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Patterns and causes of observed piñon pine mortality in the southwestern United States

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Contents

	Summary	91
I.	Introduction	91
II.	Mortality mechanisms	92
III.	Methods	92
IV.	Results	92
V.	Discussion	94
VI.	Conclusions	96
	Acknowledgements	96
	References	96

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Summary

Recently, widespread piñon pine die-off occurred in the southwestern United States. Here we synthesize observational studies of this event and compare findings to expected relationships with biotic and abiotic factors. Agreement exists on the occurrence of drought, presence of bark beetles and increased mortality of larger trees. However, studies disagree about the influences of stem density, elevation and other factors, perhaps related to study design, location and impact of extreme drought. Detailed information about bark beetles is seldom reported and their role is poorly understood. Our analysis reveals substantial limits to our knowledge regarding the processes that produce mortality patterns across space and time, indicating a poor ability to forecast mortality in response to expected increases in future droughts.

I. Introduction

In recent decades, warming and drought have been reported to increase tree mortality globally (Allen *et al.*, 2010). Recent drought and associated piñon ips (*Ips confusus* Leconte) outbreaks have led to widespread mortality of common (*Pinus edulis* Engelmann) and single-leaf (*Pinus monophylla* Torrey and Fremont) piñon pines in the southwestern United States (Breshears *et al.*, 2005). In the early 2000s, aerial surveys reported piñon pine mortality across its range, with considerable variability in mortality amounts (Fig. 1) (Meddens *et al.*, 2012). Piñon pine mortality in the mid-1990s and early 2000s is relatively well studied compared with other die-offs (Allen *et al.*, 2010; Macalady & Bugmann, 2014). However, it is unclear whether our understanding of the influences on this mortality is adequate for predicting the vulnerability of woodlands to future die-off, especially given projected warming and drying in the southwestern USA (Stocker *et al.*, 2013) and the associated challenges of managing these ecosystems under drought stress (Millar *et al.*, 2007).

We reviewed studies of piñon pine mortality caused by these recent droughts and synthesized the findings of the causes of these events. We restricted our review to studies that reported observed piñon pine mortality and explained patterns with potential causal factors in natural settings (i.e. excluding experimental studies that are limited in scope). We discuss factors that influence piñon pine mortality, including physiological mechanisms of mortality; compare spatial patterns,

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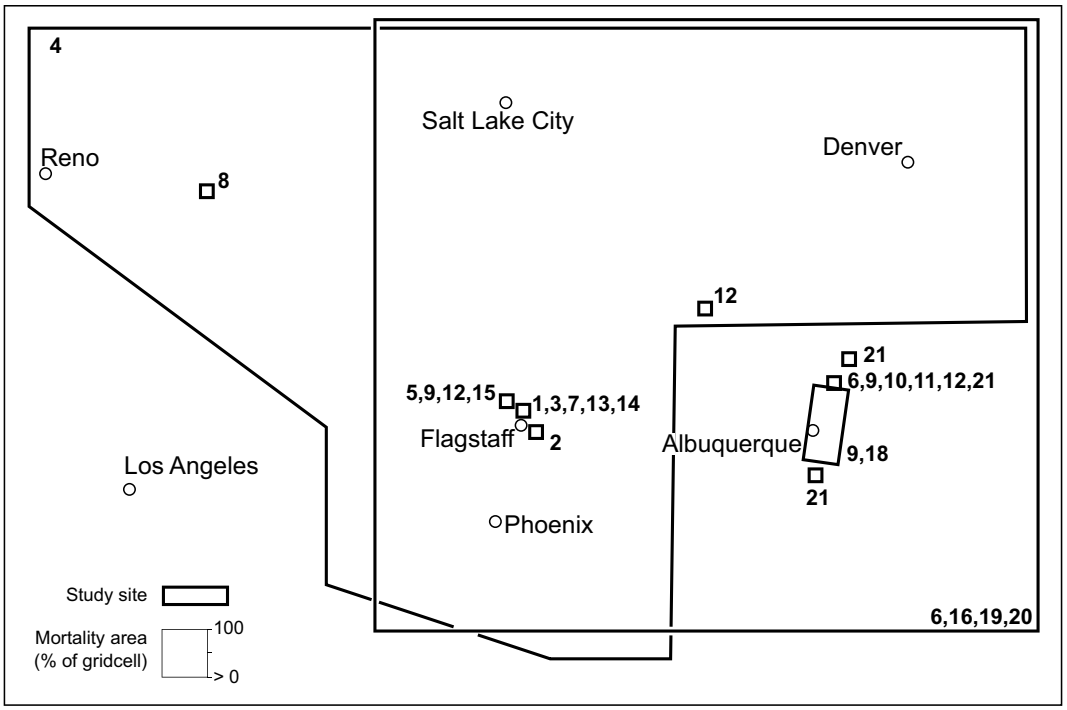

Fig. 1 Locations in the southwestern United States of observational studies of piñon pine mortality in the mid-1990s or early 2000s (black polygons); numbers correspond to studies in Supporting Information Table S1. Color bar represents 1997–2010 piñon pine canopy mortality (%) within 1-km grid cells derived from aerial detection surveys (Meddens *et al.*, 2012). Note that not all areas were surveyed each year. Blue areas show additional locations of single-leaf piñon pine; green areas show common piñon pine (http://forest.moscowfsl.wsu.edu/climate; accessed 11 December 2013; Crookston *et al.*, 2010).

extents, variability and datasets used in studies; assess agreements and disagreements of mortality influences among studies; and discuss findings and make recommendations for further research.

II. Mortality mechanisms

Drought-associated mortality is hypothesized to occur via two interrelated mechanisms. (1) Hydraulic failure may occur when water loss from transpiration exceeds available water supply from roots, leading to critically high tension in the xylem water column, cavitation, loss of conductivity and plant desiccation (Sperry *et al.*, 2002; McDowell *et al.*, 2008). (2) Carbon starvation may occur as trees close stomata to avoid water loss and cavitation, limiting photosynthesis and possibly leading to negative tree carbon balance (McDowell *et al.*, 2008). Prolonged drought may lead to death when trees run out of stored carbon or can no longer access stored carbon due to water stress in the phloem, curtailing carbon availability for vital metabolic and defense functions (McDowell *et al.*, 2011). Recent research has emphasized the interactions among carbon limitation and transport, defense metabolism, and hydraulic failure in tree mortality pathways (McDowell *et al.*, 2011, 2013; Adams *et al.*, 2013; Sevanto *et al.*, 2014). In addition to drought, bark beetles can drive tree mortality via two mechanisms (Paine *et al.*, 1997; McDowell *et al.*, 2011): (1) disruption of the transport of photosynthate associated with phloem feeding; and (2) xylem blocking by introduced fungi. Piñon ips appears to require stressed trees for successful attack (Raffa *et al.*, 2008), unlike other bark beetle species (e.g. mountain pine beetle) that can kill healthy trees.

III. Methods

For each study, we characterized the location and methods (listed in Supporting Information Table S1), and identified the potential factors considered to explain tree mortality. Based on past studies and theoretical understanding, we developed a conceptual framework with pathways and factors that influence piñon pine mortality during drought. We identified agreement and disagreement among studies for individual factors as related to our conceptual framework and to our proposed mechanisms of tree mortality.

IV. Results

Studies of observed piñon pine mortality

We found 21 observational studies of piñon pine mortality (Table S1). Most of the studies were conducted at local scales in northern New Mexico and central Arizona; a few studies described mortality at regional scales (Fig. 1). Only two studies included measurements of piñon ips outbreak dynamics (e.g. distance to nearest attacked tree), and five studies noted presence or absence of piñon ips on dead trees (Table S1). Several studies noted that dead piñon pines almost always exhibited evidence of beetle attack (Negron & Wilson, 2003; Floyd *et al.*, 2009; Macalady & Bugmann, 2014).

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The other studies were focused on the impacts of drought as the main mortality factor, yet all mentioned or described the effects of the piñon ips outbreak. Studies used a range of metrics to describe tree mortality, related to different research questions, methods and data sources. Because of different locations, extents, spatial resolution and metrics, the percent mortality varied from near 0% to > 95% (Table S1).

Conceptual framework

We developed a conceptual framework that describes how landscape, stand and tree attributes relate to observed tree mortality via the proposed physiological mechanisms of mortality. Multiple factors associated with climate, terrain, vegetation and biotic agents influence the likelihood of mortality (Fig. 2). Factors such as climate, competition among trees and understory plants, soil characteristics and topography determine tree-available soil moisture. Site factors that include topography and soil characteristics (e.g. soil texture and depth) influence soil water content and matric potential. These factors affect plant-available soil moisture directly, as well as increase vulnerability to cavitation and dieback, during drought via changes in plant rooting depths, root-to-shoot ratios and xylem characteristics (Sperry & Hacke, 2002). Bark beetles are influenced by stand structure, temperature, individual tree characteristics (e.g. size) and other biotic agents (e.g. mistletoe) (Negron & Wilson, 2003). The influence of any one factor may be weaker in very severe droughts.

Importantly, some factors influence tree mortality via multiple pathways. For example, higher temperatures increase vapor pressure deficit (VPD), which may lead to hydraulic failure and carbon starvation via influences on soil moisture and plant water relations (Breshears *et al.*, 2013), rates of photosynthesis (Weiss *et al.*, 2012), allocation to resin used as defense against bark beetle attack (Gaylord *et al.*, 2013) and respiration (Adams *et al.*, 2009). In addition, temperature determines overwintering survival and regulates the lifecycle of the piñon ips (Berryman & Stark, 1962).

Agreement and disagreement among studies

We found some agreement across the studies regarding how measured tree, stand and landscape variables related to tree mortality (Fig. 3; Table S2). All studies indicated the presence of severe drought before widespread piñon mortality (although few quantified the severity of the drought), and most studies mentioned (although few quantified) the presence of the piñon ips. Larger trees were generally linked to higher rates of tree mortality. Finally, studies revealed that complete mortality of trees within a stand was rare, even on smaller (plot- to stand-level) scale studies, indicating that some piñon pines survived on most parts of the landscape.

Despite this agreement, we also found disagreement among studies, and some findings were inconsistent with our proposed mechanisms leading to mortality (Fig. 3; Tables S2, S3). The largest disagreement was related to the influence of tree density (Table 1). We expected higher mortality with higher stand density via increased competition for resources (Table S2), and indeed some studies reported that mortality was positively related to stem density (e.g. Greenwood & Weisberg, 2008). However, other studies reported no or a slight negative relationship (e.g. Floyd *et al.*, 2009).

Other disagreements among studies were associated with the influences of elevation, topography and soil characteristics (Fig. 3; Table 1). We expected that piñon pines at lower elevations, on less favorable soils, and on south-facing slopes would experience the most drought stress (Table S2), resulting in the highest relative mortality. However, only two studies reported higher mortality rates in lower elevation areas (Santos & Whitham, 2010; Clifford

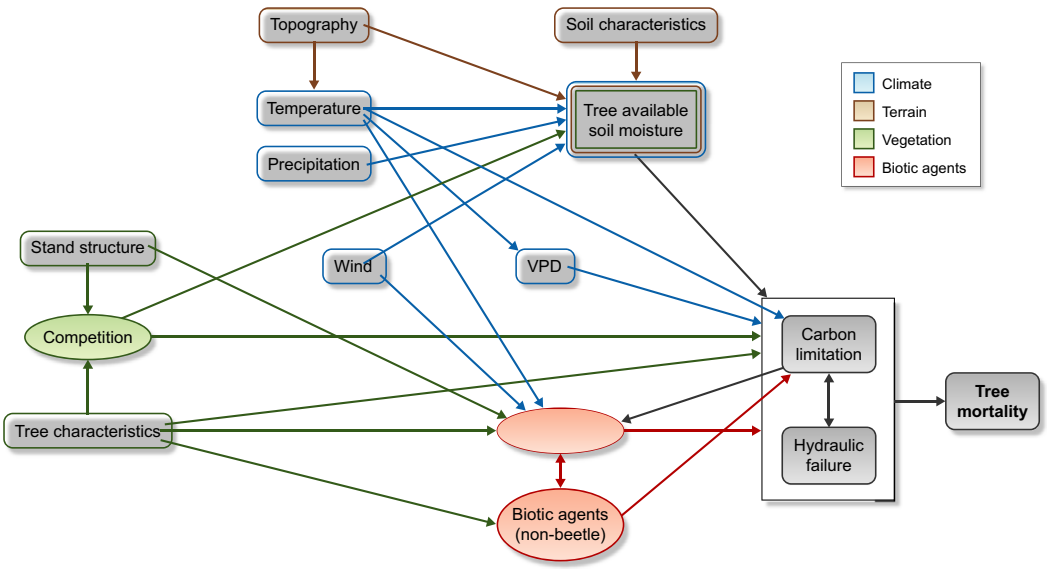

Fig. 2 Schematic representation of the factors that contribute to carbon limitation and hydraulic failure during drought, which can lead ultimately to tree mortality. Ovals indicate processes with other organisms; colored boxes represent factors related to climate (blue), terrain (brown), vegetation (green) and biotic agents (red). Many factors influence tree mortality via multiple pathways. VPD, vapor pressure deficit.

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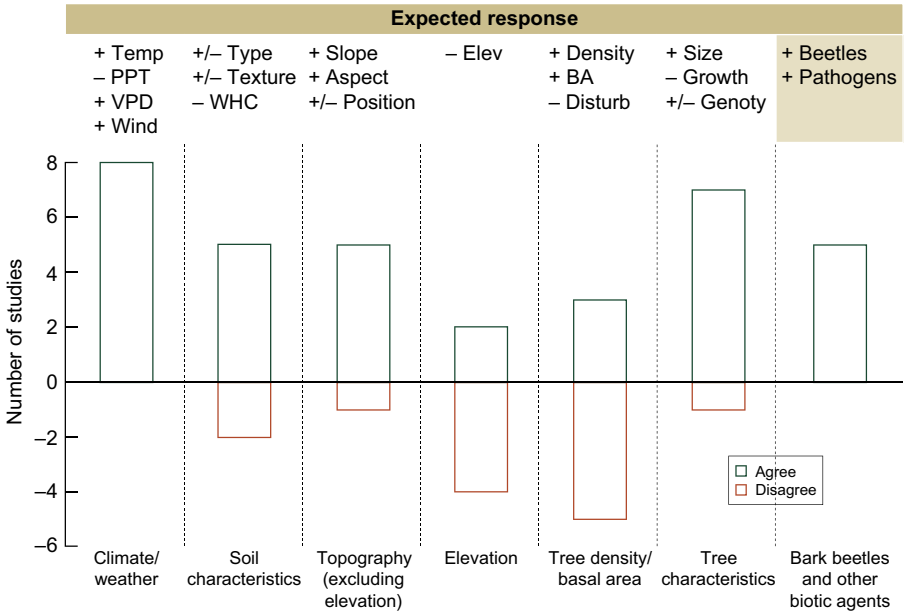

Fig. 3 Number of studies agreeing and disagreeing with expected relationships to piñon pine mortality within categories of influencing factors. The '+' or '−' indicate the expected relationships (e.g. a '+' indicates increasing mortality with increasing values of the influence) and a '+/−' indicates a nonlinear relationship between mortality and influence. See also Supporting Information Table S2 for explanation of the expected tree mortality influences and Table S3 for possible explanations of why studies disagree with these expected influences. Temp, temperature; PPT, precipitation; VPD, vapor pressure deficit; WHC, water holding capacity; Elev, elevation; BA, basal area; Disturb, past disturbance; Genoty, genotype.

et al., 2011), whereas four studies reported that the highest relative mortality did not occur at the lowest elevations (e.g. Kleinman *et al.*, 2012). Some studies reported that soil characteristics strongly influenced mortality severity (e.g. Looney *et al.*, 2012), whereas other studies did not find any effect of soil or topography (e.g. Koepke *et al.*, 2010).

V. Discussion

Agreement among studies suggests that there is good understanding of some of the processes related to piñon pine mortality (Fig. 2). For example, the importance of drought occurring before widespread tree mortality is apparent. However, the exact pathways by which drought causes piñon mortality need more refined understanding (Macalady & Bugmann, 2014). The multiple, interacting factors of drought stress and piñon ips outbreaks lead to questions about the roles of each in causing piñon pine mortality. For instance, how many piñon pines would have died in the absence of beetles, and how did beetles affect the patterns of the observed mortality?

Another agreement among the studies with high piñon pine mortality is that larger trees were more likely to die. This result contrasts with arid shrub ecosystems where smaller plants are more susceptible to drought because of shallower root systems, reduced carbohydrate reserves, and/or lower capacitance (Sperry & Hacke, 2002; Paddock *et al.*, 2013) and contrasts with a study in which smaller trees at low levels of tree mortality were preferentially killed (Looney *et al.*, 2012). Any presumed competitive advantage of larger piñon pines (e.g. greater access to soil moisture and greater carbon/water storage capacity) may be overwhelmed by: (1) greater metabolic demands and vulnerability to hydraulic failure or carbon starvation due to higher leaf area, taller stature, and reproductive maturity (McDowell *et al.*, 2005; Mueller *et al.*, 2005; Sthultz *et al.*, 2009); (2) the preference of bark beetles for larger trees (Amman & Baker, 1972); and/or (3) shallower root systems of piñon pines (West *et al.*, 2007). Further study is required to understand the mechanisms behind the vulnerability of different sized piñon pines to drought, and to quantify how changes in tree size, stand structure and soil characteristics influence mortality severity. However, the consistent finding of large-diameter piñon pine mortality during the severe 2000s drought suggests the continuation of large shifts in future tree demographics (Negron & Wilson, 2003) as drought stress and bark beetle activity increase under global warming (Williams *et al.*, 2013).

We expected higher mortality with increasing stem density because of competition for soil moisture and other resources (Fig. 2; Table S2). However, studies disagreed about the relationship between mortality severity and stem density (or basal area) (Table 1; Fig. 3). There are several possible explanations for this discrepancy. First, density-dependent mortality may have been overwhelmed by the effects of severe drought (e.g. Floyd *et al.*, 2009). Second, competition may exert only a weak influence on tree susceptibility even during less severe droughts. For example, Greenwood & Weisberg (2008) revealed a strong link between stem density and mortality severity in *P. monophylla*, but they argued that competition might not have been the most important factor. Instead, mortality of piñon pines that established in periods of relative favorable conditions on marginal microsites may confound relationships with density and therefore competition. Third, it may be important to account for species-specific stem

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Table 1 Findings about, possible explanations for and proposed future research into various influences on piñon pine mortality

Influence	Finding	Mechanisms/possible explanations	Recommendations for future research
Climate	All studies report that drought occurred before piñon mortality	Drought reduces soil moisture and increases vulnerability to carbon starvation, hydraulic failure and/or bark beetle attack	Quantify drought severity
Tree characteristics	Studies agree about increased mortality among larger trees Lower mortality in trees with higher long-term growth rates	Higher mortality among larger trees that are more vulnerable to bark beetles and hydraulic limitation Reduced vulnerability to carbon starvation	Explicitly account for stand structure, all tree size classes and growth history; landscape-scale piñon mortality studies Experiments to study soil characteristics, tree size, rooting depth and vulnerability to mortality
Piñon ips beetle	Evidence of beetle attack is present in all studies that noted the influence of beetles Few studies note the number of beetle attacks or quantified other metrics of beetle activity	Drought increases vulnerability to bark beetle attack Timing and logistics of field work (expensive and time-consuming)	Quantify bark beetle dynamics (e.g. count beetle attacks, exit holes or use pheromone traps) during ongoing mortality events Document beetle presence, attack density and attack success Quantify spatial and temporal dynamics of mortality using satellite imagery, forest inventory plots, or aerial surveys
Stem density (or competition for resources)	Studies report different relationships	Strongest competition at high stem densities, but severe droughts may mask the relationship, and insect attack dynamics are unknown	Combine findings of field observations and experiments at different locations and stem densities Quantify all influences of drought-related mortality (Fig. 2; especially drought severity and beetle attacks)
Elevation	Studies report highest mortality at different elevations	Drought stress is most severe at lower elevations, but competition and bark beetle attacks may be higher at mid-to-high elevations (with higher density stands) Different mortality metrics can lead to contradictory conclusions	Quantify all influences of mortality (Fig. 2) Analyze and report different mortality metrics Map piñon pine cover and stand structure across its range at fine resolution
Soil type and topography	Studies report different relationships between mortality and site factors	Soil depth may be more influential than soil type Severe droughts may mask relationships with soil and topography Other factors may be more influential (e.g. insect attacks)	Quantify all influences of mortality including soil texture, type and depth

density or basal area. Macalady & Bugmann (2014) found that intraspecific competition consistently reduced tree growth rates (and increased associated mortality risk), whereas reductions of tree growth rates related to competition of all trees were less apparent. Finally, bark beetles may prefer stands with greater piñon pine density and basal area because of greater food resources and dispersal opportunities (Negron & Wilson, 2003) and thus mortality patterns may reflect locations with extensive bark beetle activity rather than effects of competition. Future studies can reduce uncertainty about the relationship between tree competition and mortality by including explanatory variables representing beetle attack rate, drought severity (i.e. soil moisture anomalies) and stand characteristics.

Another disagreement was the influence of terrain factors (e.g. elevation and soil characteristics) (Table 1). A major uncertainty when comparing findings was the different metrics used to quantify mortality severity that may confound interpretation. For instance, if all piñon pines were killed on a lower elevation site that contained few piñon pines, studies of total canopy cover would report low severity (e.g. Kleinman *et al.*, 2012) but studies of percent-killed piñon pine would report high severity (e.g. Santos & Whitham, 2010). In addition, stand density and elevation are often correlated and therefore may influence findings. Future studies of tree mortality should report both total and relative mortality metrics and the range of tree densities over which the study is conducted.

In addition to the above recommendations for future studies, other aspects of piñon pine mortality warrant additional analysis. Few studies reported the metrics of beetle populations; we suggest that future studies include attacking beetle populations derived from pheromone traps or number of trees killed by beetles within a neighborhood, number of beetle attacks on host trees, number of exit holes, and/or distance to nearest attacked tree. The role of piñon ips is critical for understanding drought-related piñon mortality and future research should explicitly account for these beetle outbreak metrics when relating different variables to mortality severity (e.g. Gaylord *et al.*, 2013). Within the piñon pine range, some locations without mortality experienced similar

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drought severity as those with mortality (Breshears *et al.*, 2005; Abatzoglou & Redmond, 2014). This conclusion suggests a possible important role for beetles in influencing mortality, although the coarse spatial resolution of the analysis implies caution when interpreting results. Future landscape-scale studies that use spatially explicit datasets to examine the timing of mortality relative to drought severity and beetle populations and the spatial pattern of mortality relative to site factors will provide greater understanding of causal factors. In addition, more research of longer-term growth conditions and recovery after previous stressful events (Ogle *et al.*, 2000; Macalady & Bugmann, 2014), nutrient availability and associated tree symbioses (Swaty *et al.*, 2004), and influences of carbon allocation and defensive capabilities (e.g. Kane & Kolb, 2010) are needed. Finally, manipulative experiments (e.g. rain exclusion studies) that include studies of bark beetles can provide key information and can be used to extrapolate findings to the broader ecosystem.

VI. Conclusions

Much is understood about the plant physiological processes underlying piñon pine mortality during drought, allowing us to construct a detailed conceptual framework that shows how different biotic and abiotic factors influence mortality. Findings from observational studies of this mortality often supported this framework (Table 1). However, inconsistencies between our framework and some observational studies also occurred. Studies usually considered only a subset of potential factors, leading to higher uncertainty about their conclusions regarding the most important factors of tree mortality. The very severe drought in the early 2000s led to widespread piñon pine mortality, potentially masking relationships that may be apparent in less severe droughts. The role of bark beetles is poorly understood and understudied, and links between mortality severity and stem density or elevation are major knowledge gaps. We recommend that future studies include a broader range of potential factors to reduce uncertainties about contributing causes (Table 1).

We show that for a well-studied tree species, the influences of many factors contributing to mortality during droughts are not well understood. Expected future climate change and increased frequency and severity of warm droughts are key in setting the stage for landscape-scale mortality events (Williams *et al.*, 2013), yet significant uncertainties limit our understanding, indicating a poor ability to forecast locations of future piñon pine mortality. Increased knowledge of the mortality mechanisms and landscape influences during drought are necessary for predicting future tree mortality and designing adaptation plans for managing these ecosystems.

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Supporting Information

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

Table S1 Summary table of the different studies relating observed piñon pine mortality to factors influencing mortality severity

Table S2 Measured variables, proposed mechanisms and their expected relationship with piñon pine mortality

Table S3 Explanation of studies that disagree or were not categorized into agreeing or disagreeing with expected influences of piñon pine mortality

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***New Phytologist* Supporting Information**

Article title: **Patterns and causes of observed piñon pine mortality in the southwestern United States**

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The following Supporting Information is available for this article:

Table S1 Summary table of the different studies relating observed piñon pine mortality to factors influencing mortality severity

Table S2 Measured variables, proposed mechanisms, and their expected relationship with piñon pine mortality

Table S3 Explanation of (a) studies that disagree or (b) were not categorized into agreeing or disagreeing with expected influences of piñon pine mortality

Table S1 Summary table of the different studies relating observed piñon pine mortality to factors influencing mortality severity.

Study	Goals/ objectives	Location	Obser-vations	Timing of study	Response variable	Mortality	Important findings	Soil moisture	PDSI	Water potential	Precipitation	VPD	Temp	Wind	Soil type	Soil texture	Soil water capacity	Elevation	Slope	Aspect	Topo. position	Basal area	All tree density	Piñon density	DRC / size	Growth history	Previous mortality	Patterns of patches	Genetics	Ips presence	Ips pressure	Mistletoe	Other biota
1. Ogle *et al.*, 2000	Compare growth attributes of live and dead piñon pines	Coconino National Forest, AZ	51 transects across 3 soil types (40-50 m wide and 2-4 km long)	Fall 1996 – Spring 1997	Piñon mortality rate (% of individuals)	2.3 – 13.5% mortality	(1) Recent growth variability and overall growth rate correlated to piñon mortality; (2) mortality rates differed across soil types		n-						n-						n-					n-									
2. Negron & Wilson, 2003	Assess stand and tree attributes associated with piñon ips infestation	Coconino National Forest, AZ	87 plots (on 10 transects and radius of 5 m)	Spring 1997	Piñon infested or not (logistic regression at plot and tree level)	49.3% mortality	Higher mortality at (1) higher tree density and piñon/ha; (2) higher BA/ha; (3) lower crown ratio; (4) higher mistletoe infection; (5) larger DRC															n+	n+	n+	n+					n+	n0	n+	
3. Trotter, 2004	Model piñon mortality rates using topographic variables	820 km^2 north of Flagstaff, AZ	Unknown no. of polygons with piñon mortality >30%	1997 – 2002 (for 1996 drought)	Estimate landscape level piñon mortality	5% of the landscape contained piñon mortality	Tree mortality was spatially discrete, indicating importance of site-specific patterns. High rates of piñon mortality in regions with steep slopes, southwestern aspects, and mid-to-high elevations											n+	n+	n+								l+					
4. Shaw *et al.*, 2005	Describe extent and variability of piñon pine mortality	AZ, CO, UT, NV	Plots from Forest Inventory and Analysis (FIA)	2000 - 2004	Piñon mortality (% of BA)	2002: 1.5% 2003: 6.1% 2004: 6.3%	Cause of mortality may be best described as a complex of drought, insects, and disease (observations, no statistical relationships tested)		l-																						l+			l+
5. Mueller *et al.*, 2005	Examine the impacts of drought on piñon pine mortality	Northern AZ	11 plots (ranging from 1200 to 5000 m^2)	1999 and 2002	Stand-level piñon and juniper mortality	Piñon mortality: 25.9% (1996) 31.7% (2002)	(1) Larger trees were more likely to die than smaller trees; (2) sites with high piñon mortality in 1996 also suffered the highest mortality in 2002 (i.e., reduction in density did not buffer against mortality)																		n+		n+							
6. Breshears *et al.*, 2005	Evaluate the causes and impacts of regional-scale drought	AZ, CO, UT, NM (Northcentral NM)	AVHRR NDVI Time series of PJ vegetation type (Mesita del Buey site)	1989 - 2003 (2002 and 2003)	Change in detrended NDVI (Percentage of tree mortality)	40 – 80% (>90%)	NDVI reduction of >20% is coincident with local mortality; reductions of this magnitude observed across the piñon distribution	l-			l-		l+																					
7. Gitlin *et al.*, 2006	Investigate mortality patterns during drought	80-km radius around Flagstaff, AZ	28 transects of 100 piñon trees	Fall 2002 – Spring 2004	Piñon mortality rate (% of individuals)	41.4%	(1) Piñon mortality was greater on southerly aspects compared to northerly aspects; (2) Mortality was lower in black cinder soils (deeper) compared to red cinder soils								l-					l+														
8. Greenwood & Weisberg, 2008	Quantify biotic and abiotic influences on tree mortality	Central NV	217 plots (0.1 ha)	2005	Cumulative tree canopy mortality	18% dead crown, 7% dead trees across plots	Cumulative canopy mortality associated with high stand density and xeric site conditions									n-	l-	n+	n+	n-	n-	n+	n+		n+	l-							
9. Clifford *et al.*, 2008	Quantify the response of tree die-off	Northcentral NM and Northern AZ	53 sites (100 by 200 m) in NM	2004 - 2005	Percent piñon mortality	Piñon mortality: 1-62%	(1) Stand density did not impact mortality; (2) mortality greater in larger trees; (3) large mortality gradient across NM																n0										
10. Rich *et al.*, 2008	Quantify phenological responses to drought	Mesita del Buey Northern NM	1–50x50 m plot	2000 - 2004	Piñon canopy cover reduction	>90%	Piñon mortality was coupled to soil moisture, which in turn is coupled to temperature and preceding winter precipitation	l-			l-		l+																					
11. Breshears *et al.*, 2009	Discuss insights from long-term water potential measurements	Mesita del Buey Northern NM	One location, size unknown	1992 - 2004	Number of piñon pine trees	>90%	Piñon mortality occurred after 10 months of water potential values below the zero carbon assimilation value			n-																							
12. Floyd *et al.*, 2009	Examine relationship between stand characteristics and mortality	AZ CO NM	AZ: 53 plots (10 by 200m) CO: 24 plots (15 by 15m) NM: 32 plots (3 subplots of 100m^2)	2004 – 2005	Proportion of piñon mortality; Proportion of juniper mortality	Piñon: 32–65%, Juniper: 3–10%	(1) Inconsistent effect of tree density and basal area on mortality, with a weakly negative overall relationship; (2) severity of the drought may have masked effects of tree density and basal area on mortality															n∪	n∪		n+					n+			

Study	Goals/ objectives	Location	Obser-vations	Timing of study	Response variable	Mortality	Important findings	Soil moisture	PDSI	Water potential	Precipitation	VPD	Temp	Wind	Soil type	Soil texture	Soil water capacity	Elevation	Slope	Aspect	Topo. position	Basal area	All tree density	Piñon density	DRC / size	Growth history	Previous mortality	Patterns of patches	Genetics	Ips presence	Ips pressure	Mistletoe	Other biota
13. Santos & Whitham, 2010	Predict the spatial occurrence of piñon ips outbreaks	4 sites around Flagstaff, AZ,	12 2.5–km transects (180 trees/site)	2002	Bark beetle presence on trees	*I. confusus* on 37.5% of trees (n=120):	*I. confusus* outbreaks occurred more severely in lowland areas in favorable wind direction, at larger trees, and with stem-boring moth resistant phenotypes that had infested trees nearby							n+				n-	n+	n0		n+			n+				n+	n+	n+		
14. Koepke *et al.*, 2010	Quantify the influences of soil and vegetation type on woodland mortality	Northern AZ	180 plots (400 m^2 plots)	2004	% healthy / stressed / dead	Piñon: 12–20%	Piñon mortality not different across soil parent material, but % of stressed trees was higher on cinder material								n0																		
15. Clifford *et al.*, 2011	Assess long-term tree cover dynamics	212 km^2 site San Francisco Peaks, AZ	18 plots (10 by 200 m for RS accuracy assessment)	1936, 1959, 2002, and 2004	Amount of tree cover from remotely sensed images	55% reduction in canopy cover (for 2000s drought)	Low elevations greatest reduction in piñon cover due to drought, mid-elevations (60% of area) were more buffered against drought than lower elevations											n-					n0						nU					l0
16. Kleinman *et al.*, 2012	Quantify relationship between ips-related mortality, elevation, and land cover	AZ, CO, NM, UT	Aerial detection surveys (PJ vegetation type in AZ, CO, NM, UT)	2003	Area of ips damage and trees killed per acre form aerial detection surveys	Affected 7.4% (3 mill. ac) of PJ woodlands	(1) Greater mortality at higher elevations especially in UT, AZ, (2) greater impacts in areas where piñon pines have grown historically but may have become dense											n+					n+											
17. Looney *et al.*, 2012	Investigate tree mortality patterns and growth	Northern AZ	40 plots (0.4 ha)	2008-2009	Piñon mortality by basal area and density	14–72% by basal area 17–54% by density	Greater mortality at intermediate substrate ages and at highest piñon densities								nU							n+	n+	n+	nU								
18. Clifford *et al.*, 2013	Explore precipitation relationships with piñon pine die-off	Northern NM	95 plots (3 subplots of 100m^2) and Landsat classification (PJ area: 2437 km^2)	2005 – 2008	Piñon canopy cover die-off (from field observations & RS)	Average mortality was 42% of cover (RS), with ranges of ~2–50% (RS) and ~0-35% (plots)	(1) PPT; VPD (threshold); (2) decreasing tree density was weakly correlated with increasing tree die-off across all plots; (3) tree basal area not correlated with mortality				n-	n+					n0	n0				n0	n-										
19. Peterman *et al.*, 2013	Establish relationship between soil water holding capacity and mortality patterns	Entire piñon – Juniper extent	Aerial detection surveys	2000 – 2007 (aerial)	Tree mortality from aerial surveys	Not reported	84% and 70% of PJ recorded mortality in 2003 and 2004 on soils with soil water capacity of <150mm and with <100mm, respectively								n0		n-																
20. Williams *et al.*, 2013	Derive a forest drought stress index for measuring and predicting tree mortality	AZ, CO, NM, UT	256 ring-width datasets across study location	1000 - 2100	Ring width index	Not reported	Ring width index influenced by warm-season vapor-pressure deficit and cold-season precipitation				n-		n+	n+																			
21. Macalady & Bugmann, 2014	Analyze piñon mortality and growth patterns and relate to climate, competition, and spatial patterns	NM (4 sites)	Individual trees (98 dead and 69 live trees (2000)) (26 dead and 25 live trees (1950))	2000s and 1950s	Tree status (live or dead) and radial tree growth; mortality % within plots and sites	1950s: 46.5–64.5% 2000s: 19.9–99.6% (At the site level)	(1) Decades-long growth divergences and lower average growth rates in dead trees; (2) Greater mortality with larger year-to-year growth variability; (3) mortality % was higher among larger trees; (4) tree density and basal area weakly and variably related to mortality				n-	n+									n0	n0	n+	n+	n-				n+			

Symbols: ‘n’ indicates quantitative relationship found between piñon pine mortality and variable; ‘l’ indicates qualitative relationship found; ‘+’ indicates positive relationship between mortality and variable; ‘-’ indicates negative trend between mortality and variable; ‘0’ indicates no trend found between mortality and variable; ‘ ∪ ’ indicates non-linear or categorical response between mortality and variable; empty gray boxes indicate that the variable was not measured or related to mortality. The colors across the top indicate factors related to climate (blue), terrain (brown), vegetation (green), and biotic agents (red). BA, basal area; VPD, vapor pressure deficit; PPT, precipitation; RS, remote sensing; PJ, piñon-juniper; NDVI, normalized difference vegetation index; PDSI, Palmer drought severity index; DRC, diameter root collar.

Table S2 Measured variables, proposed mechanisms, and their expected relationship with piñon pine mortality. Studies that measured a given variable are categorized as agreeing or disagreeing with the expected relationship. Study numbers refer to the studies listed in the left column of Table S1 with bold and underlined numbers indicating agreement with the expected relationship.

Group	Factor	Measured variable	Proposed mechanisms leading to mortality	Expected relation-ship with mortality	Studies that measured this	# of studies	% agreement with expected relationship	Potential confounding factors
Vege-tation	Stand Structure	Tree density	Higher mortality at higher tree density that increases competition for resources	+	**2**, **8**, 9, 12, 15, **16**, **17**, 18, 21	9	44%	(1) Different measurements of mortality (% or absolute) may confound relationship; (2) bark beetle activity may change mortality severity; (3) sites with greater moisture stress may have lower tree density but higher mortality; (4) drought duration and severity may mask competition effects
		Piñon pine density	Higher mortality at higher piñon pine density that increases competition for resources	+	**2**, **17**, **21**	3	100%	Same as above
		Basal area	Higher mortality at higher basal area that increases competition for resources	+	**2**, **8**, 12, **13**, **17**, 18, 21	7	57%	Same as above
		Earlier disturbance	Lower mortality with earlier disturbances that reduces tree density and competition for resources	-	5	1	0%	Disturbance decreases carbon reserves or the potential to rebound
		Patch structure	Lower mortality with more patchiness that decreases landscape connectivity and increases heterogeneity, potentially leading to reduced bark beetle mortality	-	3, 15	2	0%	More patchiness might indicate less favorable growing conditions, leading to higher mortality severity
	Tree charac-teristics	Tree size	Higher mortality among larger trees that are more vulnerable to bark beetles	+	**2**, **5**, **8**, **12** **13**, 17, **21**	7	86%	Dominate resources (e.g., deeper rooting depths)
			Higher mortality among larger, taller trees that are more vulnerable to hydraulic limitation	+	**2**, **5**, **8**, **12**, **13**, 17, **21**	7	86%	Same as above
			Lower mortality among larger trees that dominate resources	-	N/A	0	N/A	Larger trees more vulnerable to bark beetles and hydraulic limitation
		Long-term growth rate	Lower mortality in trees with higher long-term growth rates, reflecting reduced vulnerability to carbon starvation due to enhanced photosynthetic capacity, water status, and/or carbon reserves	-	**1**, **21**	2	100%	Trees with higher growth rates may be more vulnerable to hydraulic limitation
		Genotype	Increased mortality of genotypes resistant to stem-boring moth (less optimal tree architecture)	+	**13**	1	100%	

Group	Factor	Measured variable	Proposed mechanisms related to mortality	Expected relation-ship with mortality	Studies that measured this	# of studies	% agreement with expected relationship	Potential confounding factors
Terrain	Topography	Slope	Higher mortality at steeper slopes with less favorable soil conditions	+	**3**, 8, **13**	3	67%	Tree density, soil types
		Aspect (southwest-ness)	Higher mortality at higher values (increased temperatures and VPD)	+	**3**, **7**, **8**	3	100%	Same as above
		Elevation	Higher mortality at lower and drier sites	-	3, 8, **13**, **15**, 16, 18	6	33%	Tree density (competition from more trees) at middle elevations, bark beetles
		Topographic position	Lower mortality when located lower in watershed (increased area contributing to run-off and therefore higher soil moisture)	-	**1**, **8**	2	100%	Tree density, soil types
	Soil charac-teristics	Soil type	Lower mortality with increased fertility and soil water holding capacity	-	**1**, **7**, 13, 17, 19	5	40%	Tree density, precipitation
		Depth	Lower mortality with deeper soils that hold more soil moisture	-	N/A	0	N/A	Tree density, precipitation
		Texture	Lower mortality with texture that holds more soil moisture	-	**8**	1	100%	Tree density, precipitation
		Fertility	Lower mortality at fertile soils that increases nonstructural carbon reserves	-	N/A	0	N/A	Tree density
		Water holding capacity	Lower mortality at sites that hold more soil moisture	-	**8**, 18, **19**	3	67%	Tree density, precipitation
Climate	Temperature	Temperature	Higher mortality via direct temperature effects on carbon assimilation and respiration	+	**6**, **10**, **20**	3	100%	Respiration rate
			Higher mortality via influence of temperature on soil moisture and VPD, which causes stomatal closure, lower carbon assimilation, and/or increased hydraulic limitation	+	**6**, **10**, **20**	3	100%	
			Optimal temperatures lead to increased vigor of bark beetle populations	U	N/A	0	N/A	
	Precipitation	Precipitation	Lower mortality with increased precipitation (increased available soil moisture and decreased atmospheric moisture demand)	-	**1**, **4**, **6**, **10**, **18**, **20**, **21**	7	100%	Soil characteristics
	VPD	VPD	Higher mortality via stomatal closure (reduced photosynthesis and carbon assimilation) and hydraulic limitation	+	**18**, **20**, **21**	3	100%	Soil moisture

Group	Factor	Measured variable	Proposed mechanisms related to mortality	Expected relation-ship with mortality	Studies that measured this	# of studies	% agreement with expected relationship	Potential confounding factors
Climate (cont.)	Wind	Derived from DEM	Higher mortality with higher winds leading to more bark beetle dispersion	+	**13**	1	100%	
			Higher mortality at higher winds leading to less available soil moisture	+	N/A	0	N/A	
Biotic Agents	Bark beetles	Presence	Higher mortality with more beetle attacks through hydraulic limitation	+	**2**, **4**, **12**, **13**, **21**	5	100%	
		Pressure	Higher mortality with more beetle attacks through hydraulic limitation	+	**13**	1	100%	More resistant phenotypes
	Other biotic agents	Pathogens	Higher mortality through reduced carbon reserves and reduced growth	+	**4**, **15**	2	100%	Bark beetles
		DMT	Higher mortality through reduced carbon reserves and reduced growth	+	**2**	1	100%	Bark beetles
		Mycorrhizae	Lower mortality through increased non-structural carbon reserves and increased growth	-	N/A	0	N/A	

U, non-linear relationship with mortality; N/A, not available or not measured; VPD, vapor pressure deficit; DEM, digital elevation model; DMT, dwarf mistletoe.

Table S3 Explanation of (a) studies that disagree or (b) were not categorized into agreeing or disagreeing with expected influences of piñon pine mortality.

(a) Studies that disagreed with expected influences		
Variable (category from Figure 3)	**Study**	**Possible explanation**
Soil characteristics	Greenwood & Weisberg (2008)	Soil texture only played a small role, possibly because of incomplete classification of spatial layer (inhibiting assessment of spatial variation); soil depth hypothesized as more important
	Koepke *et al.* (2010)	Piñon pine mortality not different across soil parent material, because: (1) Cinder type soils may allow deeper water infiltration and deeper soil horizons may allow water storage not predicted by a priori expectations (2) Bark beetles may be more important to mortality severity than soil type
	Looney *et al.* (2012)	Piñon pine mortality severity not linearly related to substrate age because piñon density might be more influential on mortality severity
	Peterman *et al.* (2013)	(1) The resolution of the soil (SSURGO) dataset may have been too coarse to attribute causality (2) Most evaluation sites on locations with high water-holding capacity (>250 mm)
Topography	Greenwood & Weisberg (2008)	Higher mortality on lower slopes, due to soil and other topographic characteristics
Elevation (elevation)	Trotter (2004)	Tree mortality higher at mid- to high elevations, because: (1) Competition (due to higher stand densities) for water and other resources may be greater at mid- to high elevations. (2) Lower piñon pine water-use efficiencies may occur at mid-elevations
	Greenwood & Weisberg (2008)	Positive correlation between stand density and elevation (higher stand densities at higher elevations) and increased beetle activity at these locations may lead to increased mortality severity
	Kleinman *et al.* (2012)	Greater mortality at higher elevations (especially in UT, AZ), because: (1) They reported total tree canopy mortality, not % piñon mortality (2) There may be higher competition at middle elevations.
	Clifford *et al.* (2013)	No relation between elevation and mortality severity, because availability of soil moisture was more important
Tree density (tree density, basal area)	Clifford *et al.* (2008)	No effect between tree density and mortality severity or decreasing tree density was slightly correlated to increasing tree die-off, because: (1) Drought severity and length may overwhelm the influences of competition and thus the relationship of density-dependent mortality severity (2) Bark beetle attacks and drought susceptibility of trees might be more profound in more open stands with older trees
	Floyd *et al.* (2009)	
	Clifford *et al.* (2011)	
	Clifford *et al.* (2013)	
	Macalady & Bugmann (2014)	
Tree size	Looney *et al.* (2012)	Smaller trees died preferentially at lower mortality severity, due to reduced access to soil moisture
(b) Studies that were not categorized into agreement or disagreement		
Variable	**Study**	**Explanation**
Ips presence (bark beetles and other biotic agents)	Negron & Wilson (2003)	Ips presence was not actually tested but implied in the study

SSURGO, Soil Survey Geographic Database, USDA Natural Resources Conservation Service.

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