by piñon and juniper (Natural Resources Conservation Service, 2006). Both of these soil complexes are characterized as well-drained soils derived from sandstone with a depth ranging from 0.5 to > 1.5 m (Natural Resources Conservation Service, 2006; and see Supporting Information Table S1 for soil texture and soil organic matter data for each site). To select sites, we first used Geographic Information Systems to locate areas within southwestern Colorado that were of the two soil complexes, between 2000 and 2200 m in elevation, had a slope of < 10% and were located on federally owned land. We then used Google Earth (Version 7.0; Google Inc., Mountainview, CA, USA) imagery taken in 2011 to identify areas of high and low mortality that were within 1 km of a road. Following this, we selected 15 sites that were located on Wetherill soils and 15 sites that were located on Gladel–Pulpit soils, half of which were considered to be high-mortality (> 60% mortality) sites and half of which were considered to be low-mortality (< 40% mortality) sites. All sites were generally at least 2 km apart (Fig. 1). However, we included stands that were within 2 km of one another if they differed in percentage mortality or differed by the Natural Resources Conservation Service soil map unit and vegetation characteristics. At our sites, the only two tree species were piñon and juniper. The common shrub species were antelope bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus montanus*) and sagebrush (*Artemesia* spp.).

Data collection

At each site, we established three 50-m-long transects, spaced 25 m apart. We surveyed for all tree juveniles, which included seedlings (basal diameter < 2.5 cm) and saplings (basal diameter
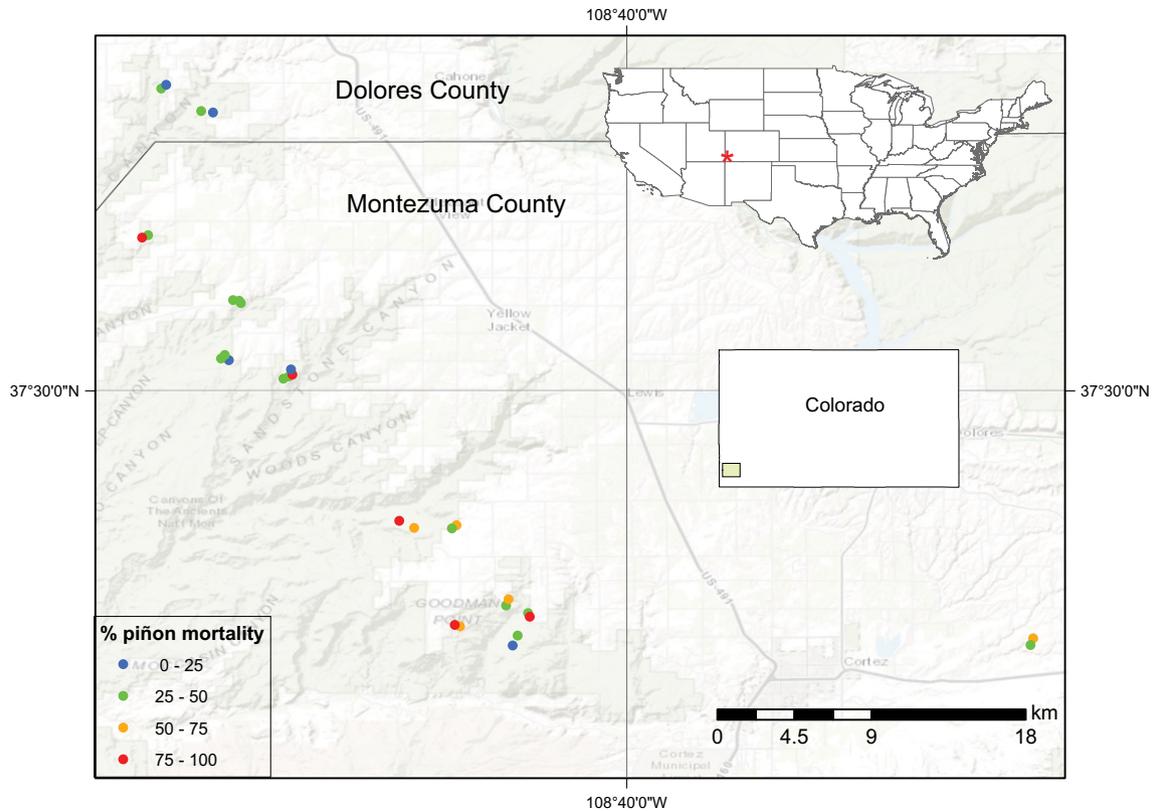
Fig. 1 Map of the 30 sites sampled in the USA. Different colored circles illustrate the different levels of adult piñon mortality that occurred at each site based on adult stem density.

≥ 2.5 and < 5 cm), along a 10-m belt at each transect (i.e. 1500 m^2 surveyed for tree juveniles per site). For all tree juveniles encountered, we recorded the species, status (dead or alive), basal diameter (diameter at the root collar) and microsite (beneath canopy vs canopy interspace). In addition, for each piñon seedling, we estimated whether the seedling established before the mortality event (i.e. ≥ 10 yr, which we refer to as an advanced seedling) or after the mortality event (i.e. ≤ 8 yr, which we refer to as a new seedling) by counting the number of annual whorls along the main stem, a method that has been used to age piñon (Sthultz et al., 2007) and other pine species (Collins et al., 2011).

To quantify tree and shrub density, cover, basal area (BA) and mortality, at each site we established five circular plots of 7 m in radius. One circular plot was located in the center of the middle transect and the other four circular plots were located at each end of the outer transects. We measured the height, two perpendicular canopy widths (live only), basal diameter (trees only) and status (live vs dead) for each tree and shrub species located within each circular plot. For all dead trees, we also noted whether the tree mortality was recent (≤ 10 yr) by following the guidelines in Jacobi et al. (2005), which were based on piñon in southwestern Colorado. Trees were considered to be recently (≤ 10 yr) dead if 33% or less of the branches were broken, most small limbs were present and at least 50% of the bark was attached and not > 2 mm from the tree.

To examine whether piñon and juniper juveniles were randomly distributed within a site or were associated with specific microsites, we first determined the relative availability of microsites using the line point intercept method. Every 50 cm along

each transect, we recorded the microsite (tree and/or shrub presence vs interspace), for a total of 100 points/transect and 300 points/site. We used the line point intercept method, rather than data from our circular plots, to determine the relative availability of microsites, because tree and shrub canopies often overlapped. Therefore, the circular plot data probably overestimated canopy cover.

At each site, soil cores were taken from 0–10 cm soil depth at each transect end (six per site) to estimate soil available water capacity in surface soils. Soil cores were 2.5 cm in diameter and taken 1 m out from the canopy edge of juniper and/or piñon. Within a month of collection, soil samples were taken back to the University of Colorado, where they were dried for 48 h at 60°C, weighed, sieved through a 2-mm sieve and re-weighed. The six soil samples taken at each site were then combined, and organic matter content (%) was estimated using the loss on ignition method (Ball, 1964; Ben-Dor & Banin, 1989) with a muffle furnace set at 580°C. Percentage sand, silt and clay were estimated following Kettler et al. (2001). Using our estimates of percentage sand, silt, clay and organic matter content (see Table S1 for these data), we calculated soil available water capacity by subtracting the wilting point (θ_{1500}) from the field capacity (θ_{33}), which we calculated using the equations in table 1 of Saxton & Rawls (2006).

Data analyses

We divided tree seedlings into two size classes on the basis of their basal diameter (new seedlings, basal diameter ≤ 0.5 cm;

Table 1 The predictor variables and their ecological function used in each stepwise multiple linear regression for each size class

Predictor variable	Ecological function
Live piñon basal area	Piñon seed availability and microsites after mortality
Live + dead piñon basal area	Piñon seed availability and microsites before mortality
Percentage piñon mortality	Microsite changes (dead piñon microsites)
Live shrub cover	Microsite
Live juniper cover (P only)	Microsite
Soil available water capacity	Water availability
Live juniper basal area (J and %P only)	Juniper seed availability and microsite

Predictor variables only used to predict piñon juvenile density, juniper juvenile density or piñon juvenile dominance are denoted by 'P', 'J' and '% P', respectively. Piñon mortality was calculated on the basis of basal area rather than stem density. All of the vegetation predictor variables were calculated using the pooled circular plot data.

advanced seedlings, basal diameter > 0.5 and < 2.5 cm), because we were unable to age all of the tree seedlings. These size classes were chosen using piñon seedling size–age data across our 30 sites (see Fig. S1), which indicate that 78% of the seedlings of ≤ 0.5 cm were < 9 yr old (i.e. established post-mortality), whereas 98% of seedlings of > 0.5 cm were > 10 yr old (i.e. established before mortality). We were unable to date juniper seedlings using the annual whorl method. However, piñon and juniper trees in southern Utah have a similar relationship between basal diameter and tree age among juveniles with a basal diameter of ≥ 2.0 cm (Fig. S2; M. D. Redmond, N. S. Cobb, M. Miller & N. N. Barger, unpublished). This suggests that the size–age relationship among piñon and juniper seedlings may also be similar. Because we divided seedlings into age classes (new seedlings and advanced seedlings) on the basis of their size for the analyses, it is important to note that some seedlings may be incorrectly classified, which may reduce our ability to detect differences in vegetation associations between new seedlings and advanced seedlings.

We evaluated the vegetation and soil characteristics associated with piñon and juniper recruitment by performing stepwise multiple linear regression analyses for each juvenile size class (new seedlings, advanced seedlings and saplings). For these analyses, we used each site as a replicate by pooling and then averaging transect and circular plot data. In each linear regression model, juvenile density was used as a response variable and various vegetation and soil characteristics that were identified a priori were used as predictor variables (see Table 1 for a list of all predictor variables used and their hypothesized function). It should be noted that we used piñon BA rather than canopy cover as a predictor variable for all regression analyses, because we did not collect canopy cover data of dead piñon trees. Further, live piñon BA is a strong predictor of live piñon canopy cover (simple linear regression, $R^2 = 0.91$, $P < 0.0001$). We also used juniper BA rather than canopy cover as a predictor variable for the regression analyses with juniper juveniles (Table 1), because juniper often did not grow vertically, and so canopy cover probably overestimated seed availability in these cases.

Each complete model was simplified using the stepAIC procedure as part of the package MASS (Venables & Ripley, 2002) in R (R Development Core Team, 2011) following the procedure outlined in Zuur et al. (2007). The stepAIC procedure examines all predictor variables using backward selection to produce a final model based on the minimization of the Akaike Information Criterion (AIC; Akaike, 1973). Piñon new seedlings and juniper saplings were log transformed to meet the assumptions of these tests.

Following the same procedure as above, we examined the vegetation and soil characteristics associated with piñon dominance for each juvenile size class to determine potential changes in future stand composition across our study sites (see Table 1 for the list of predictor variables). Piñon dominance was calculated as:

$$\text{Piñon dominance}_{\text{size class X}} = \frac{(\text{Piñon Density}_{\text{size class X}})}{(\text{Piñon Density}_{\text{size class X}} + \text{Juniper Density}_{\text{size class X}})}$$

To determine whether recent increases in aridity and recent mortality had shifted piñon dominance, we first examined whether juvenile piñon dominance had shifted relative to adult piñon dominance, regardless of piñon mortality levels. To do this, we performed paired Student's t-tests to compare juvenile piñon dominance at each size class (new seedling, advanced seedling and sapling) with adult piñon dominance before recent mortality (calculated using live and dead tree density). To determine whether recent mortality had shifted juvenile piñon dominance relative to adult piñon dominance, we performed regression analyses to examine whether the difference in dominance between juveniles and adults (response variable) was affected by piñon mortality (predictor variable). We calculated the difference in dominance between juveniles at each size class and adults by dividing juvenile piñon dominance$_{\text{size class X}}$ by adult piñon dominance before recent mortality.

To determine whether overstory trees and shrubs had a facilitative or competitive effect on piñon and juniper recruitment, and how this effect may differ between the two species and between the three juvenile size classes, we used the relative interaction index proposed by Armas et al. (2004). The interaction index reveals whether competition or facilitation is occurring within each microsite by representing the relative difference in seedling density occurring beneath tree and shrub canopies and in the interspace, and is calculated as:

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

Thus, the interaction index ranges from −1 to 1, with a positive interaction index representing a facilitative effect of canopy microsites on recruitment, and a negative interaction index representing a competitive effect of canopy microsites. For each species and each juvenile size class, we estimated the juvenile density at each microsite by dividing the total number of juveniles found underneath the canopy (or interspace) microsite by the total cover of live and dead shrubs and trees (or the total

cover of area with no trees and shrubs), which was calculated using the line point intercept data. Because we wanted to compare how the interaction index varies between the two species and the three juvenile size classes, we only used sites that had a sufficient number of juveniles sampled in each size class and each species. To do this, we only used sites that, given a uniform distribution of juveniles, we would expect at least one individual of each size class and each species to be located beneath the canopy (i.e. total number of individuals$_{\text{species X, size class Y}}$ × proportion canopy cover ≥ 1). We omitted 14 sites from the analysis as these sites did not meet the criteria. Using the 16 sites that met our criteria, we calculated the interaction index at each site for each species and each juvenile size class. We then performed a series of non-parametric paired Wilcoxon signed rank tests (nine paired tests in total) to determine whether the interaction index differed between piñon and juniper within each juvenile size class (three paired tests) and whether the interaction index differed between each juvenile size class within each species (six paired tests). We used non-parametric paired Wilcoxon signed rank tests rather than a paired two-way ANOVA because of the non-normality of the data, even after transformations.

We also examined the effect of canopy presence on piñon sapling survival by comparing the interaction indices of live piñon saplings and dead piñon saplings beneath the canopy of trees and shrubs. Similar to above, we only used sites that had a sufficient number of live and dead piñon saplings, such that, given a uniform distribution, we would expect to find at least one live and dead sapling underneath the canopy. Using the 18 sites that met our criteria, we performed a paired Wilcoxon signed rank test to determine whether the interaction index differs between live and dead piñon saplings.

As multiple comparisons (10) were conducted using interaction indices, we applied the false discovery rate (FDR) correction using a standard step-up procedure to control the inflation of type I error derived from repeated testing (Benjamini & Hochberg, 1995; García, 2004). All analyses were performed in R (R Development Core Team, 2011), with $\alpha = 0.05$.

Results

As intended, our study sites spanned a gradient of adult piñon mortality levels, with mortality ranging from 16% to 100% based on BA (9–100% based on stem density). In addition, there was high variability in shrub cover (0–14%), tree density (169–1105 stems ha^{-1}) and tree BA (12–52 m^2 ha^{-1}) across our study sites (Tables 2, S2), as well as some variability in soil available water capacity (11–16%; Table S2). Piñon and juniper juvenile (i.e. seedlings and saplings) densities were also highly variable across our study sites, with juvenile densities ranging from 27 to 948 stems ha^{-1} for piñon and 40 to 827 stems ha^{-1} for juniper (Table 2). Among both piñon and juniper, the density of advanced seedlings (i.e. seedlings that probably established before adult mortality) was over 2.5-fold higher than the density of new seedlings (i.e. seedlings that probably established following adult mortality), on average (Table 2). However, the difference in density between new seedlings and advanced seedlings was highly variable across the 30 study sites (Table S2), such that, at some sites, new seedlings were over 1.4 times more abundant than advanced seedlings, whereas, at others, advanced seedlings were over 25 times more abundant than new seedlings (Table S2).

Vegetation and soil characteristics associated with tree recruitment

The density of piñon new seedlings was positively associated with live shrub cover, live piñon BA and live juniper cover ($R^2 = 0.63$, $P < 0.0001$; Table 3; Fig. 2a). Notably, there was no relationship between percentage piñon mortality and piñon new seedling density. Given that live piñon BA was strongly associated with piñon new seedling density, our results suggest that only current live piñon abundance influences new seedling establishment.

The density of piñon advanced seedlings was also positively associated with live shrub and juniper cover (Table 3; Fig. 2b). However, unlike piñon new seedlings, the density of piñon advanced seedlings was positively associated with piñon BA before adult mortality and soil available water capacity (final model $R^2 = 0.64$, $P < 0.0001$; Table 3; Fig. 2b). Given that piñon BA before adult mortality was a strong predictor of piñon advance seedling density, these results suggest that recent mortality did not affect the abundance of advanced seedlings.

Although there was a strong association between the density of piñon seedlings and vegetation structure (Table 3), piñon sapling density was only positively associated with live shrub cover ($R^2 = 0.31$, $P = 0.001$; Table 3).

Juniper juveniles were more weakly associated than piñon juveniles with vegetation and soil characteristics. Juniper new seedling density was positively associated with live piñon BA and live juniper BA, whereby 26% of the variability of juniper new seedlings could be explained by these two variables (Table 3). Unlike juniper new seedlings, there was no relationship between

Table 2 Stem density and piñon dominance across our 30 sites

Size class	Piñon density (stems ha^{-1})	Juniper density (stems ha^{-1})	Piñon dominance (%)
New seedlings	67 ± 16 (0–300)	34 ± 5 (0–107)	54 ± 5 (0–100)
Advanced seedlings	194 ± 20 (13–480)	193 ± 19 (6–333)	51 ± 3 (22–93)
Sapling	137 ± 16 (0–327)	90 ± 16 (0–480)	58 ± 5 (0–100)
Adult (pre-mortality)	488 ± 54 (78–1039)	447 ± 25 (169–753)	49 ± 3 (13–77)
Adult (post-mortality)	268 ± 34 (0–623)	421 ± 24 (155–727)	35 ± 4 (0–70)

Data are means ± 1SE. The range is included in parentheses.

Table 3 Results of the best linear models based on stepAIC used to predict piñon and juniper densities and piñon dominance in each juvenile size class

	Size class	R^2	P value	Predictor variables	β_s	P value
Piñon	New seedling	0.63	<0.0001	Live shrub cover	0.50	**0.001**
				Live piñon basal area	0.47	**0.002**
				Live juniper cover	0.36	**0.01**
	Adv. seedling	0.64	<0.0001	Live shrub cover	0.70	**< 0.001**
				Live + dead piñon basal area	0.55	**0.004**
				Live juniper cover	0.38	**0.01**
				Soil available water capacity	0.31	**0.03**
	Sapling	0.31	0.001	Live shrub cover	0.56	**0.001**
Juniper	New seedling	0.26	0.02	Live piñon basal area	0.40	**0.02**
				Live juniper basal area	0.34	0.05
	Adv. seedling	0.09	0.11	Soil available water capacity	0.30	0.11
	Sapling	0.21	0.01	Live juniper basal area	−0.46	**0.01**
Piñon dominance	New seedling	0.32	0.002	Live shrub cover	0.56	**0.002**
	Adv. seedling	0.35	0.01	Live shrub cover	0.39	**0.02**
				Live juniper basal area	0.33	0.06
				Live + dead piñon basal area	0.30	0.08
	Sapling	0.59	<0.0001	Live juniper basal area	0.56	**0.0002**
				Live shrub cover	0.46	**0.001**
				Live + dead piñon basal area	0.30	**0.03**

The standardized regression coefficient (β_s) and P value are given for each predictor variable used in the final model based on stepAIC. $n = 30$ (except $n = 28$ for piñon dominance of new seedlings because of a lack of new seedlings at two sites).
P-values of statistically significant predictor variables are shown in bold ($P <0.05$).

juniper advanced seedling density and the predictor variables ($R^2 = 0.09$, $P = 0.11$; Table 3). There was weak evidence that the presence of adult junipers may inhibit the advancement of junipers to the sapling size class: juniper sapling density was weakly and negatively related to juniper BA ($R^2 = 0.21$, $P = 0.01$; Table 3).

Vegetation and soil characteristics associated with juvenile piñon dominance

Juvenile piñon dominance across our study sites was highly variable, ranging from 19% to 86% (Table 2). Piñon dominance among new seedlings was positively influenced by live shrub cover ($R^2 = 0.32$, $P = 0.002$; Table 3). Dominance of both piñon advanced seedlings and piñon saplings was positively associated with live shrub cover, live juniper BA and live + dead piñon BA ($R^2 = 0.35$ and 0.59 for advanced seedlings and saplings, respectively; Table 3). These results highlight how tree and shrub microsites are important for juvenile piñon dominance, and suggest that percentage piñon mortality did not influence juvenile piñon dominance.

There were no significant differences between adult piñon dominance before recent mortality and juvenile piñon dominance among all size classes (paired Student's t-tests; $P > 0.09$; Fig. 3; Table 2), suggesting that there was no directional shift in juvenile piñon dominance relative to adult piñon dominance across our 30 sites. There was also no relationship between piñon mortality and the difference in piñon dominance among juveniles and adults ($R^2 < 0.1$; $P > 0.1$; Fig. 3). Although there was some variability in the relationship between juvenile piñon dominance and adult piñon dominance (Fig. 3), our results suggest that, overall, the juvenile tree community is similar to that of the adult tree community before the recent mortality (Fig. 3).

Net effects of facilitation and competition by trees and shrubs

Consistent across all juvenile size classes, both piñon and juniper were more likely to be found beneath tree and shrub canopies than in the interspace, as evidenced by the high positive interaction indices (indicating facilitation) between shrub and tree cover and juvenile piñon and juniper trees (Fig. 4). In addition, although piñon and juniper new seedlings had high interaction indices (> 0.90), with over 90% of new seedlings occurring beneath trees and shrubs, piñon and juniper saplings had significantly lower interaction indices (0.76 and 0.40, respectively; Fig. 4). Unlike new seedlings, piñon advanced seedlings and saplings had significantly higher interaction indices than juniper (Fig. 4), suggesting that, at these larger juvenile size classes, juniper is less able to survive than piñon beneath tree and shrub canopies.

Both live and dead piñon saplings were more likely to be found beneath the canopy of a tree or shrub than in the interspace, as evidenced by the high positive interaction indices between shrub and tree cover and piñon sapling densities (mean interaction index ± 1SE = 0.76 ± 0.06 and 0.83 ± 0.07 for live and dead piñon saplings, respectively). However, interaction indices did not differ between live and dead piñon saplings (paired Wilcox signed rank test, $P = 0.3$), indicating that piñon sapling survival was the same in both canopy and interspace microsites.

Discussion

Vegetation and soil characteristics associated with tree recruitment

Our results suggest that recovery following recent piñon mortality will be dependent on advanced regeneration, findings which are consistent with other studies examining tree regeneration

(a)

(b)
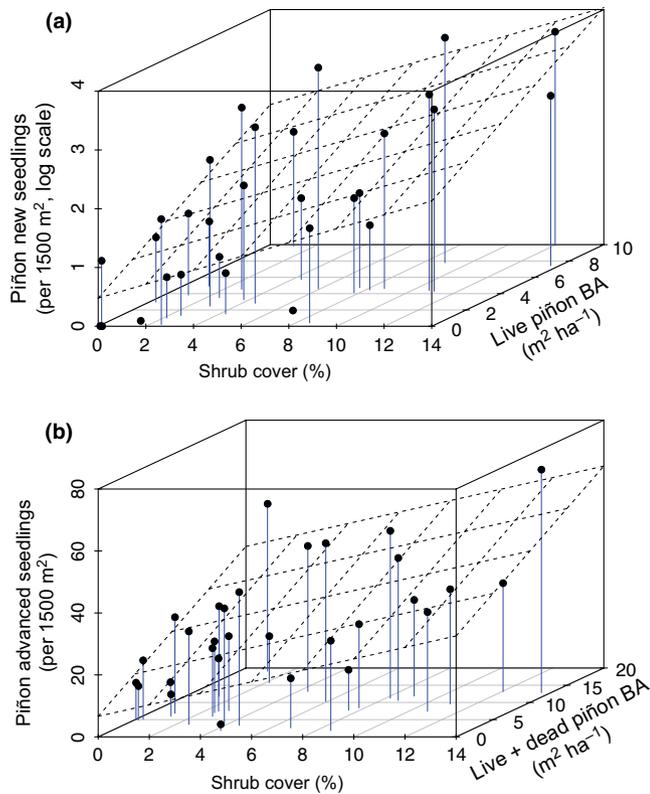
Fig. 2 (a) Plot of the logarithm of the density of piñon new seedlings (i.e. seedlings with a basal diameter ≤ 0.5 cm, which probably established after adult mortality) against percentage shrub cover and live adult piñon basal area (BA), the two strongest predictor variables. (b) Plot of the density of piñon advanced seedlings (i.e. seedlings with a basal diameter > 0.5 cm, which probably established before adult mortality) against percentage shrub cover and live and dead adult piñon basal area, the two strongest predictor variables. Dashed grid represents the multiple linear regression model using the two strongest predictor variables in the regression models presented in Table 3.

Fig. 3 The relationship between juvenile piñon dominance and adult piñon dominance across the 30 sampled sites in the USA. Different colored circles illustrate the different levels of adult piñon mortality that occurred at each site based on adult basal area. The line illustrates where juvenile piñon dominance is equal to adult piñon dominance.

Fig. 4 The interaction indices between shrub and tree cover and live juvenile piñon (gray bars) and juniper (black bars) trees. Interaction indices between 0 and 1 represent a facilitative effect of shrub and tree cover on piñon and juniper recruitment, with increasingly positive values representing an increasingly facilitative effect. Asterisks denote significant differences between piñon and juniper juveniles within each size class, and different letters denote significant differences between juvenile size classes within each species. Error bars are ± 1SE.

following drought- and insect-induced tree mortality (Veblen *et al.*, 1991; Axelson *et al.*, 2009; Collins *et al.*, 2011; Diskin *et al.*, 2011; Kayes & Tinker, 2012). New (post-mortality) piñon recruitment was strongly positively associated with live adult piñon density (Table 3; Fig. 2a), and was thus negatively affected by recent piñon mortality. The low levels of new piñon recruitment following high mortality are probably a result of seed limitations, as piñon seed viability declines rapidly after the first year (Meeuwig & Bassett, 1983), and may also be caused by declines in canopy microsites. Notably, piñon advanced (pre-mortality) seedlings and saplings were not affected by overstory piñon mortality and, instead, were positively associated with piñon density at the time of establishment (i.e. live + dead piñon BA; Table 3). These results highlight the importance of advanced regeneration for piñon recovery, and support previous findings of low juvenile piñon mortality in areas with high adult piñon mortality (Negrón & Wilson, 2003; Mueller *et al.*, 2005). The relatively high levels of advanced regeneration following drought- and beetle-induced mortality in this study and others (Veblen *et al.*, 1991; Axelson *et al.*, 2009; Collins *et al.*, 2011; Diskin *et al.*, 2011; Kayes & Tinker, 2012) suggest that there is a greater bottleneck in

obtaining new recruitment, which is dependent on seed production, dispersal, germination and seedling establishment, as compared with advanced regeneration, which is only dependent on juvenile survival following recent mortality.

Shrub and juniper cover was strongly positively associated with piñon juvenile density (Table 3), which supports our hypothesis that trees and shrubs facilitate piñon establishment and is consistent with other field observations and experimental studies (Floyd, 1982; Chambers, 2001; Mueller *et al.*, 2005; Sthultz *et al.*, 2007). The shading provided by trees and shrubs reduces solar radiation, leading to lower soil temperatures and less evapotranspiration (Breshears *et al.*, 1997; Chambers, 2001; Royer *et al.*, 2010, 2012), and may result in higher soil water contents

(Chambers, 2001). Higher nutrient availability and higher organic matter content have also been reported underneath trees and shrubs in piñon–juniper woodlands (Padien & Lajtha, 1992; Chambers, 2001), which may also positively influence piñon recruitment.

In addition to vegetation structure, our results suggest that high soil available water capacity may be important for the promotion of piñon juvenile survival. Regionally, there was greater adult piñon mortality in areas with lower soil available water capacity (Peterman et al., 2012). Although the range of soil available water capacity across our sites was relatively narrow compared with other studies (Peterman et al., 2012), there was a positive association between soil available water capacity and piñon advanced seedling density (Table 3). This positive association may be caused by greater piñon seedling survival during the 2002–2003 drought in areas with higher soil available water capacity. Because piñon recovery following high adult mortality will probably be dependent on advanced regeneration, these results suggest that areas with lower soil available water capacity may have less piñon regeneration following high adult mortality.

Juniper juveniles were not as strongly associated with vegetation structure as piñon, and were also more commonly found in the canopy interspaces than piñon (Table 3; Fig. 4). These results support our hypothesis that piñon is more dependent on overstory trees and shrubs to facilitate seedling establishment and survival, and are consistent with previous field studies (Chambers et al., 1999). However, juniper new seedlings were still strongly facilitated by overstory trees and shrubs, unlike juniper advanced seedlings and saplings (Table 3; Fig. 4). This suggests that competition for light and, potentially, water may be more important than the facilitative effects of overstory trees and shrubs once juniper seedlings become established.

Shifts in the juvenile tree community

Counter to our predictions, piñon mortality resulted in no shift in the juvenile tree community (Table 2; Fig. 3), suggesting that future woodland composition may be similar to the woodland composition in the past. The lack of a shift in the juvenile tree community is in contrast with other studies that have examined tree regeneration patterns following drought- and/or beetle-induced mortality (Veblen et al., 1991; Suarez & Kitzberger, 2008; Collins et al., 2011; Kayes & Tinker, 2012). However, all of these studies examined tree regeneration following the mortality of relatively shade-intolerant species, such as lodgepole pine (Pinus contorta). In contrast, piñon is more shade tolerant than juniper (Barney & Frischknecht, 1974; Chambers et al., 1999), which, we hypothesize, enabled piñon to have higher juvenile densities before mortality, leading to sufficient advanced regeneration. Recovery following drought- and insect-induced tree mortality will be largely dependent on juveniles present in the community before the mortality event (Veblen et al., 1991; Suarez & Kitzberger, 2008; Collins et al., 2011). Thus, there may be greater shifts in the juvenile tree community following overstory mortality of shade-intolerant tree species because of little advanced regeneration.

Juvenile piñon dominance was still highly variable across our study sites (Table 2; Fig. 3), and was positively related to tree and shrub cover (Table 3). This suggests that there may be a shift in the juvenile tree community in the future. Once more dead piñon snags fall, piñon dominance may become negatively impacted by the loss in canopy microsites. There has also been significant shrub mortality and juniper dieback in piñon–juniper woodlands in northern Arizona following recent droughts (Gitlin et al., 2006; Koepke et al., 2010), which could further reduce suitable microsites and affect future piñon dominance. In addition, drought- and insect-induced mortality events are predicted to increase in the southwestern USA (Williams et al., 2013). These predicted future mortality events may result in a shift in juvenile piñon dominance. In particular, as these older juveniles grow, they will probably become more susceptible to bark beetle attack and less likely to survive future droughts (Floyd et al., 2009), which may result in less advanced regeneration.

Net effects of facilitation and competition by trees and shrubs

Juveniles of both piñon and juniper across all size classes were more likely to be found underneath the canopy of trees and shrubs than in the adjacent interspace (Fig. 4), which supports the hypothesis that trees and shrubs facilitate piñon and juniper establishment (Miller & Rose, 1995; Chambers, 2001; Mueller et al., 2005; Sthultz et al., 2007). The high percentage of piñon and juniper seedlings underneath tree and shrub canopies may also be partly a result of the caching of seeds underneath trees and shrubs by birds and small mammals (Vander Wall & Balda, 1977; Vander Wall, 1997).

New seedlings of piñon and juniper were more likely than saplings to be found underneath the canopy of trees and shrubs (Fig. 4). There are two, non-mutually exclusive, hypotheses for why there is a decline in the positive association between shrub and tree canopies and tree juveniles with juvenile age. One hypothesis is that, as juveniles become older, increased competition with overstory trees and shrubs may outweigh the facilitative effects. In support of this hypothesis, both juniper and various shrub species have been reported to negatively impact adult piñon growth through below-ground competition (Haskins & Gehring, 2004; McHugh & Gehring, 2006), and shifts from facilitation to competition are known to occur among a variety of plant species with changes in life stages (Callaway & Walker, 1997). Another hypothesis is that these older juveniles established during cooler, wetter climate conditions, and thus were not as dependent on tree and shrub microsites at the time of establishment. In support of this hypothesis, previous research on piñon (Sthultz et al., 2007) and other tree species (Greenlee & Callaway, 1996; Kitzberger et al., 2000) has found that the net effects of competition and facilitation vary across spatial and temporal gradients of abiotic stress.

Interestingly, there was no difference in survival between piñon saplings located beneath the canopy of a tree or shrub and those located in the canopy interspace. This suggests that, at this

life history stage, facilitation and competition were equal between canopy microsites and piñon saplings in our study area. However, piñon sapling density was positively associated with shrub cover (Table 3). This may be caused by the facilitative effects of shrubs on piñon seedling establishment (Fig. 4) and the above-ground competitive release that occurs once the sapling grows taller than the shrub.

Conclusion

Drought- and insect-induced piñon mortality events have dramatically altered woodland structure across the southwestern USA (Breshears et al., 2005; Mueller et al., 2005), affecting water and energy fluxes and carbon stocks (Royer et al., 2011; Adams et al., 2012; Hicke et al., 2012). Our results indicate that piñon mortality does not strongly affect successional trajectories in piñon–juniper woodlands because of advanced regeneration. Accordingly, this landscape appears to be resilient to recent drought- and beetle-induced mortality because of the high densities of juveniles that survived the drought. However, piñon and juniper have slow growth rates in these semi-arid ecosystems (Despain, 1989; Barger et al., 2009), which suggests that ecosystem processes and function may be altered in high-mortality stands for 50 yr or more. As hypothesized, trees and shrubs appear to facilitate both piñon and juniper seedling establishment, and piñon juveniles were more dependent than juniper on tree and shrub microsites. Piñon advanced seedlings were also positively associated with soil available water capacity, unlike juniper. These results highlight the greater drought tolerance of juniper relative to piñon (Linton et al., 1998; West et al., 2007; Breshears et al., 2008; McDowell et al., 2008), and suggest that tree and shrub microsites may become increasingly important for future piñon recruitment, given the predicted increases in aridity across the southwestern USA (Seager et al., 2007; Williams et al., 2013).

References

Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, Villegas JC, Breshears DD, Zou CB, Troch PA, Huxman TE. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proceedings of the National Academy of Sciences, USA 106: 7063–7066.

Adams HD, Luce CH, Breshears DD, Allen CD, Weiler M, Hale VC, Smith A, Huxman TE. 2012. Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. Ecohydrology 5: 145–159.

Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. Second International Symposium on Information Theory. Budapest, Hungary: Akademiai Kiado.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259: 660–684.

Anderegg WRL, Kane JM, Anderegg LDL. 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change 3: 30–36.

Armas C, Ordiales R, Pugnaire FI. 2004. Measuring plant interactions: a new comparative index. Ecology 85: 2682–2686.

Axelson JN, Alfaro RI, Hawkes BC. 2009. Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. Forest Ecology and Management 257: 1874–1882.

Ball DF. 1964. Loss-on-ignition as an estimate of organic matter and organic carbon in non-calcareous soils. Journal of Soil Science 15: 84–92.

Barger NN, Adams HD, Woodhouse C, Neff JC, Asner GP. 2009. Influence of livestock grazing and climate on pinyon pine (Pinus edulis) dynamics. Rangeland Ecology & Management 62: 531–539.

Barney MA, Frischknecht NC. 1974. Vegetation changes following fire in the pinyon–juniper type of west-central Utah. Journal of Range Management 27: 91–96.

Ben-Dor E, Banin A. 1989. Determination of organic matter content in arid-zone soils using a simple 'loss-on-ignition' method. Communications in Soil Science and Plant Analysis 20: 1675–1695.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B (Methodological) 57: 289–300.

Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J et al. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences, USA 102: 15144.

Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, McDowell NG, Pockman WT. 2008. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. Frontiers in Ecology and the Environment 7: 185–189.

Breshears DD, Rich PM, Barnes FJ, Campbell K. 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. Ecological Applications 7: 1201–1215.

Brown JH, Whitham TG, Ernest SKM, Gehring CA. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. Science 293: 643–650.

Brown M, Black TA, Nesic Z, Foord VN, Spittlehouse DL, Fredeen AL, Grant NJ, Burton PJ, Trofymow JA. 2010. Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia. Agricultural and Forest Meteorology 150: 254–264.

Callaway RM, DeLucia EH, Moore D, Nowak R, Schlesinger WH. 1996. Competition and facilitation: contrasting effects of Artemisia tridentata on desert vs. montane pines. Ecology 77: 2130–2141.

Callaway RM, Walker LR. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958–1965.

Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proceedings of the National Academy of Sciences, USA 108: 1474–1478.

Chambers JC. 2001. Pinus monophylla establishment in an expanding Pinus–Juniperus woodland: environmental conditions, facilitation and interacting factors. Journal of Vegetation Science 12: 27–40.

Chambers JC, Vander Wall SB, Schupp EW. 1999. Seed and seedling ecology of piñon and juniper species in the pygmy woodlands of western North America. *Botanical Review* 65: 1–38.

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG *et al.* 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491: 752–755.

Collins BJ, Rhoades CC, Hubbard RM, Battaglia MA. 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *Forest Ecology and Management* 261: 2168–2175.

Despain DW. 1989. *Radial growth relationships in Utah juniper (Juniperus osteosperma) and pinyon pine (Pinus edulis)*. PhD thesis, University of Arizona, Tuscon, AZ, USA.

Diskin M, Rocca ME, Nelson KN, Aoki CF, Romme WH. 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research* 41: 782–792.

Everett R, Ward K. 1984. Early plant succession on pinyon–juniper controlled burns. *Northwest Science* 58: 57–68.

Floyd ME. 1982. The interaction of piñon pine and gambel oak in plant succession near Dolores, Colorado. *Southwestern Naturalist* 27: 143–147.

Floyd ML, Clifford M, Cobb NS, Hanna D, Delph R, Ford P, Turner D. 2009. Relationship of stand characteristics to drought-induced mortality in three southwestern piñon–juniper woodlands. *Ecological Applications* 19: 1223–1230.

García LV. 2004. Escaping the Bonferroni iron claw in ecological studies. *Oikos* 105: 657–663.

Gitlin AR, Sthultz CM, Bowker MA, Stumpf S, Paxton KL, Kennedy K, Muñoz A, Bailey JK, Whitham TG. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology* 20: 1477–1486.

Greenlee JT, Callaway RM. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *American Naturalist* 148: 386–396.

Guardiola-Claramonte M, Troch PA, Breshears DD, Huxman TE, Switanek MB, Durcik M, Cobb NS. 2011. Decreased streamflow in semi-arid basins following drought-induced tree die-off: a counter-intuitive and indirect climate impact on hydrology. *Journal of Hydrology* 406: 225–233.

Haskins KE, Gehring CA. 2004. Interactions with juniper alter pinyon pine ectomycorrhizal fungal communities. *Ecology* 85: 2687–2692.

Hicke JA, Allen CD, Desai AR, Dietze MC, Hall RJ, Hogg EH, Kashian DM, Moore D, Raffa KF, Sturrock RN *et al.* 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology* 18: 7–34.

Jacobi WR, Kearns HSJ, Johnson DW. 2005. Persistence of pinyon pine snags and logs in southwestern Colorado. *Western Journal of Applied Forestry* 20: 247–252.

Johnsen T. 1959. Longevity of stored juniper seeds. *Ecology* 40: 487–488.

Kayes LJ, Tinker DB. 2012. Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. *Forest Ecology and Management* 263: 57–66.

Kettler TA, Doran JW, Gilbert TL. 2001. Simplified method for soil particle-size determination to accompany soil-quality analyses. *Soil Science Society of America Journal* 65: 849.

Kitzberger T, Steinaker DF, Veblen TT. 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* 81: 1914–1924.

Koepke DF, Kolb TE, Adams HD. 2010. Variation in woody plant mortality and dieback from severe drought among soils, plant groups, and species within a northern Arizona ecotone. *Oecologia* 163: 1079–1090.

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik L. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452: 987–990.

Linton MJ, Sperry JS, Williams DG. 1998. Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. *Functional Ecology* 12: 906–911.

McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG *et al.* 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* 178: 719–739.

McHugh TA, Gehring CA. 2006. Below-ground interactions with arbuscular mycorrhizal shrubs decrease the performance of pinyon pine and the abundance of its ectomycorrhizas. *New Phytologist* 171: 171–178.

Meehl GA, Tebaldi C. 2004. More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* 305: 994–997.

Meeuwig RO, Bassett RI. 1983. *Pinyon–juniper. Silviculture systems for the major forest types of the United States*. Washington, DC, USA: Agriculture Handbook US Dept. of Agriculture No. 455.

Miller RF, Rose JA. 1995. Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon. *Western North American Naturalist* 55: 37–45.

Mueller RC, Scudder CM, Porter ME, Talbot Trotter R, Gehring CA, Whitham TG. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology* 93: 1085–1093.

Natural Resources Conservation Service. 2006. Major land resources area: southwestern plateaus, mesas and foothills. Natural Resources Conservation Service. http://www.ut.nrcs.usda.gov/technical/technology/range/mlra35.html

Negrón JF, Wilson JL. 2003. Attributes associated with probability of infestation by the piñon ips, *Ips confusus* (Coleoptera: Scolytidae), in piñon pine, *Pinus edulis*. *Western North American Naturalist* 63: 440–451.

Padien DJ, Lajtha K. 1992. Plant spatial pattern and nutrient distribution in pinyon–juniper woodlands along an elevational gradient in northern New Mexico. *International Journal of Plant Sciences* 153: 425–433.

Peterman W, Waring RH, Seager T, Pollock WL. 2012. Soil properties affect pinyon pine–juniper response to drought. *Ecohydrology*. doi: 10.1002/eco.1284.

Pfeifer EM, Hicke JA, Meddens AJH. 2011. Observations and modeling of aboveground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. *Global Change Biology* 17: 339–350.

R Development Core Team. 2011. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Redmond MD, Cobb NS, Miller ME, Barger NN. (2013). Long-term effects of chaining treatments on vegetation structure in piñon–juniper woodlands of the Colorado Plateau. *Forest Ecology & Management* 305: 120–128.

Redmond MD, Forcella F, Barger NN. 2012. Declines in pinyon pine cone production associated with regional warming. *Ecosphere* 3: 120.

Royer PD, Breshears DD, Zou CB, Cobb NS, Kurc SA. 2010. Ecohydrological energy inputs in semiarid coniferous gradients: responses to management- and drought-induced tree reductions. *Forest Ecology and Management* 260: 1646–1655.

Royer PD, Breshears DD, Zou CB, Villegas JC, Cobb NS, Kurc SA. 2012. Density-dependent ecohydrological effects of piñon–juniper woody canopy cover on soil microclimate and potential soil evaporation. *Rangeland Ecology & Management* 65: 11–20.

Royer PD, Cobb NS, Clifford MJ, Huang CY, Breshears DD, Adams HD, Villegas JC. 2011. Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: primary and secondary ecological implications. *Journal of Ecology* 99: 714–723.

Saxton KE, Rawls WJ. 2006. Soil water characteristic estimates by texture and organic matter for hydrologic solutions. *Soil Science Society of America Journal* 70: 1569.

Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C *et al.* 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316: 1181–1184.

Sthultz CM, Gehring CA, Whitham TG. 2007. Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytologist* 173: 135–145.

Suarez ML, Kitzberger T. 2008. Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. *Canadian Journal of Forest Research* 38: 3002–3010.

Tausch RJ, Tueller PT. 1977. Plant succession following chaining of pinyon–juniper woodlands in eastern Nevada. *Journal of Range Management* 30: 44–49.

Van Mantgem PJ, Stephenson NL. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters* 10: 909–916.

Van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH *et al.* 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323: 521–524.

Vander Wall SB. 1997. Dispersal of singleleaf piñon pine (*Pinus monophylla*) by seed-caching rodents. *Journal of Mammalogy* 78: 181–191.

Vander Wall SB, Balda RP. 1977. Coadaptations of the Clark's Nutcracker and the piñon pine for efficient seed harvest and dispersal. *Ecological Monographs* 47: 89–111.

Veblen TT, Hadley KS, Reid MS, Rebertus AJ. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72: 213–231.

Venables WN, Ripley BD. 2002. *Modern Applied Statistics with S.* New York, NY, USA: Springer.

Walton A. 2012. *Provincial-level projection of the current mountain pine beetle outbreak. Update of the infestation projection based on the provincial aerial overview surveys of forest health conducted from 1999 through 2011 and the BCMPB model (year 9).* British Colombia Ministry of Forests, Land and Natural Resource Operations. [WWW document] URL: http://www.for.gov.bc.ca/ftp/hre/external/!publish/web/bcmpb/year9/BCMPB.v9.BeetleProjection.Update.pdf [accessed on 20 May 2013].

West AG, Hultine KR, Jackson TL, Ehleringer JR. 2007. Differential summer water use by *Pinus edulis* and *Juniperus osteosperma* reflects contrasting hydraulic characteristics. *Tree Physiology* 27: 1711–1720.

Williams AP, Allen CD, Macalady AK, Griffin D, Woodhouse CA, Meko DM, Swetnam TW, Rauscher SA, Seager R, Grissino-Mayer HD *et al.* 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3: 292–297.

Worrall JJ, Marchetti SB, Egeland L, Mask RA, Eager T, Howell B. 2010. Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *Forest Ecology and Management* 260: 638–648.

Zuur AF, Ieno EN, Smith GM. 2007. *Analysing ecological data.* New York, NY, USA: Springer.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Piñon seedling size–age relationship.

Fig. S2 Size–age relationship among piñon and juniper juveniles at two sites in southern Utah.

Table S1 Location, soil texture and organic matter data for each site

Table S2 Vegetation characteristics, soil available water capacity and tree recruitment data for each site

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.