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Precipitation thresholds and drought-induced tree die-off: insights from patterns of *Pinus edulis* mortality along an environmental stress gradient

Michael J. Clifford¹, Patrick D. Royer^{2,3}, Neil S. Cobb⁴, David D. Breshears⁵ and Paulette L. Ford⁶

¹Earth and Environmental Science Department, Lehigh University, Bethlehem, PA 18015, USA; ²Columbia Basin Groundwater Management Area, Kennewick, WA 99366, USA; ³Intera Geoscience and Engineering, Richland, WA 99354, USA; ⁴Merriam-Powell Center for Environmental Research, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA; ⁵Department of Ecology & Evolutionary Biology, School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 85721, USA; ⁶USDA Forest Service Rocky Mountain Research Station, Albuquerque, NM 87102, USA

Author for correspondence:

Michael J. Clifford

Tel: +1 610 758 1242

Email: mjc709@lehigh.edu

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Summary

- Recent regional tree die-off events appear to have been triggered by a combination of drought and heat – referred to as ‘global-change-type drought’. To complement experiments focused on resolving mechanisms of drought-induced tree mortality, an evaluation of how patterns of tree die-off relate to highly spatially variable precipitation is needed.
- Here, we explore precipitation relationships with a die-off event of pinyon pine (*Pinus edulis* Engelm.) in southwestern North America during the 2002–2003 global-change-type drought. Pinyon die-off and its relationship with precipitation was quantified spatially along a precipitation gradient in north-central New Mexico with standard field plot measurements of die-off combined with canopy cover derived from normalized burn ratio (NBR) from Landsat imagery.
- Pinyon die-off patterns revealed threshold responses to precipitation (cumulative 2002–2003) and vapor pressure deficit (VPD), with little to no mortality (< 10%) above 600 mm and below warm season VPD of c. 1.7 kPa. [Correction added after online publication 17 June 2013; in the preceding sentence, the word ‘below’ has been inserted.]
- Our results refine how precipitation patterns within a region influence pinyon die-off, revealing a precipitation and VPD threshold for tree mortality and its uncertainty band where other factors probably come into play – a response type that influences stand demography and landscape heterogeneity and is of general interest, yet has not been documented.

Introduction

Disturbance events are important drivers of ecosystem patterns and processes (Turner, 1989), and understanding the patterns associated with such events allows for a greater understanding of the variability within a system. Particularly concerning are recent tree die-off events at up to regional scales, apparently triggered by a combination of drought and heat – previously referred to as ‘global-change-type drought’ (Breshears *et al.*, 2005) – in some cases associated with pests and pathogens (Allen *et al.*, 2010). The physiological mechanisms associated with drought-induced mortality remain a major uncertainty, and appear to be related to complex interrelationships between plant hydraulics and carbon metabolism (McDowell *et al.*, 2008, 2011; Zeppel *et al.*, 2012). Nonetheless, the fundamental drivers of such die-off patterns often appear to be a combination of reduced precipitation, warmer temperature and associated increased atmospheric demand. There is a need for improved relationships, even if empirical rather than mechanistic, that can aid in prediction of forest vulnerability to future

climate. While controlled experiments are being used to untangle the mechanisms of drought-induced tree mortality (Adams *et al.*, 2009; Plaut *et al.*, 2012), simultaneously broad-scale analyses are needed that utilize extensive available data sets on climate drivers that affect tree die-off. Indeed, recent synthesis of ecosystem responses to severe drought reveals strong cross-biome patterns associated with precipitation (Ponce Campos *et al.*, 2013).

Among the most studied examples of drought-induced tree mortality is the die-off of the pinyon pine (*Pinus edulis*) in the southwestern USA during drought occurring around the year 2000. In the semiarid southwestern USA, drought disturbance has altered vegetation patterns and forest and woodland dynamics (Allen & Breshears, 1998; Mueller *et al.*, 2005), and has persisted in areas since the mid-1990s (Breshears *et al.*, 2005; Shaw *et al.*, 2005), with extreme drought conditions occurring between 2002 and 2004. Drought, coupled with increased temperatures (Breshears *et al.*, 2005; Adams *et al.*, 2009) and an associated bark beetle (*Ips confusus*) outbreak in pinyon pine, a co-dominant tree species of the pinyon–juniper woodlands (*Juniperus* spp.), caused

widespread pinyon die-off occurring between 2002 and 2003 (Breshears *et al.*, 2005).

Most regional climate models predict increasing future temperatures and decreased precipitation in the southwestern USA (Seager *et al.*, 2007; Overpeck & Udall, 2010). Persistent drought conditions and increased temperatures will continue to alter vegetation patterns as dominant overstory species trees continue to die (Adams *et al.*, 2009; Allen *et al.*, 2010), especially as water budgets become more stressed (Seager *et al.*, 2007). Temperatures during the drought of 2002 and 2003 were higher than in the previous recorded drought of similar magnitude, which occurred in the 1950s (Breshears *et al.*, 2005). The elevated temperatures combined with decreased precipitation increase the vapor pressure deficit (VPD), causing substantial negative impacts on the physiology of the tree, and increasing the potential for carbon starvation or xylem cavitation (Adams *et al.*, 2009; McDowell *et al.*, 2011; Choat *et al.*, 2012), ultimately leading to death.

Elevated temperature can cause increased die-off risks through physiological mechanisms in trees; however, temperatures also affect insect physiology and life cycles (Raffa *et al.*, 2008). Warmer temperatures can increase the populations of many outbreak-type insect species (Swetnam & Lynch, 1993; Logan *et al.*, 2003; Bigler *et al.*, 2006). These outbreaks occur as vegetation becomes stressed and host plant defense mechanisms are unable to keep herbivorous insects from attacking (Waring & Cobb, 1992). The effect of temperature and the associated change in atmospheric demand (as reflected in vapor pressure deficit) has recently been shown to contribute to patterns of regional variability in die-off (Weiss *et al.*, 2009, 2012). However, other recent studies suggest that this effect should be related to precipitation amount. Edaphic variables such as soil topography (Kleinman *et al.*, 2012) and soil water-holding capacity (WHC) (Peterman *et al.*, 2012) have been shown to be important controls on the patterns of pinyon die-off. Edaphic variables controlling die-off appear to be related to factors that control available moisture over varying temporal scales, and have also been shown to control overall canopy cover in water-limited woodlands (Kerkhoff *et al.*, 2004). Precipitation patterns probably underlie these responses, affecting plant-available water and associated plant water stress.

In summary, several studies have documented the impacts of drought, increased temperatures, and bark beetle infestation on die-off in pinyon–juniper woodlands since the die-off event of 2002 and 2003 (Negron & Wilson, 2003; Breshears *et al.*, 2005; Mueller *et al.*, 2005; Shaw *et al.*, 2005; Huang *et al.*, 2010; Clifford *et al.*, 2011; Royer *et al.*, 2011; Gaylord *et al.*, 2013), but no studies have examined pinyon die-off along a selected precipitation gradient. In this study, we identified spatial gradients of die-off using an extensive network of field sites and extrapolated to the entire area using remote sensing and asked the question: How do environmental patterns alter pinyon pine die-off dynamics over a region that experienced a gradient of mortality? In addition to correlating die-off patterns to regional climatic variation, we discuss our results in the context of a recently reported relationship of pinyon die-off to soil WHC (Peterman *et al.*, 2012) and VPD (Williams *et al.*, 2013), as well as stand-level variables

identified in other studies (Negron & Wilson, 2003; Floyd *et al.*, 2009) that could potentially promote die-off in pinyon pine.

Materials and Methods

Meteorological station data as reference points

The study area comprised *c.* 10 000 km² in the Middle Rio Grande Basin (MRGB) in central New Mexico, USA, and was located along a *c.* 180-km north–south precipitation gradient that occurred during the years 2002 and 2003. To describe the differences in precipitation and temperature between the extreme northern and southern portions of the study area, we used a time series of temperature and precipitation obtained from two weather stations. The northern station was located in Los Alamos, New Mexico (station number 295084; 35.8°N, –106.3°E) and the southern station in Mountainair, New Mexico (station number 295965; 34.5°N, –106.2°E). These stations were chosen as they were expected to show the largest variation in climate because of the latitudinal layout of our study area and are found at the end-members along a precipitation gradient. The time series of annual temperature and precipitation records from each station for 1970 to 2007 were standardized with *z*-scores to control for differences in temperature or precipitation caused by the topographic location of the weather station (e.g. the northern station was at 2230 m elevation and the southern station at 1980 m elevation). *z*-scores were used to examine the duration and magnitude of deviations from mean climate conditions.

Study site, stand characteristics, and environmental correlates of tree die-off

We sampled 95 pinyon–juniper woodland sites between 2005 and 2008 within the *c.* 10 000 km² study area in central New Mexico (Fig. 1). We followed a stratified random protocol for site selection. Site 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 only requirement of site selection was the presence of at least one pinyon pine (*Pinus edulis* Engelm.) per site; otherwise there was no preconceived selection of die-off levels or stand characteristics during site selection, as we were interested in describing the extent and heterogeneity of die-off and woodland structure within the study region. Sites were distributed across all elevation ranges (e.g. 1673–2313 m) and one location was not biased over another. Three 100-m² square subplots were established at each site. Subplots were placed in a triangular formation, 75 m apart (Floyd *et al.*, 2009). The tree species found on our sites included pinyon pine, one-seeded juniper (*Juniperus monosperma* Engelm.), alligator juniper (*Juniperus deppeana* Steud.), ponderosa pine (*Pinus ponderosa* Dougl. ex C. Lawson), and oak (*Quercus* spp.).

To determine whether there were nonclimatic environmental predictors of die-off or stand characteristics that could have increased die-off in pinyon pine, data from each subplot were averaged to the site level so that sites were representative of the general stand, and the average values were used for analyses.

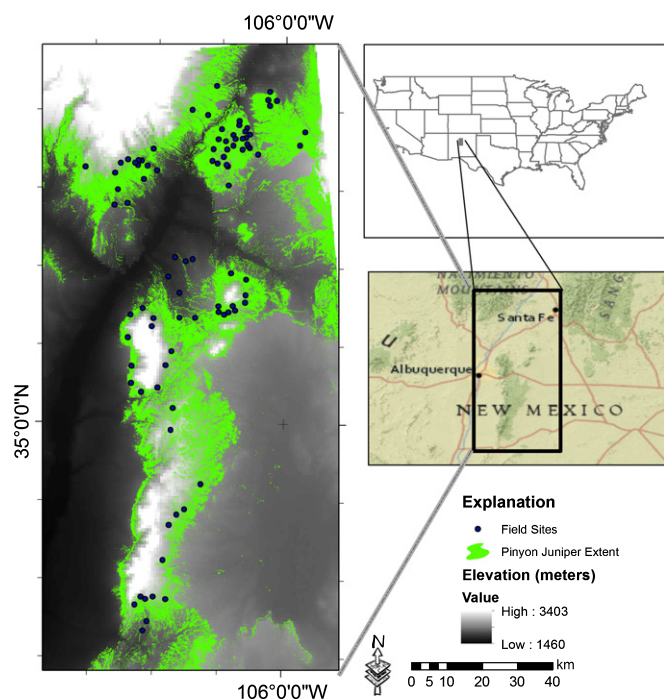


Fig. 1 The location of the study area in central New Mexico, USA. Inset shows the location of field sites (circles) overlaid on pinyon–juniper woodlands (green) and digital elevation model (grayscale).

Within each subplot, all trees were measured by two recorders for basal trunk diameter (btd), tree height, canopy area and tree status (e.g. dead or alive), following methods used in Floyd *et al.* (2009) and Clifford *et al.* (2011). btd was recorded using tree calipers and tree crown area was estimated from two perpendicular measurements of basal crown diameter. Canopy cover for each site was calculated as the sum of crown areas. Tree density was based on all individuals (including seedlings) and is shown as a measure of trees per 100 m², while basal area was calculated as $\pi \times (\text{btd}/2)^2$ (see Floyd *et al.*, 2009 for additional details). From basal area calculations, the loss of above-ground carbon content was also calculated based on equations in Huang *et al.* (2010) to examine the regional impacts on carbon dynamics of tree die-off.

Plot-level analyses of environmental, climate, and stand variables

Multiple regressions were performed to determine the relationship between per cent pinyon die-off derived from plot-level measurements and environmental and climate variables and stand characteristics. Per cent pinyon die-off was used as the dependent variable in all analyses, while independent variables included stand density (including all tree species found in a plot), basal area, and elevation, which are likely stressors, and were chosen because of the potential to magnify the impacts of drought conditions and they have also been examined in other studies (Negron & Wilson, 2003; Floyd *et al.*, 2009; Clifford *et al.*, 2011). To explore the relationships of die-off to soil WHC, we used a method similar to that of Peterman *et al.* (2012), where WHC to a depth of 100 cm was extracted from a multilayer soil character data set for the conterminous USA (CONUS-SOIL; Miller &

White, 1998) derived from the Natural Resources Conservation Service Soil Geographic Database (SSURGO) data set for each of our sites, and regression analyses were used to examine the relationships.

We used the parameter-elevation regressions on independent slopes model (PRISM) data to examine how precipitation and temperature related to per cent pinyon die-off at each site (Daly *et al.*, 2002). PRISM data are 4-km resolution data sets interpolated from participating weather stations (<http://prism.oregon-state.edu/>). Precipitation and temperature obtained from PRISM were used to predict die-off for the years 2002 and 2003. These climatic variables were used because precipitation is a major limiting factor for plant growth in the semi-arid southwestern USA and increased temperatures cause further water stress on plants. Similarly, we calculated warm season water vapor deficit, the difference between saturation water pressure and actual vapor pressure, and evaluated this variable in relationship to die-off. Warm season water vapor deficit was estimated by obtaining monthly maximum temperature, monthly minimum temperature and average dew-point temperature from PRISM for May, June, July, and August using methods derived from Williams *et al.* (2013). We also examined the relationships between annual maximum temperature, warm season maximum temperature, annual precipitation, warm season precipitation, and cold season precipitation to further understand how seasonality of climate variables impacted pinyon die-off. However, for much of the analyses, we used the cumulative precipitation between 2002 and 2003 because the linear relationship between precipitation in 2002 and that in 2003 was good (Supporting Information Fig. S1) and the drought was most extreme during these 2 yr. Using only 2002 or 2003 precipitation did not change the patterns of the results.

Remote sensing and regional die-off

Landsat imagery was obtained from 5 June 2001 to represent pre-die-off conditions and 13 June 2004 to represent post die-off conditions at row path combinations of 33/35, 34/35, 33/36, and 34/36 from Landsat 5 TM/EMT from the USGS Landsat archive. We chose Landsat imagery in June because it is the driest month of the year, in which pinyon–juniper tree canopies are most easily delineated from understory ground cover. Data from each time period were obtained with *c.* 0% cloud cover. We corrected and converted band images to top of the atmosphere reflectance values using the COST method (Chavez, 1996). To evaluate die-off in a larger spatial context and assess inferences and applications of remote sensing relative to field-based values, several different analyses were performed. We used a spectral index with band 4 (0.76–0.90 μm) and band 7 (2.08–2.35 μm) known as the normalized burn ratio (NBR; Key & Benson, 2006), which contrast bands 4 and 7:

$$\text{NBR} = (\text{Band 4} - \text{Band 7}) / (\text{Band 4} + \text{Band 7}).$$

This index has been used to characterize bark beetle impacts on tree die-off, and is particularly useful for capturing

disturbance impacts in general, especially those of wildfires (Cohen & Yang, 2010; Kennedy *et al.*, 2010; Meigs *et al.*, 2011). We calculated the absolute difference between pre-die-off NBR and post-die-off NBR, hereafter referred to as dNBR. We used the final dNBR grid as a basis for illustrating die-off intensity and developing pixel-based image classification to estimate die-off and non-die-off to the full extent of pinyon–juniper woodlands within our study region.

The extent of pinyon–juniper woodlands was identified using SWreGAP (<http://earth.gis.usu.edu/swgap/landcover.html>). Both the Landsat imagery and the SWreGAP data set have the same 30 m × 30 m pixel size, and consequently neither was re-sampled. Each pixel in the dNBR grid was classified as die-off and non-die-off using a maximum likelihood supervised classification with field data as the basis for training and validation sites. Twenty-seven die-off sites of the 95 total die-off field sites were randomly selected and used as ‘training’ sites for areas where die-off occurred, and 52 remaining die-off sites were used for cross-validation. Sixteen of our sites, which had zero die-off, were used as training sites for non-die-off. Classification accuracy for die-off sites was assessed against the validation sites using a binomial test for proportional accuracy and standard deviation (Feller, 1968).

The results of dNBR classification were then mapped to pinyon–juniper woodland extent within the study area, with each pixel represented as die-off or non-die-off. To further assess remote sensing and classification results, field-data-based per cent die-off was plotted against Landsat-based per cent die-off. To calculate per cent die-off at a spatial magnitude that could be compared with field sites, we used a 100-m circular buffer at each field location and the total number of pixels classified as die-off was divided by the sum of pixels in each area within the 100-m buffer (Fig. S2; 34 pixels on average). Partially overlapping pixels were included in estimations only if > 50% of the pixel fell within the buffer boundary. A supplemental test was carried out to assess Landsat-based dNBR by correlating the natural log of total canopy loss in the field with relative dNBR.

Results

Climate along north–south gradient

Weather stations at the extreme north end (Los Alamos, New Mexico) and south end (Mountainair, New Mexico) of our study region showed pronounced differences in precipitation patterns leading up to, and through, the die-off event (Fig. 2). Overall, the drought was more severe in the northern region, with the magnitude of drought conditions or deviation from the mean being much greater. Precipitation at the northern station decreased by 41% from the 38-yr mean from 2002 to 2003, while that at the southern station decreased by 21% over the same period of time. The regions did not differ substantially in patterns of temperature, but both weather stations recorded elevated temperatures during the drought and pinyon die-off event, consistent with the findings of others (Breshears *et al.*, 2005; Adams *et al.*, 2009; Weiss *et al.*, 2009, 2012).

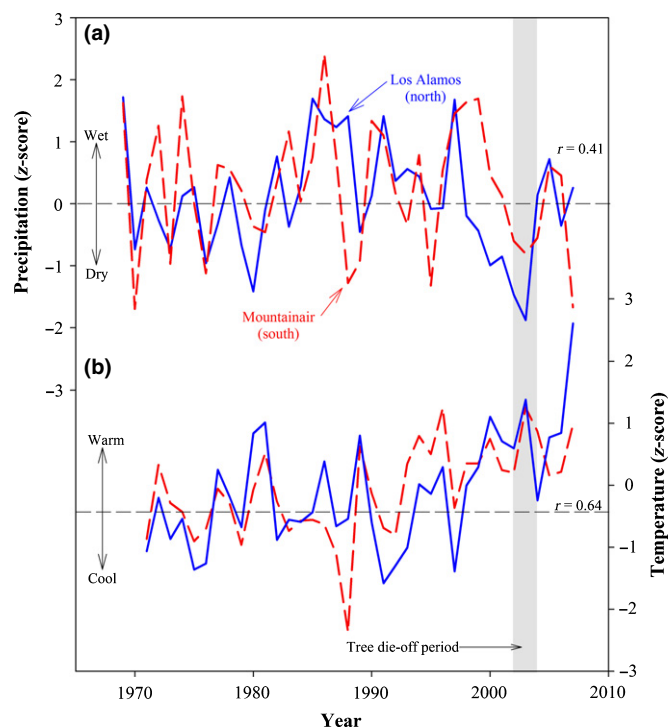


Fig. 2 Time series of normalized precipitation, $r = 0.41$ (a), and temperature, $r = 0.64$ (b), from two weather stations at the extreme northern (Los Alamos; blue solid line) and extreme southern (Mountainair; red dashed line) ends of the study area in New Mexico, USA, expressed as z-scores. The period when extensive pinyon die-off occurred in 2002 and 2003 is shaded in gray.

Regional patterns of die-off

The proportional accuracy of dNBR pixels classified as die-off based on training and validation sites was 78.8% (standard deviation ± 5.6). The correlation between per cent canopy die-off estimated in the field and estimated with remote sensing at similar extents was $r^2 = 0.59$, and the correlation between field-based canopy loss and dNBR was $r^2 = 0.54$ (Fig. S3). At the regional extent, total tree die-off and severity increased from south to north, along the latitude and precipitation gradient, consistent with general patterns in die-off related to climate drivers (Fig. 3). The total area designated as pinyon–juniper woodland in the study area was 2437 km², while the total area classified as die-off was 1029 km², corresponding to a total 42% change in cover (Fig. 3). Few sites in the northern portion of the study area (four of 64, or 6%) were above the cumulative precipitation threshold of 600 mm, while sites to the south were generally above this threshold (15 of 31, or 48%). Die-off intensity and total die-off generally increased with higher overall initial canopy cover, consistent with field data.

Environmental correlates of tree die-off

Extensive pinyon pine die-off along the precipitation gradient altered the canopy cover dynamics of the region and may have had lasting effects on the pinyon–juniper woodland ecosystem

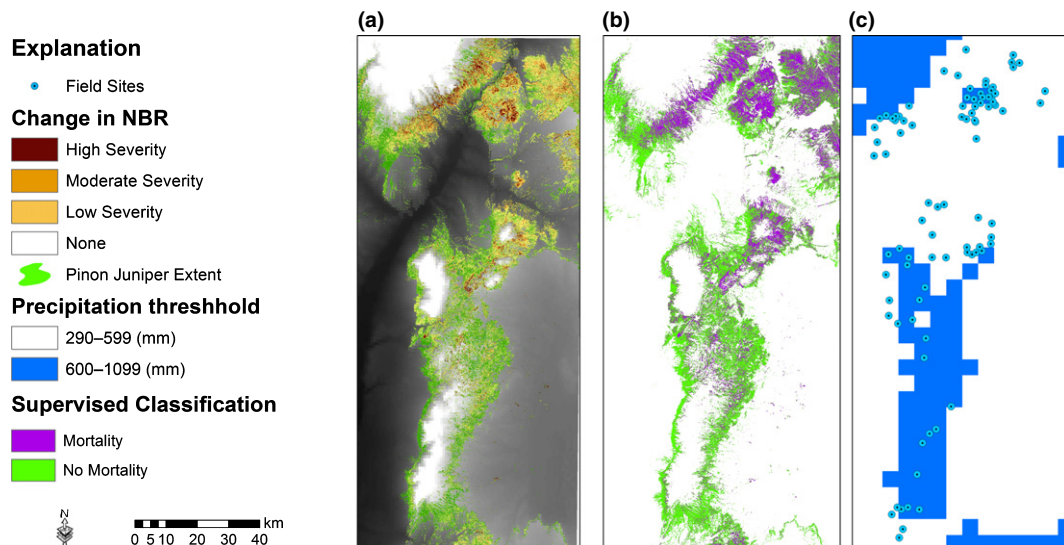


Fig. 3 (a) Extent of pinyon–juniper woodlands (green) shown with the die-off intensity (orange to brown gradient) detected with normalized burn ratio (NBR) between 2001 and 2004. The gray background is non-pinyon–juniper woodlands and shows the elevation, where dark is low and light is high. (b) Extent of pinyon–juniper woodlands showing a binary classification of areas where die-off occurred (purple) or did not (green). (c) Extent of area with < 600 mm of cumulative precipitation (white) from 2002 to 2003 and extent of area with > 600 mm of precipitation (blue); field site locations are shown as dots.

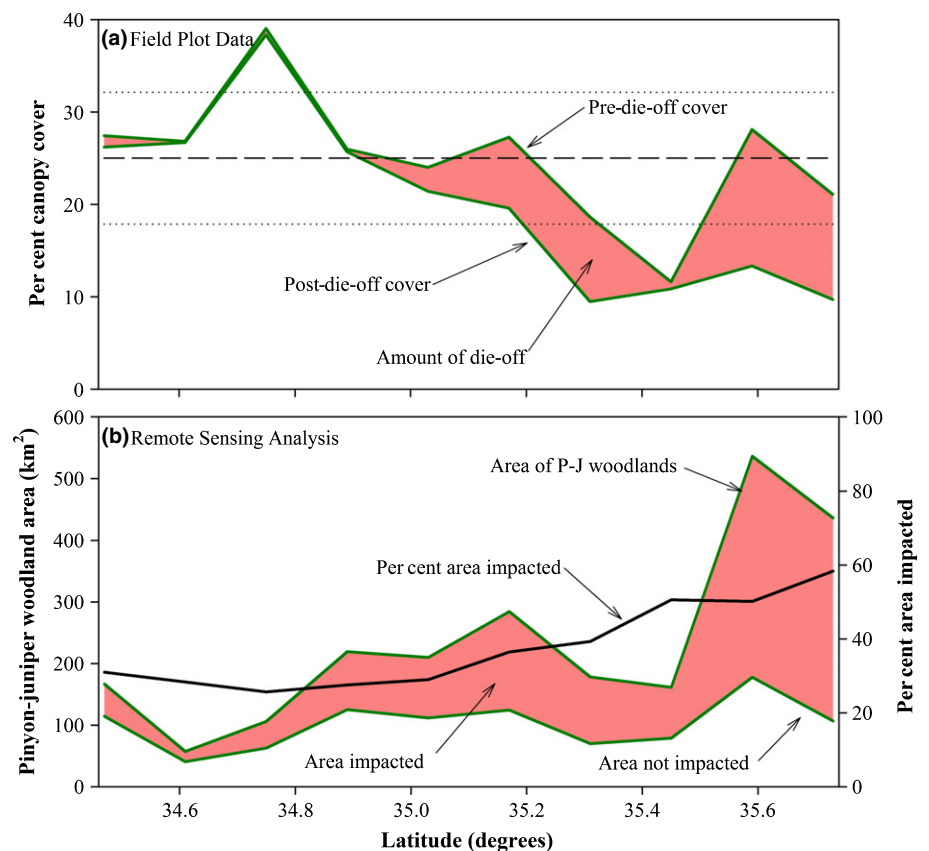


Fig. 4 (a) Latitudinal change in canopy cover pre- and post-die-off obtained from field plots. The red shaded region shows the amount of canopy cover killed by drought. Dashed and dotted lines are the mean and standard deviation, respectively, of pre-die-off canopy cover for all sites. (b) Area of pinyon–juniper (P-J) woodland from the SWReGAP data set, area of woodland impacted as detected through normalized burn ratio (NBR) analysis, and per cent of area impacted by die-off along a latitudinal gradient.

(Fig. 4). Both the field sites and remote sensing analyses showed similar patterns, where field sites showed a decrease in overall canopy cover from south to north and remote sensing analyses showed that there was more woodland in the north, in which a

greater percentage of woodlands experienced die-off from south to north. Patterns of pinyon die-off within the MRGB study area generally followed the latitudinal patterns of precipitation from 2002 to 2003 (Fig. 5), where precipitation at each site decreased

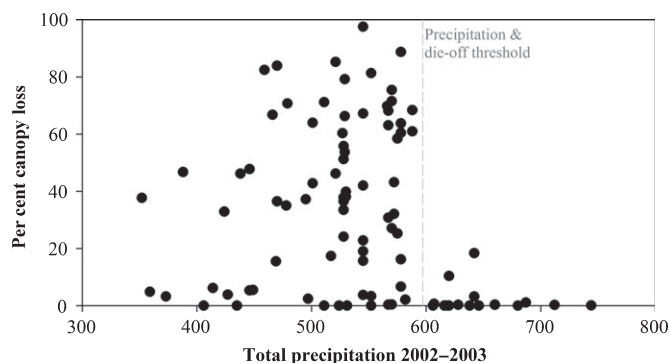


Fig. 5 The relationship of canopy cover loss to cumulative precipitation from 2002 to 2003 in the pinyon–juniper woodland field sites.

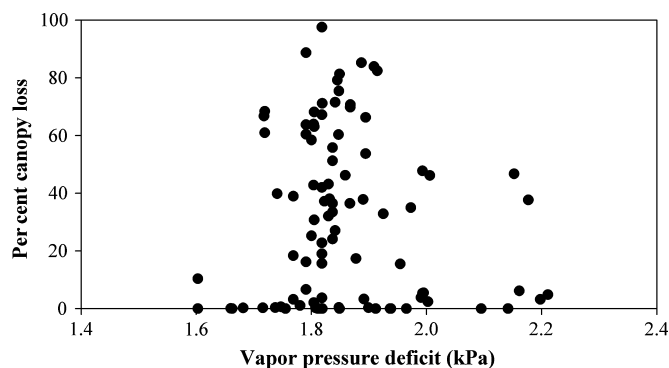


Fig. 6 Relationship between per cent canopy loss and average warm season vapor pressure deficit between 2002 and 2003 from the pinyon–juniper woodland field sites.

when moving from south to north. Furthermore, cumulative precipitation from 2002 to 2003 suggests that pinyon pines experience a threshold, where sites that experienced > 600 mm of precipitation had remarkably low die-off rates, while sites that experienced < 600 mm of cumulative precipitation had the possibility of substantially higher die-off rates (Fig. 3). The precipitation threshold is consistent whether data are displayed as total canopy cover lost from die-off or per cent canopy cover lost from die-off. Additionally, warm season VPD from 2002 and 2003 suggests a similar threshold in pinyon die-off to that for precipitation (Fig. 6). When the mean warm season VPD from 2002 to 2003 was < 1.7 kPa, a similar pattern emerged with low levels of die-off, but when VPD became > 1.7 kPa, variability and levels of die-off increased dramatically. [Correction added after online publication 17 June 2013; in the preceding sentence, > 1.7 kPa was corrected to < 1.7 kPa, to read ‘When the mean warm season VPD from 2002 to 2003 was < 1.7 kPa . . .’.]

We examined nonclimatic characteristics of environmental stress that other studies found were associated with pinyon die-off (Floyd *et al.*, 2009). Tree basal area was not a significant predictor of tree die-off, while decreasing tree density was correlated with increasing tree die-off (Table S1). Furthermore, we used 32 sites included in Floyd *et al.* (2009), with an additional 63 sites in this study, but report similar relationships to die-off. Additionally, we found similar amounts of above-ground carbon loss, 13.4

to $15.4 \text{ Mg C ha}^{-1}$, as found in Huang *et al.* (2010). Per cent pinyon die-off had no relationship to elevation and little relationship to soil WHC in our study region. Most of our sites (77%) occurred on soils that hold > 250 mm of water, but die-off varied substantially across all soil WHC levels, especially those with > 250 mm WHC, which was the highest category that Peterman *et al.* (2012) used in their soil classifications.

Discussion

We show a pattern of pinyon die-off along a precipitation gradient during a drought, where the most notable pattern was a strong threshold response of die-off to precipitation; sites above a 600-mm threshold of cumulative precipitation during the drought period had little to no die-off, while sites < 600 mm were highly variable but included areas with high levels of die-off. Furthermore, this threshold response in die-off had a distinct south to north pattern, where reduced precipitation occurred in more northerly sites. Data from weather stations at the extreme north and south ends of the study region showed that the northern portion experienced earlier drying and a more severe drought than the southern portion (Fig. 2). The tree responses below the *c.* 600-mm threshold provide a key insight regarding a survival threshold. Decreases in precipitation across the gradient of our sites were *c.* 100 mm over 2 yr. This precipitation-related threshold for survival is also notable in the context of recent syntheses highlighting the point that many tree species persist at the brink of tolerable water potential deficits (Choat *et al.*, 2012). Notably, we also detected a die-off threshold related to VPD, with mortality occurring at a warm season (May–August) mean VPD of *c.* 1.7 kPa. This result reinforces the important interaction between atmospheric demand and drought, highlighted experimentally (Adams *et al.*, 2009) and in recent regional analysis and projection (Williams *et al.*, 2013). In addition to the patterns in cumulative climate metrics, there was also evidence for such thresholds in seasonal data, for both precipitation and VPD (Figs S4, S5).

Because precipitation and VPD were important climatic metrics of die-off, we examined WHC as a further link to understand the patterns of mortality. However, we did not find a strong relationship between die-off and soil WHC, as was detected in Peterman *et al.* (2012). Our sites covered a much smaller spatial extent and our methods of pinyon die-off detection was different from those used in Peterman *et al.* (2012), which may explain the differences in our results. Thus, over the extent of pinyon pine distribution, existing WHC data may be an important predictor of pinyon die-off, but at more local scales, where WHC varies less, a combination of other variables apparently had greater control over pinyon die-off. The relatively coarse detail of the SSURGO data set compared with the spatial scale used in our study may limit our ability to detect a WHC effect; there was not much variability in the data set and most of our sites are near the upper end of the classifications used in Peterman *et al.* (2012; W. Peterman, pers. comm.).

We also did not find any compelling relationships between tree die-off and stand characteristics that would explain either the

threshold response or variation in die-off among sites that received <600 mm precipitation. We found a significant, but weak increase in die-off with decreasing stand density. This finding is consistent with two other studies of the die-off event (Floyd *et al.*, 2009; Clifford *et al.*, 2011), but contrasts with results from other studies that have reported positive associations between tree density and increased pinyon die-off (Negron & Wilson, 2003; Weisberg *et al.*, 2007; Greenwood & Weisberg, 2008). As discussed in Floyd *et al.* (2009) and Clifford *et al.* (2011), there are several reasons why die-off might increase or decrease with density, including the level of tree mortality, the tree species involved, and the range of stand densities.

We extrapolated field and Landsat estimates of die-off to estimate regional impacts on carbon, and land surface–atmospheric flux and feedback. Regarding carbon loss, our estimates are lower than, but comparable to, those of Huang *et al.* (2010), implying that, while the stand characteristics differ between Colorado and New Mexico (Floyd *et al.*, 2009), drought and die-off had similar effects on carbon loss. We expect that the regional loss in canopy cover will correspond to an increase in shortwave albedo, and a suppression of longwave radiation, similar to the impact of changes in semi-arid forests on climate systems at the same latitude (Rotenberg & Yakir, 2010). The offset of carbon loss to a cooling effect resulting from increased albedo and suppressed longwave radiation could be further quantified with respect to total climate forcing with the inclusion of flux data (beyond the scope of this study). We note that the relationship between landsat-based canopy cover and dNBR to field-based canopy cover may be vastly improved with higher resolution imagery (Greenwood & Weisberg, 2009; Royer *et al.*, 2011). Consequently, the relationship between climate variables and spectral signatures produced by remote sensing would potentially align more closely to field-based climate variables.

Insights from pinyon–juniper woodlands may have broader relevance, in that distribution is tightly linked to water balance in general, and particularly mortality events (Kerkhoff *et al.*, 2004; Breshears *et al.*, 2005, 2009b); consequently, they may provide insights for other water-limited systems. They can also span a large range of canopy cover from open savannah through dense woodland (Kerkhoff *et al.*, 2004; Breshears, 2006), which may provide insights in the context of mixed woody–herbaceous ecosystems (House *et al.*, 2003). More generally, tree die-off driven by drought and associated factors, such as pests and pathogens and anomalously warm conditions, remains a fundamental challenge to predict (Breshears & Allen, 2002; McDowell *et al.*, 2008, 2011; Allen *et al.*, 2010). Much effort is currently focused on resolving the mechanistic details associated with mortality, including the interrelationships between hydraulic failure, carbon starvation and biotic agents, and associated water balance and carbon metabolism dynamics (McDowell *et al.*, 2011; Choat *et al.*, 2012). Also emerging are mortality-related linkages that span the continuum from precipitation and soil moisture, plant water potential and conductance, photosynthesis and respiration to associated plant hydraulics and carbon metabolism. Arguably these relationships are most exhaustively documented for *Pinus edulis*, which could serve as a model species for conifer responses

(Martinez-Vilalta *et al.*, 2012). The amount and timing of reductions in precipitation, concurrent with anomalously warm temperatures, resulted in regional-scale die-off for this species (Breshears *et al.*, 2005; Shaw *et al.*, 2005) and also resulted in soil moisture levels that were below plant available thresholds for most of the time during extreme dry years preceding mortality (Breshears *et al.*, 2009a). Consequently, plant water potential dropped below a threshold of stomatal closure (Breshears *et al.*, 2009b), resulting in reduced conductance, transpiration and respiration (McDowell *et al.*, 2008, 2011). This can result in die-off that appears to be related, at least in part, to carbon metabolism, based on a glasshouse experiment (Adams *et al.*, 2009, 2013), but also highlights the interrelationship of plant hydraulics and carbon metabolism (McDowell *et al.*, 2011; Plaut *et al.*, 2012). Nonetheless, precipitation and related metrics such as soil WHC, in association with temperature data, are the most widely accessible data associated with the drivers of die-off events and if interpreted appropriately, may aid in revealing key aspects of drought mortality thresholds (Breshears *et al.*, 2009a; Peterman *et al.*, 2012), especially when analyses control for climatic gradients, as was done here.

In conclusion, climate variability has played a dominant role in the dynamics of stand development and population structure of pinyon–juniper woodlands of the southwest (Swetnam & Betancourt, 1998; Barger *et al.*, 2009; Clifford *et al.*, 2011). Our data suggest that within-region climate variability can be an important source of woodland heterogeneity, where extensive drought in one location of a region can lead to greater die-off and more radically altered vegetation structure than another location (Allen & Breshears, 1998). In further studies, drought- and bark beetle-induced die-off in pinyon pines was more common in larger, mature trees (Mueller *et al.*, 2005; Clifford *et al.*, 2008), suggesting that changes in demography and recruitment will occur in coming decades (Redmond & Barger, 2013). Through such changes in demographics, some areas such as the northern portion of our study area will probably be comprised of a much younger pinyon pine population (Mueller *et al.*, 2005), whereas others will have less dense stands compared with areas in the southern part of the study area (Fig. 4). Furthermore, a litany of ecosystem-level and biophysical changes to forest productivity have likely occurred in the northern region (Anderegg *et al.*, 2012; Edburg *et al.*, 2012). Numerous studies suggest that rapid die-off alters carbon cycling (Huang *et al.*, 2010; Hicke *et al.*, 2012), hydrological cycles (Guardiola-Claramonte *et al.*, 2011; Adams *et al.*, 2012), and near-ground insolation and evapotranspiration (Royer *et al.*, 2011) which greatly affect regional-scale Earth systems feedbacks (Adams *et al.*, 2010). Our results refine how precipitation patterns within a region influence pinyon die-off, revealing a precipitation and VPD envelope for tree mortality and its uncertainty band where other factors probably come into play – a response type that influences stand demography and landscape heterogeneity and that is of general interest yet has rarely been documented. Understanding the processes behind the patterns of die-off and how these will impact the cascade of Earth systems feedbacks will be vital to modeling the future of forested regions in the southwestern USA under a changing climate.

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Supporting Information

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

Fig. S1 Linear relationship between precipitation from 2002 and precipitation from 2003.

Fig. S2 Field-based plot design and remote sensing-based overlay of site extent.

Fig. S3 The relationship between plot-level canopy die-off and die-off detected through remote sensing.

Fig. S4 Relationship between warm season, cold season, and annual precipitation and canopy loss for 2002 and 2003.

Fig. S5 The relationship between vapor pressure deficits (VPDs) during the 2002 warm season and the 2003 warm season.

Table S1 Multiple regression analysis using per cent pinyon die-off as the dependent variable

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Commentary

Climate-driven tree mortality: insights from the piñon pine die-off in the United States

The global climate is changing, and a range of negative effects on plants has already been observed and will likely continue into the future. One of the most apparent consequences of climate change is widespread tree mortality (Fig. 1). Extensive tree die-offs resulting from recent climate change have been documented across a range of forest types on all forested continents (Allen *et al.*, 2010). The exact physiological mechanisms causing this mortality are not yet well understood (e.g. McDowell, 2011), but they are likely caused by reductions in precipitation and increases in temperatures and vapor pressure deficit (VPD) that lead to enhanced soil moisture deficits and/or increased atmospheric demand of water from plants. When plant stomata close because of a lack of available soil water or high atmospheric demand, the plant cannot photosynthesize (leading to carbon (C) starvation) and/or cannot move water from roots to leaves (hydraulic limitation); either mechanism reduces growth, potentially leading directly to mortality and/or to reduced capacity to defend against insect or pathogen attack. Regardless of the mechanisms, few studies have documented relationships between climate and large-scale tree die-offs. In this issue of *New Phytologist* (pp. 413–421) Clifford *et al.* address this gap by reporting on a study of climate conditions during widespread piñon pine mortality that occurred in the early 2000s. This die-off occurred across 1.2 Mha of the southwestern United States (Breshears *et al.*, 2005) and killed up to 350 million piñon pines (Meddens *et al.*, 2012; Fig. 2). A combination of low precipitation, high temperatures and VPD, and bark beetles was reported to cause the mortality (Breshears *et al.*, 2005).

‘... the complexity of forest die-offs will challenge scientists to describe, explain, and model these events.’

Clifford *et al.* focused on tree mortality along a 180-km transect across northern New Mexico, USA. The authors combined field observations at 95 plots and remotely sensed imagery to quantify tree mortality in this area, and related mortality to climate in 2002 and 2003. Key to this transect was a gradient of precipitation trends in which greater reductions occurred in the north than the south (the entire study area experienced warming). In addition to this climate gradient, a tree mortality gradient, which increased from

south to north, was documented by both the field measurements and remote sensing.

Past studies have argued that quantifying thresholds of mortality are needed to allow us to predict which plants will be more susceptible to drought mortality (McDowell *et al.*, 2011; Zeppel *et al.*, 2013). Clifford *et al.* related cumulative 2002–2003 precipitation values to field measurements of tree mortality, finding a threshold of 600 mm for cumulative 2-yr precipitation, above

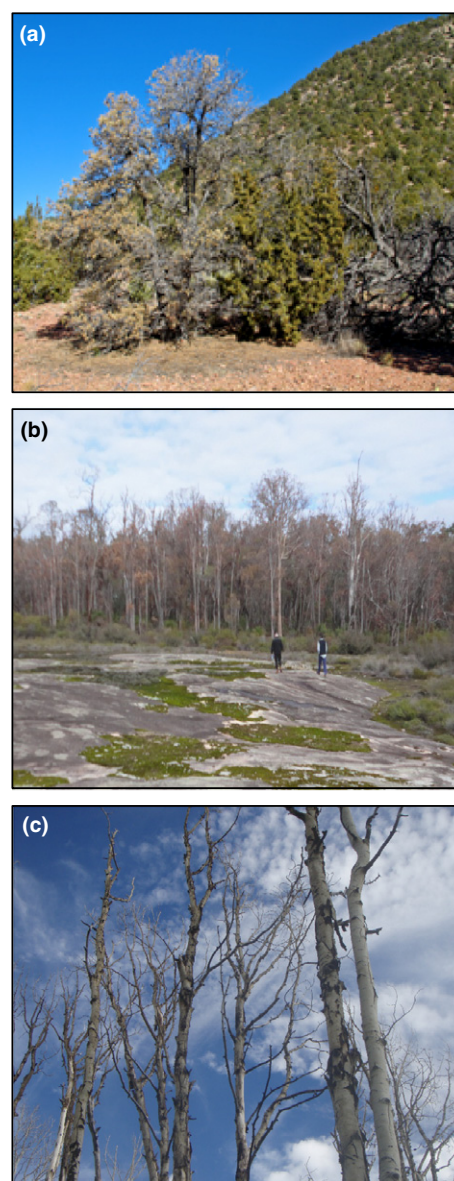


Fig. 1 Tree mortality during recent die-off events: (a) piñon pine, New Mexico, USA (photograph courtesy of A. Mack); (b) *Eucalyptus*, New South Wales, Australia (photograph courtesy of P. Mitchell); and (c) trembling aspen, Colorado, USA (photograph courtesy of W. Anderegg).

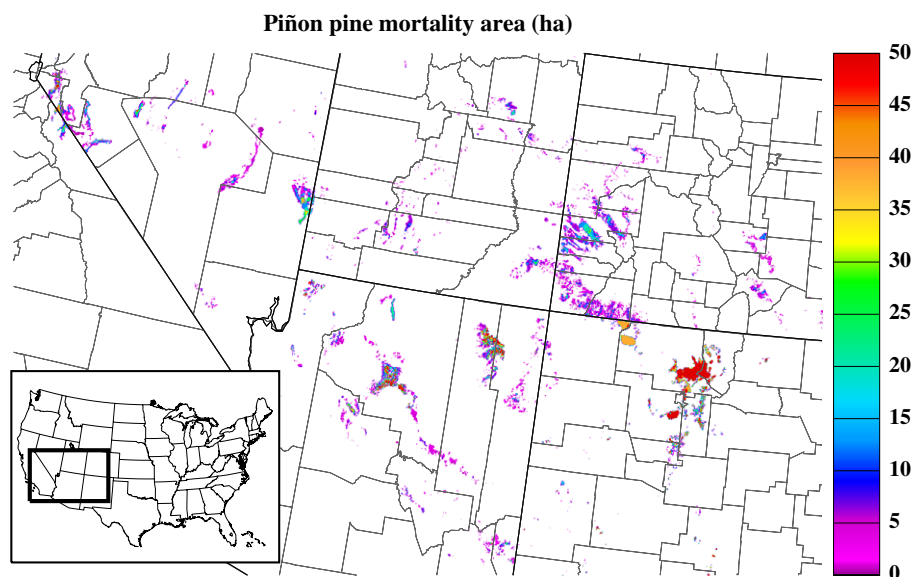


Fig. 2 Piñon pine mortality area in south-western United States (ha within 1-km² grid cells) from the early 2000s (Meddens *et al.*, 2012).

which little or no mortality occurred. Conversely, substantial mortality occurred within some sites with < 600 mm. The authors also reported a VPD threshold of 1.7 kPa, above which sites experienced tree mortality. This VPD threshold contrasts with the threshold of 3.0 kPa for increased risk of mortality in the broad-leaf evergreen *Eucalyptus globulus* (Mendham *et al.*, 2005). The contrasting mortality thresholds for these conifers and broadleaf evergreens imply differences across plant functional types, and highlight the need for further research. Clifford *et al.* did not have any success modeling climate–stand structure–tree mortality relationships with linear regression, illustrating the complexity and perhaps nonlinear nature of the climate–plant relationships.

This study is novel for several reasons. The authors covered extensive spatial gradients in climate and tree mortality, using widespread field sampling in conjunction with remote sensing to examine variability along these gradients. A combination of methods including field observations of mortality and stand structure, remote sensing, and analyses of climate station and gridded climate data allowed them to ascertain climate influences on mortality. Multiple climate factors were considered that represented both soil moisture and atmospheric demand. Finally, the study used various analytical methods, including examining relationships with multivariate linear regression modeling (which produced insignificant results and low goodness-of-fit) and empirical analysis (which identified simple thresholds in precipitation and VPD).

The authors make significant contributions to understanding mechanisms of tree mortality. Yet the study also raises important questions. First is a set of questions related to the characteristics of the piñon pine die-off. How widely applicable are these results? Determining whether the reported precipitation and VPD thresholds are similar in other areas of piñon pine mortality and for other woodland tree species or other plant functional types is critical for successful modeling of other die-off events. How much stress can piñon pines (and other plants) undergo before succumbing to death? How long before a severely stressed tree recovers to 'normal' growth?

Second, important questions remain about the mechanisms causing tree mortality. What is the relative importance of reductions in precipitation vs increases in VPD? In their study Clifford *et al.* found substantial variability in tree mortality beyond the precipitation and VPD thresholds, and the authors were unsuccessful at modeling mortality with multivariate linear regression methods. What is the source of this variability? Clearly microsite differences contributed, but to what extent? What are the important predisposing factors that might be considered by future studies? Perhaps using variables that better represent drivers, such as modeled soil moisture or climatic water deficit, would yield improved relationships. The authors reported similar warming at the ends of their mortality gradient, suggesting that precipitation or humidity may have played more important roles than temperature in driving tree mortality.

Bark beetles were also an important factor in the piñon pine die-off (Breshears *et al.*, 2005). Climate influences beetle outbreaks through drought stress of host trees and accelerated beetle life cycles from higher temperatures. The beetle species involved, piñon ips (*Ips confusus*), does not kill healthy trees, unlike some other major bark beetle species. Instead, ips populations increase with drought stress and decline when drought is relieved (Raffa *et al.*, 2008; Gaylord *et al.*, 2013). Beyond this simple characterization, however, we lack the basic knowledge about the population dynamics of these beetles and interactions with climate change. Furthermore, we need a better understanding of the role these beetles played in this piñon pine die-off: what proportion of trees would have survived in the absence of beetles?

A third set of questions concerns predicting die-offs. What are the prospects for modeling future tree mortality given expected increased tree stress associated with future climate change (Williams *et al.*, 2013)? Models are urgently needed to inform resource managers, policy makers, and the public about which forests will be vulnerable to mortality in the coming decades. The findings of Clifford *et al.* on precipitation and VPD thresholds offer a first step toward predictions, yet the complexity of these relationships suggest challenges to building robust models. Other

regions in western North America, Europe, South America, and Australia have experienced tree mortality as well. These other events have challenges of their own. Some cases, such as sudden aspen decline, appear to be primarily driven by physical climate changes (e.g. drought; Anderegg *et al.*, 2012), implying that modeling may be easier. Other cases, such as lodgepole pine mortality caused by mountain pine beetles, involve a combination of climate, beetle population dynamics, and host–beetle interactions (Raffa *et al.*, 2008), suggesting more complex modeling is required.

Significant challenges exist for obtaining useful data for analyses of tree mortality. Clifford *et al.* invested substantial time in measuring 95 plots, and similar intensive fieldwork will provide valuable information for future studies. Clifford *et al.* also used remotely sensed imagery to map mortality. Interestingly, the field data the authors used to build their remote sensing-based model covered only 1% of the imagery area at each location, yet the authors achieved good accuracy with their remote sensing-based model. Use of satellite imagery for mapping tree mortality is desirable for extending study areas, though tests of these methods to other regions are needed. Finally, Clifford *et al.* relied on gridded climate data at reasonably fine spatial resolution (4 km) to examine precipitation and VPD at their field sites. Such data sets work well for variables that generally vary smoothly in space, although patchier summer precipitation from convective storms, potentially important in delivering needed moisture to trees, may not be well represented. Furthermore, such fine-resolution data sets that vary in time cover only limited regions globally, yet studies of impacts in mountainous regions require fine detail to capture steep gradients in complex terrain.

Die-offs are significant events for humans and natural systems. Services to humans, biogeochemical cycling (including C and water), energy fluxes, and wildlife habitat are among the processes severely affected by die-offs (Breshears *et al.*, 2011; Anderegg *et al.*, 2013). Widespread tree mortality is an indicator of climate change clearly visible not only to scientists but also decision makers and the general public. Our ability to accurately predict how forests will respond to warming, and the impacts that will cascade through ecosystems, relies on our understanding of how climate influences trees. The Clifford *et al.* study advances this knowledge, suggesting and inspiring future studies that build from these results. However, the complexity of forest die-offs will challenge scientists to describe, explain, and model these events. Research is needed that: is interdisciplinary in nature, involves tree physiologists, forest and landscape ecologists, climatologists, and entomologists; covers a range of plant functional types and biomes; and considers multiple spatial scales, from leaves to whole trees to landscapes to the globe.

Jeffrey A. Hicke^{1*} and Melanie J. B. Zeppel²

¹Department of Geography, University of Idaho, Moscow, ID 83844, USA;

²Department of Biological Sciences, Macquarie University, Sydney, NSW, 2109, Australia

(*Author for correspondence: tel +1 208 885 6240; email jhicke@uidaho.edu)

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