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A Dirty Dozen Ways to Die: Metrics and Modifiers of Mortality Driven by Drought and Warming for a Tree Species

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Tree mortality events driven by drought and warmer temperature, often amplified by pests and pathogens, are emerging as one of the predominant climate change impacts on plants. Understanding and predicting widespread tree mortality events in the future is vital as they affect ecosystem goods and services provided by forests and woodlands, including carbon storage needed to help offset warming. Additionally, if extensive enough, tree die-off events can influence not only local climate but also climate and vegetation elsewhere via ecoclimate teleconnections. Consequently, recent efforts have focused on improving predictions of tree mortality. One of the most commercially important genera of trees is *Pinus*, and the most studied species globally for drought-induced tree mortality is piñon pine, *Pinus edulis*. Numerous metrics have been developed in association with predicting mortality thresholds or variations in mortality for this species. In this article, we compiled metrics associated with drought and warming related mortality that were developed for *P. edulis* or for which *P. edulis* was a key example species used in a calculation or prediction. We grouped these metrics into three categories: (i) those related to simple climate variables, (ii) those related to physiological responses, and (iii) those that require multi-step calculations or modeling using climate, ecohydrological, and/or ecophysiological data; and we identified the spatial-temporal scale of each of these metrics. We also compiled factors shown to modify rates or sensitivities of mortality. The metrics to predict mortality include empirical ones which often have implicit linkages to expected mechanisms, and more mechanistic ones related to physiological drivers. The metrics for *P. edulis* have similarities with those available for other species of *Pinus*. Expected future mortality events will provide an opportunity to observationally and experimentally test and compare these metrics related to tree mortality for *P. edulis* via near-term ecological forecasting. The metrics for *P. edulis* may also be useful as potential analogs for other genera. Improving predictions of tree mortality for this species and others will be increasingly important as an aid to move toward anticipatory management.

Keywords: climate change, die-off, drought, mortality, *Pinus edulis*, tree

INTRODUCTION

One of the major impacts of climate change on terrestrial ecosystems is tree mortality events caused by drought and warmer temperature, often exacerbated by pests and pathogens (Allen et al., 2010, 2015; IPCC et al., 2014). Tree mortality impacts ecosystem services provided by forests, including carbon storage that helps offset warming impacts of emissions (Bonan, 2008; Kurz et al., 2008; Breshears et al., 2011; Anderegg et al., 2013; Ma et al., 2013). Tree mortality events can cause ecosystem state changes (Cobb et al., 2017) and, if extensive enough, can influence not only local climate but also climate and associated vegetation elsewhere—termed ecoclimate teleconnections (Garcia et al., 2016; Stark et al., 2016; Swann et al., 2018).

Recent reviews of rapidly expanding literature on tree mortality related to drought and warming include: compilation of observational case studies globally (Allen et al., 2010, updated sequentially in IPCC et al., 2014; Allen et al., 2015; Hartmann et al., 2018); physiological responses of plants (McDowell et al., 2008, 2011; Choat et al., 2012, 2018) including a synthesis specific to experimental results (Adams et al., 2017b) and one specific to tree functional traits (O'Brien et al., 2017); drought-insect interactions (Anderegg et al., 2015); ecological (Anderegg et al., 2013) and hydrological (Adams et al., 2012) consequences of tree die-off events; and dynamics and management options post die-off (Cobb et al., 2017).

One of the most important genera in terms of extent (Richardson and Rundel, 1998) and commercial value in forestry (LeMaitre, 1998) is *Pinus*, and the most studied species globally of *Pinus* relative to drought-related mortality is the piñon pine *Pinus edulis* (Allen et al., 2015; Meddens et al., 2015; Adams et al., 2017b). This species has been studied with respect to most key categories related to mortality (Allen et al., 2015). In this article, we summarize metrics and modifiers associated with mortality driven by drought and warming for *P. edulis*, explicitly describe the relevant spatial-temporal scales for each, relate these to other results for *Pinus*, and highlight their potential utility for other genera and for near-term ecological forecasting—where predictions are made iteratively and publicly shared and then tested by subsequent observations, updating the predictions as new information becomes available and factoring lessons learned back into predictions (Clark et al., 2001; Dietze, 2017; Dietze et al., 2018). This review focuses on compiling the broad set of relevant metrics related to mortality for *P. edulis*, complementing that of Meddens et al. (2015), which focused on meta-analysis of different physiographic and biotic drivers of mortality.

METRICS ASSOCIATED WITH MORTALITY DRIVEN BY DROUGHT AND WARMING FOR *Pinus edulis*

We compiled metrics associated with drought- and warming-related mortality that were developed for *P. edulis* or for which *P. edulis* was a key species used in a calculation or prediction (**Table 1**). These metrics were grouped into: (i) those driven solely by climate variables, (ii) physiological responses, and (iii) those that require multi-step calculations and modeling. The spatial-temporal scale of each of these metrics was explicitly identified (**Figure 1**). We also compiled factors shown to modify *P. edulis* mortality (**Table 1**). Many of these metrics and modifiers are related to one another directly or indirectly, but we group them together only if they use the same predictor variables or are complex ecosystem models requiring multiple inputs. A key figure illustrating each is provided in **Supplementary Table S1**. Many of these metrics are associated with the early 2000s drought in the Southwestern US (Breshears et al., 2005) and may be overly tied to those specific drought conditions. Important characteristics of the 2000s drought were that it was almost as severe as the 1950s drought in terms of low precipitation (with the 1950s drought being the worst drought in Southwest USA since the 1500s), but it was also warmer (Breshears et al., 2005)—the consequences of which become more evident when Vapor Pressure Deficit (VPD) is considered (Weiss et al., 2009). Importantly, the warmer conditions associated with the 2000s drought are expected to be somewhat indicative of future drought (Breshears et al., 2005; Allen et al., 2015). Time series of plant water potential and soil moisture pre-drought and through mortality provide additional details about this event (Breshears et al., 2005, 2009a,b). Also included are diverse experimental results (Adams et al., 2009, 2017a; Plaut et al., 2012; Krofcheck et al., 2014; Pangle et al., 2015).

Metrics Driven Primarily by Climatic Variables

Metric 1: Standardized Precipitation Evaporation Index (SPEI)

SPEI includes both a precipitation input component and an evaporative demand component (Vicente-Serrano et al., 2010), a common theme among some of the metrics. After considering all possible months of the year to begin in and SPEI durations of 1–24 mo, SPEI with a duration of 11 months starting in July was found to be most strongly positively correlated with *P. edulis* and *P. ponderosa* growth, with SPEI below −1.64 identified as a threshold to trigger mortality (Huang et al., 2015).

TABLE 1 | Compilation of key published metrics to predict *Pinus edulis* mortality (upper portion), which can be used in near-term ecological forecasting, followed by modifiers (lower portion) which need to be used in conjunction with additional information.

Metric #	Mortality = f(....)	Threshold, Mode, or Relationship	Data	Drought/Warming source	References
METRICS					
Metrics Driven Primarily by Climatic Variables					
1	Standardized Precipitation Evaporation Index (SPEI)	SPEI of −1.64 corresponds to no growth and regional mortality	SPEI from September thru July	Climate data from 2000s drought	Huang et al., 2015
2	Forest Drought-Stress Index (FDSI)	FDSI of −1.41 corresponds to regional mortality events	Prior winter PPT and current and prior summer VPD	1500s droughts	Williams et al., 2013
3	Precipitation (PPT) and Vapor Pressure Deficit (VPD) Thresholds	Below 600 mm PPT threshold and above 1.7 kPa VPD threshold	Annual precipitation and warm season VPD	Observations of 2000s drought	Clifford et al., 2013
4	Bioclimatic Envelope for Mortality	At higher temperature can die at wetter soil moisture	Climate, soil moisture	Field Transplant Experiment	Law et al., in press
Nature Metrics Based on Direct Ecohydrological or Physiological Thresholds					
5	Water Potential (ψ) Threshold	Exceeded thresholds	Predawn water potential	Literature review	Adams et al., 2017b
6	Percent Loss Conductivity (PLC)	60% PLC threshold as mortality tipping point	Predawn water potential with PLC relationship	Literature review; Observations from 2000s drought	West et al., 2007; Koepke and Kolb, 2013; Adams et al., 2017b
7	Minimal Protracted Frequency of Plant Available Water (PAW)	Low frequency of plant available water over growing season	Soil moisture by depth	Observations of 2000s drought	Breshears et al., 2009a
8	Duration of Water Potential below Point of Stomatal Closure (Time ψ ↓)	Plant water potential below stomatal closure >10 Mo	Predawn water potential	Observations of 2000s drought	Breshears et al., 2009b
9	Multispectral Remote-Sensing Measures	Plant water content and plant water potential	Remotely sensed multispectral indices	Observations of 2000s drought	Breshears et al., 2005; Rich et al., 2008; Huang et al., 2010; Krofcheck et al., 2014
Metrics Based on Multi-Step Modeling of Climate, Ecohydrology, and/or Ecophysiology					
10	Climate suitability during drought and historic reference (ECSxHCS)	Low ECS (Episodic Climate Suitability) and high HCS (Historic Climate Suitability)	Climate during drought relative to long-term mean	2000s drought in context of historical (28 year) climate	Lloret and Kitzberger, 2018
11	Integrated Ecophysiology	Ecophysiological threshold exceeded	Climate, Predawn water potential	Miscellaneous studies	McDowell et al., 2008
12	Regional processes	Critical mortality threshold of −2.4 MPa	Climate, Other parameters	Miscellaneous studies	McDowell et al., 2016
MODIFIERS					
Drought Properties					
1	Temperature	Faster when warmer by 5% per °C	Climate	Growth Chamber Experiment	Adams et al., 2017a
Soil Properties					
2	Topographic Moisture Index and Elevation	Lower and drier sites experienced more mortality	Topographic position (slope, elevation, aspect)	1950s drought	Allen, 1989; Allen and Breshears, 1998
3	Soil Available Water Capacity (AWC)	Areas with a soil AWC < 100 mm have greater mortality	Soil AWC	Observations of 2000s drought	Peterman et al., 2013
4	Soil Parent Material	Cinder exacerbates drought more than basalt or sedimentary parent material	Soil parent material	Observations of 2000s drought	Koepke et al., 2010
Tree Phenotype And Genotype					
5	Tree Size	Large trees more susceptible	Demography	Observations of 2000s drought	Floyd et al., 2009
6	Phenotypic Plasticity and Sequence of Events	Reduction of biomass/variable growth rates	Dendrochronology, Demography	Observations of 2000s drought	Ogle et al., 2000; Macalady and Bugmann, 2014

(Continued)

TABLE 1 | Continued

Modifiers	Mortality = f(....)	Threshold, Mode, or Relationship	Data	Drought/Warming Source	References
7	Prior Patterns of Growth Rates	Long term growth rate, variability, and number of abrupt increases predict mortality	Demography, Dendrochronology	1950s, 1990s, and 2000s droughts	Ogle et al., 2000; Macalady and Bugmann, 2014;
8	Resin Ducts	Smaller resin ducts increase likelihood of mortality	Resin flow, Dendrochronology	Observations of 2000s drought	Gaylord et al., 2013, 2015
9	Genetics	Mortality of trees resistant to moth was 3 times higher than for moth-susceptible trees	Genetics	Observations of 2000s drought	Sthultz et al., 2009
Biotic Interactions					
10	Competition	Mixed evidence	Demography	Literature Review	Meddens et al., 2015
11	Facilitation	Facilitation reduces threshold	Demography, Microclimate	Observations of 2000s drought	Royer et al., 2010; Redmond et al., 2015
12	Outbreaks	Selectivity for larger trees	Beetle populations	Experimental drought	Gaylord et al., 2013

Metric 2: Forest Drought-Stress Index (FDSI)

FDSI is an annual index that includes winter-spring precipitation and vapor pressure deficit during the early summer of the current year and the late summer of the year prior, and is standardized by applying a ratio of the current conditions to the long-term mean (Williams et al., 2013). FDSI strongly correlates to regional trends of tree growth and regional patterns of drought-related mortality agents, including bark beetle outbreaks and area burned by tree-killing wildfire. A FDSI ≤ -1.41 is thought to have resulted in widespread mortality (Williams et al., 2013), based on FDSI during the driest half of years during Southwest USA "megadrought" events (Swetnam and Betancourt, 1998).

Metric 3: Precipitation (PPT) and Vapor Pressure Deficit (VPD) Thresholds

Field observations of *P. edulis* mortality across central NM, USA in response to the 2000s drought were highly variable with two thresholds for mortality identified: sites with 2-year precipitation > 600 mm or for warm season (May-August) mean VPD over 2 years of < 1.7 kPa, had little to no mortality ($<10\%$), whereas at sites with < 600 mm or > 1.7 kPa, plant mortality was highly variable (0% to ∼100%; Clifford et al., 2013).

Metric 4: Bioclimatic Envelope for Mortality

A new type of bioclimatic envelope that focuses exclusively on mortality events for *P. edulis* was developed for saplings and small reproductively mature sized trees, based largely on climate manipulation experiments that varied precipitation and temperature (Law et al., in press). This bioclimatic envelope estimates a boundary between survival and mortality as a function of length of a dry period and growing season temperature. It indicates that at warmer temperatures (or greater VPD), the duration that *P. edulis* can survive is reduced.

Metrics Based on Direct Ecohydrological or Physiological Thresholds

Metric 5: Water Potential (ψ) Threshold

Plant water stress as reflected in more negative plant water potential, usually measured at the twig scale for *P. edulis*, has been used to identify threshold values at which tree mortality occurs (Sperry et al., 1988; McDowell et al., 2008) and can be measured in the field. Although the plant water potential for stomatal closure varies somewhat (Breshears et al., 2009b), values associated with greater stress may be more variable among sites (Linton et al., 1998; West et al., 2007; Koepke and Kolb, 2013). A review of experimental studies of drought found that this metric occurred in association with mortality of every tree species studied (Adams et al., 2017b).

Metric 6: Percent Loss of Conductivity (PLC)

Increased stress associated with more negative plant water potential is also associated with loss in conductivity due to embolism intrusion, usually measured in stems in the lab, leading to disruptions of the hydraulic water column that can lead to mortality (Sperry et al., 1988; McDowell et al., 2008). Empirical and theoretical models suggest that this tightly coupled relationship accurately estimates loss of conductivity across species spanning an isohydry-anisohydry gradient (Cochard, 1992; Linton et al., 1998). A recent meta-analysis determined a key threshold of 60% PLC as a mortality tipping point (Adams et al., 2017b), for which site-specific relationships to *P. edulis* predawn water potential can be developed prior to drought (Linton et al., 1998; West et al., 2007; Koepke and Kolb, 2013).

Metric 7: Minimal Protracted Frequency of Plant Available Water (PAW)

Long-term soil moisture data obtained by neutron probe measurements that extended below the topsoil and into tuff bedrock (Breshears et al., 2005, 2009a) were adjusted for soil

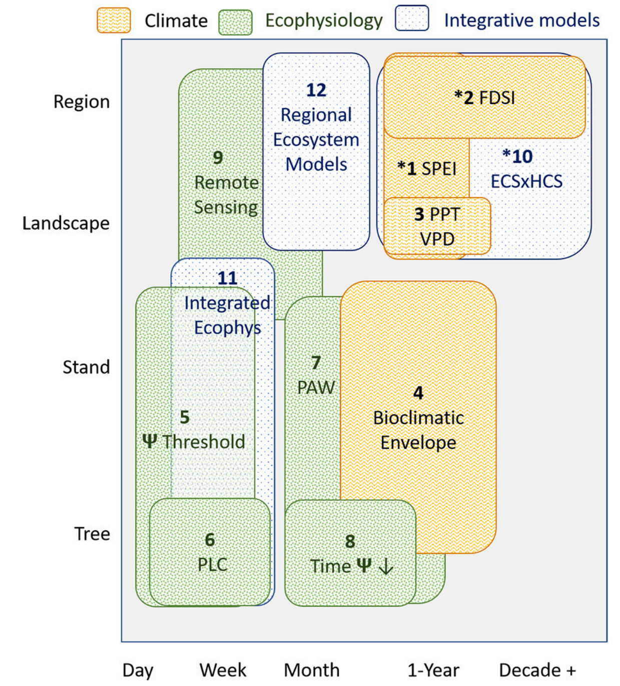

FIGURE 1 | Spatial and temporal scale of each key metric (see section Metrics Associated With Mortality Driven by Drought and Warming for *Pinus edulis*) to predict tree mortality. Spatial scale of each metric is based on the spatial scale at which that metric was developed. The temporal scale of each metric is based on the frequency at which the metric can be updated and used for near-term ecological forecasting. Pattern denotes the metric category as climate (section Metrics Driven Primarily by Climatic Variables), ecophysiology (ecohydrological and physiological thresholds; section Metrics Based on Direct Ecohydrological or Physiological Thresholds) or integrative models (section Metrics Based on Multi-step Modeling of Climate, Ecohydrology, and/or Ecophysiology). "*" indicates long-term (15+ years) temporal data is needed for the predictions.

texture to estimate thresholds at which soil moisture above bedrock tuff becomes relatively unavailable to plants. During the 2000s drought, soil moisture above the bedrock tuff was below an availability threshold for 14 consecutive months, during which time tree mortality occurred (Breshears et al., 2009a).

Metric 8: Duration of Water Potential Below Point of Stomatal Closure (Time ψ ↓)

For relatively more isohydric species, such as *P. edulis*, trees close stomata at a given level of water stress and then attempt to survive the duration of the drought, paying respiration costs during that period. Predawn plant water potential for *P. edulis* at the same site as *Metric 7* was <-2.2 MPa, the point of stomatal closure (Lajtha and Barnes, 1991), for 10 consecutive months preceding tree mortality (Breshears et al., 2009b). Similarly, a field experiment removing 50% of ambient precipitation resulted in *P. edulis* mortality after 7 consecutive months of near zero conductance (Plaut et al., 2012).

Metric 9: Multispectral Remote-Sensing Measures

Multispectral assessments of whole-ecosystem responses of post-die-off can detect *P. edulis* die-off (e.g., Breshears et al., 2005; Rich et al., 2008; Huang et al., 2010; Krofcheck et al., 2014). Further, multispectral data for *P. edulis* needles alone revealed strong correlations between either plant water content or plant water potential with each of 5 multispectral indices for needles spanning healthy through dead (Stimson et al., 2005).

Metrics Based on Multi-Step Modeling of Climate, Ecohydrology, and/or Ecophysiology

Metric 10: ECSxHCS

Using climate data, extended species distribution modeling was applied to assess whether *P. edulis* mortality during drought was greater in areas with lower historical climatic suitability (HCS; i.e., species distribution modeling using long-term average climate conditions) or with lower climatic suitability during a multi-year drought [episodic climatic suitability, ECS) (Lloret and Kitzberger, 2018). Highest mortality was found in areas with both high HCS and low ECS, suggesting trees have acclimated to the conditions historically experienced and are thus most sensitive to abrupt changes in climate.

Metric 11: Integrated Ecophysiology

Models based on plant ecophysiology have been developed to predict mortality based on known detailed physiological relationships (i.e., stomatal responses to limited water availability) of *P. edulis* (McDowell et al., 2008) coupled with information on temperature, drought intensity/duration and the role of biotic agents (hydraulic aspects of mortality, drawing on Sperry et al., 1988 are reviewed in Choat et al., 2018; see Adams et al., 2013 for carbohydrate results for *P. edulis*). The interactions among these specific drivers can push plants to mortality via combinations of carbon starvation, hydraulic failure, and/or pests and pathogens (McDowell et al., 2011; Anderegg et al., 2015).

Metric 12: Regional Ecosystem Models

Regional *P. edulis* mortality projections among three ecosystem models all predicted widespread die-off, after verifying the ability of each to reproduce predawn water potential accurately (McDowell et al., 2016 and references therein): (1) TREES, a dynamic ecosystem model of water and carbon flows, plant water balance and cavitation was coupled with stomatal conductance, photosynthesis, and evaporation (Mackay et al., 2003, 2010; Samanta et al., 2007; Loranty et al., 2010); (2) MuSICA, a multilayer, multi-leaf process-based biosphere-atmosphere exchange model, included detailed root water uptake, plant water storage dynamics, soil water hydraulic redistribution, root cavitation, and plant NSC storage dynamics (Ogée et al., 2003); and (3) ED(X), which tracks cohorts of trees based on their sizes, simulated tree mortality of cohorts based on carbon starvation and hydraulic failure, accounting for plant water storage and hydraulic conductivity (Moorcroft et al., 2001 with modifications described by Fisher et al., 2010; McDowell et al., 2013; and Xu et al., 2013). All three models used a critical mortality threshold of growing season predawn plant water potential associated with stomatal closure (−2.4 MPa) derived from a field experiment (Pangle et al., 2012; SI 5 in McDowell et al., 2016).

MODIFIERS OF RATES OR SENSITIVITY OF *P. edulis* MORTALITY

We also identified four categories of "modifiers" that influence the likelihood of *P. edulis* mortality (drought properties, soil properties, tree phentoype and genotype, and biotic interactions) that differ from "metrics" in that they cannot be used to independently estimate mortality without additional factors, nor can they be iteratively updated for near-term ecological forecasting.

Drought Properties

Modifier 1: Temperature

The first modifier focuses on how temperature explicitly drives mortality. *Pinus edulis* was the first species for which warmer conditions during drought were shown to hasten tree mortality for a reproductively mature-sized tree (Adams et al., 2009). Further, *P. edulis* seedlings exhibited a similar slope in hastening of time-to-mortality of ∼5% per °C increase in temperature across a wide range of temperatures (Adams et al., 2017a).

Soil Properties

Modifier 2: Topographic Moisture Index and Elevation

Spatial patterns of *P. edulis* mortality in response to the 1950s drought were a function of a topographic moisture index and elevation, with increased mortality at drier and lower sites (Allen, 1989; additional details in Allen and Breshears, 1998). Slope aspect and position influenced mortality in piñon-juniper woodlands in general, but the effects of elevation were mixed (Meddens et al., 2015).

Modifier 3: Soil Available Water Capacity (AWC)

Using publicly available soil data (SSURGO; scale of 1:20,000), *P. edulis* stands had greater mortality during the 2002–2003 drought where soil AWC (calculated based on soil texture and depth) was <100 mm (Peterman et al., 2013). However, a smaller-scale study conducted in NM found no relationship between soil AWC and *P. edulis* mortality (Clifford et al., 2013), suggesting this metric may be more applicable across large geographic areas that vary greatly in soil AWC.

Modifier 4: Soil Parent Material

P. edulis mortality from the 2002–2003 drought was greater on soil parent material derived from volcanic cinder than from flow basalt or sedimentary substrate (Koepke et al., 2010).

Tree Phenotype and Genotype

Modifier 5: Tree Size

Physical characteristics like size are expected to be modifiers of mortality (Bennett et al., 2015; McDowell and Allen, 2015). Larger diameter *P. edulis* trees have experienced greater levels of drought-related mortality (Floyd et al., 2009; Meddens et al., 2015), likely due to combinations of bark beetle selectivity for large diameter trees (Santos and Whitham, 2010; Gaylord et al., 2013), a greater vulnerability of taller trees to hydraulic failure (McDowell and Allen, 2015), and carbon starvation from increased metabolic demands (Mueller et al., 2005).

Modifier 6: Phenotypic Plasticity and Sequence of Events

Phenotypic plasticity, including climate-induced variability in leaf area, sapwood area (Limousin et al., 2015), and tree-ring growth (Williams et al., 2013) can result in structural overshoot risks during rapid transitions from wet to dry periods (Jump et al., 2017), while the duration and sequencing of good and bad growth years affect both short- and long-term tree mortality risk (Ogle et al., 2000; Macalady and Bugmann, 2014).

Modifier 7: Prior Patterns of Growth Rate

Evaluating the 1950s, 1996, and the 2000s droughts, the best predictors for growth-mortality models of *P. edulis* included long-term (10–30 year) average growth rate combined with a metric of growth variability from the past 15 years and the number of abrupt growth increases over the past 10 years (Ogle et al., 2000; Macalady and Bugmann, 2014).

Modifier 8: Resin Ducts

Investment in resin ducts represent a proxy for defense against insects and may vary in response to tree size and age dynamics. *P. edulis* trees that produce smaller and/or fewer resin ducts are more likely to die during drought (Kläy, 2011; Gaylord et al., 2013, 2015).

Modifier 9: Genetics

A study of *P. edulis* mortality during drought for trees that exhibited genetically-based resistance or susceptibility to the moth *Dioryctria albovittella* found that drought-related mortality of trees resistant to the moth was three times higher than for moth-susceptible trees (Sthultz et al., 2009).

Biotic Interactions

Modifier 10: Competition

The effects of stand tree density (i.e., both intra- and inter-specific competition) on *P. edulis* mortality are mixed, with more studies not detecting density effects (Meddens et al., 2015). A study on juvenile *P. edulis* survival during drought found that mortality of juveniles located in the canopy interspace of overstory trees and shrubs was greater in areas with higher grass cover (Redmond et al., 2015).

Modifier 11: Facilitation

Adult trees in piñon-juniper woodlands provide substantial shading below tree canopies and as a function of the overall tree density (Royer et al., 2010, 2011). Facilitation by adults increases the mortality threshold to more extreme conditions relative to non-facilitated plants (Sthultz et al., 2007; Redmond et al., 2015).

Modifier 12: Outbreaks

Bark beetle *(Ips confusus)* outbreaks are usually associated with field observations and experiments of *P. edulis* mortality (Meddens et al., 2015). Note, however, that *P. edulis* mortality during drought has occurred in the absence of bark beetles (Mueller et al., 2005) and controlled experiments quantify rates of mortality caused by drought in the absence of bark beetles (Adams et al., 2009, 2017a; Anderegg and Anderegg, 2013).

RELATIONSHIPS TO STUDIES OF OTHER *PINUS* SPECIES

The metrics and modifiers for *P. edulis* mortality share consistencies with other species in the *Pinus* genus. Several of the above metrics and modifiers (e.g., *Metrics 1–2* and *Modifier 1*) were also predictive of *P. ponderosa* mortality. For instance, the increase of hastening in time-to-mortality for *P. edulis* of ∼5% per °C also applies to *P. ponderosa*, as does the linear relationship of this response to a wide range of warming during drought (Adams et al., 2017b). Mortality of five European species of *Pinus* depended on warming and water limitation (Matias et al., 2017), consistent with the climate metrics for *P. edulis,* which include both a warming or evaporative demand component and a precipitation component; these species also differed in sensitivity between montane and lowland sites. Other *Pinus* species have similar ecophysiological characteristics as *P. edulis* (Olson et al., 2018) and are also vulnerable to bark beetles, particularly when under water stress (Anderegg et al., 2015). The effect of elevated CO_2 on mortality has not been studied for *P. edulis*, but results for *P. radiata* found it did not extend time-to-mortality (Duan et al., 2015).

CONCLUSION

There are more studies of drought-related mortality for *P. edulis* than for any other tree species, yet the many interrelated and often untested metrics and modifiers indicate a need to determine which are the most robust, accounting for tradeoffs between robustness and data or computational requirements. Expected future mortality events will provide an opportunity to observationally and experimentally test and compare these metrics related to tree mortality for *P. edulis* via near-term ecological forecasting (Clark et al., 2001; Dietze, 2017; Dietze et al., 2018). Given that many current projections of *P. edulis* mortality predict extensive mortality in coming decades (e.g., Adams et al., 2009, 2017a; Williams et al., 2013; McDowell et al., 2016), we need to test these metrics and modifiers with upcoming droughts. These metrics and modifiers reinforce that *Pinus*, a widely distributed and commercially important genus, is likely to be sensitive to future hotter drought. These metrics also serve as potential analogs for species in other genera or trait groups. Improving predictions of tree mortality will be increasingly important in moving toward anticipatory management under warming climate (Bradford et al., 2018).

AUTHOR CONTRIBUTIONS

DB provided a first rough draft of the synthesis table and the manuscript. All authors contributed to substantial revision and identifying and summarizing key metrics and modifiers, as well as editing and refinement of the text, tables and figure.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2018.00004/full#supplementary-material

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