Dead again: predictions of repeat tree die-off under hotter droughts confirm mortality thresholds for a dryland conifer species

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Abstract

Tree die-off, driven by extreme drought and exacerbated by a warming climate, is occurring rapidly across every wooded continent—threatening carbon sinks and other ecosystem services provided by forests and woodlands. Forecasting the spatial patterns of tree die-off in response to drought is a priority for the management and conservation of forested ecosystems under projected future hotter and drier climates. Several thresholds derived from drought-metrics have been proposed to predict mortality of Pinus edulis, a model tree species in many studies of drought-induced tree die-off. To improve future capacity to forecast tree mortality, we used a severe drought as a natural experiment. We compared the ability of existing mortality thresholds derived from four drought metrics (the Forest Drought Severity Index (FDSI), the Standardized Precipitation Evapotranspiration Index, and raw values of precipitation (PPT) and vapor pressure deficit, calculated using 4 km PRISM data) to predict areas of P. edulis die-off following an extreme drought in 2018 across the southwestern US. Using aerial detection surveys of tree mortality in combination with gridded climate data, we calculated the agreement between these four proposed thresholds and the presence and absence of regional-scale tree die-off using sensitivity, specificity, and the area under the curve (AUC). Overall, existing mortality thresholds tended to over predict the spatial extent of tree die-off across the landscape, yet some retain moderate skill in discriminating between areas that experienced and did not experience tree die-off. The simple PPT threshold had the highest AUC score (71%) as well as fair sensitivity and specificity, but the FDSI had the greatest sensitivity to die-off (85.9%). We highlight that empirically derived climate thresholds may be useful forecasting tools to identify vulnerable areas to drought induced die-off, allowing for targeted responses to future droughts and improved management of at-risk areas.

1. Introduction

Tree die-off (or mass-mortality events of trees) driven by extreme drought, exacerbated by a warming climate, and frequently associated with forest pests and pathogens, presents a global-scale challenge to maintaining forested ecosystems under accelerating climate warming (Breshears et al. 2005, Allen et al. 2010, 2015). Forecasting tree die-off has the potential to inform management goals like the provisioning of ecosystem services, developing treatments to increase forest resiliency during or prior to drought, and planning recovery efforts following drought, as well as scientific questions like carbon sink-source dynamics, global climate circulation, and species distributions (e.g. Anderegg et al. 2013, Bradford et al. 2018, Swann et al. 2018, Jackson 2021). But forecasting tree die-off remains a major challenge, as tree die-off events
are relatively infrequent, long-lasting, and slow developing in comparison to many other forest disturbances like fires or hurricanes (Redmond et al. 2019). Thus, while the study of tree mortality is often a retrospective exercise, advancing forecasts of tree die-off requires iteratively testing existing hypotheses to refine future predictions, highlight areas of uncertainty, and evaluate our understanding of ecological processes (Dietze 2017).

‘Hotter droughts’ or ‘hot droughts’ (Allen et al. 2015; originally ‘global-change-type-droughts’, Breshears et al. 2005) greatly increase the likelihood of tree die-off, due in part to the positive exponential relationship between maximum temperature and saturation vapor pressure (Breshears et al. 2013, Grossiord et al. 2020). Hotter temperatures exponentially increase the water stress experienced by plants during periods of drought (e.g. vapor pressure deficit (VPD), Anderson 1936, Grossiord et al. 2020), therefore continued and accelerating climate warming greatly increases the vulnerability of trees to mortality from bark beetles, pathogens, hydraulic failure of the xylem, and carbon starvation (McDowell et al. 2008, 2011, Adams et al. 2009, Breshears et al. 2013, Gaylord et al. 2013). Identifying temperature and moisture thresholds associated with tree die-off (i.e. mortality thresholds) has been the focus of much recent research (e.g. Clifford et al. 2013, Huang et al. 2015, Hammond et al. 2019) in part because this would allow scientists and managers to better predict how, when, and where trees are most likely to die following hotter droughts. However, the wide variation in physiological vulnerability and drought exposure makes individual-tree mortality exceedingly difficult to predict (Trugman et al. 2021). Ultimately, it is unclear whether empirically derived threshold responses, often retrospectively identified from a single drought event, produce transferrable and repeatable results in future drought events of differing severity, or whether such predictions are consistent across large geographic areas.

One of the best-documented examples of tree die-off occurred in the southwestern United States during the early 2000s (Breshears et al. 2005, Floyd et al. 2009, Meddens et al. 2015). An outbreak of piñon Ips beetles (Ips confusus), occurring in combination with a hot drought event, resulted in high levels of regional-scale mortality of piñon pine (Pinus edulis), an iconic conifer species in dry woodlands and forests of the region. This event motivated a substantial amount of research on drought and warming-driven die-off. In the last 20 years, over a dozen metrics and their associated thresholds have been proposed as predictors of piñon pine die-off (reviewed in Breshears et al. 2018). Many of these metrics require detailed ecophysiological and hydraulic data to predict individual-level mortality (Breshears et al. 2018), though such data are not widely available, especially over long periods of time or across broad spatial areas. However, four of these metrics are amenable to broad-scale forecasting efforts: the Forest Drought Severity Index (FDSI), the Standardized Precipitation Evapotranspiration Index (SPEI), and absolute values of precipitation (PPT) and VPD (Breshears et al. 2018). Yet, the applicability of these metrics and their associated thresholds to predict piñon pine mortality have not been field-tested in subsequent droughts. Such metrics also share similarities with those available for other species of Pinus (e.g. Williams et al. 2013, Breshears et al. 2018) and field-validating such relationships will improve our ability to forecast forest die-off in other systems and species.

We used a recent hot drought as a natural experiment to evaluate our ability to predict areas experiencing piñon pine die-off using these four existing mortality thresholds. Our primary objective was to assess whether thresholds derived from these four regional-scale drought metrics could successfully predict the spatial patterns of piñon pine die-off in advance of aerial surveys of tree die-off the following year. We highlight the importance of testing existing mortality thresholds, which have yet to be independently validated in subsequent drought events, and discuss how these results bear on our ability to develop future forecasts of tree die-off.

2. Methods and materials

2.1. Study species and area

Piñon pine occupies low elevation, semi-arid forests and woodlands of the southwestern United States and Mexico. The study area comprised the distribution of piñon pine (from Little 1971) in the US states of Colorado, New Mexico, Utah, and Arizona (hereafter the southwestern US). Trees of the genus Pinus are some of the most commercially important species worldwide, and piñon pine specifically has been used in a large majority of studies examining hotter drought driven die-off, making it a model species (Breshears et al. 2018). It has been estimated that half of a million hectares of piñon pine woodlands and forests in the southwestern US (14% of the total area of the species) have been affected by tree die-off between 2000–2018 (Hicke et al. 2020), with some areas experiencing near total loss of mature piñon pine trees (Breshears et al. 2005, Floyd et al. 2009, Clifford et al. 2013).

The climate of the southwestern US is characterized by cold winters, warm summers, and highly seasonal precipitation. Annual PPT averages around 400 mm per year (PRISM Climate Group, 1981–2010) and is highly seasonal. In the north and western portion of the study area, PPT falls mostly as snow during the cool-season (October–April) and the warm-season is dry. Heading south and east, PPT is more strongly influenced by the North American monsoon (Notaro et al. 2010). In these areas, half or more of the annual PPT may fall during the summer...
months of July, August, and September (which are usually the driest months in the north and west portions of the study area, PRISM Climate Group 2021).

Much of this area has experienced a persistent hydrological drought for two decades, the driest such period since in at least 1200 years (Park et al. 2022), and climate models predict continued warming and drying trends in the future (Bradford et al. 2020b, Cook et al. 2021). The 2018 hot drought in the south-west US was an acute event that was overlaid on this extended hydrological drought. About half of the study area experienced PPT deficits greater than 50% of the climatological normal (e.g. 1981–2010), and annual mean temperatures in 2018 across the region were on average 0.5 °C–2 °C warmer relative to 1981–2010 climate averages (PRISM Climate Group 2021). Despite several drought events that occurred between 2002 and 2018, the 2018 drought event was at the time the most severe drought since 2002 (figure 1).

2.2. Quantifying tree-die-off—aerial detection surveys (ADS)

To quantify tree die-off across the study area, we used ADS (USDA Forest Service 2019). These surveys are flown by the United States Forest Service each year, usually in mid-summer, and are widely used in studies of tree mortality at coarse spatial grains (ca. 1 km²) and at regional extents (Coleman et al. 2018, Hicke et al. 2020, Meddens et al. 2012, Preisler et al. 2017, Masek et al. 2013, Hart et al. 2017). Trained surveyors sketch polygons of areas affected by tree mortality, representing stand-level mortality at spatial scales greater than 0.4 ha, and then estimate the attributes of these polygons including the approximate area, severity category (five categories based on the percentage of dead or dying trees), tree species, and mortality agent. Detection of mortality often lags at least a year behind drought; therefore, we examined ADS surveys flown in summer 2019 to assess the impacts of the 2018 hotter drought (similar to Hicke et al. 2020, Meddens et al. 2012). Previous work also suggests that the background rate of mortality in these systems is 1%–3% annually (van Mantgem et al. 2009); therefore, to be confident that we were describing mortality events that exceeded background mortality rates, we excluded observations where fewer than 15 trees died in areas <0.4 ha in size (point observations) and stand-level observations labeled as <10% mortality (ADS severity classes 1–2). Finally, we masked all data surveyed by ADS teams in 2019 to the extent of piñon pine (Little 1971). All analyses were carried out in R 4.1.0 (R Core Team 2021) using functions from the raster (Hijmans 2021) and sf (Pebesma 2018) packages. Data visualizations were made in ggplot2 (Wickham 2016) with scico, PNWcolors, and patchwork packages (Lawlor 2020, Pedersen 2020, Pedersen and Cramer 2020), and data carpentry was performed using data table (Dowle and Srinivasan 2021).

We calculated the total number of acres affected by tree die-off by summing the area of all polygons in each severity class. However very few of these polygons were in the most severe mortality class (i.e. >50% mortality of live trees, n = 9). Therefore, summing the total area affected would overestimate the total area directly affected by tree die-off. To account for this, we multiplied each polygon by a constant corresponding to the upper, middle, and lower bounds of each severity class. For example, the acreage of polygons described as experiencing 11%–29% mortality (the lowest severity class included in this study, ‘Severity class 3—Moderate’) were multiplied by 11% (lower bound), 29% (upper bound), and 20% (middle estimate). For comparison with gridded climate data (below) we transformed ADS polygon data to a 4 km resolution raster of presence/absence and aligned with the gridded climate data (figure 2). We then calculated the total acres affected by tree die-off

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**Figure 1.** Running 6 month SPEI values between 1 January, 1989, and 1 December, 2018 averaged across all piñon pine woodlands in the southwestern US. Each bar represents the difference in PPT and evapotranspiration for the prior 6 month period, standardized to the long-term mean (since 1901). Positive values (blue) indicate cooler and wetter than average conditions, and negative values (red) indicate hotter and drier than average conditions. SPEI was calculated with a Thornthwaite type water balance using PRISM derived PPT and mean temperature at a 4 km resolution, and the distribution of piñon pine woodlands was described by Little (1971). Dashed line indicates 1 standard deviation below the average (fainter line, = –1.5) as benchmarks of drought stress. Drought conditions in 2018 (minimum 6 month SPEI value = –1.81) were the most severe in this area since 2002 (minimum 6 month SPEI value = –2.10). A long-term drought in 2012 briefly reached a minimum 6 month SPEI value of –1.69, but overall, the 2012 event was less severe than the 2002 or 2018 droughts.
Figure 2. Panel A shows tree die-off (i.e. observations of mortality exceeding 10% of the affected area) of piñon pine in 2019 as quantified by ADS. Gray shading shows the distribution of piñon pine across the U.S. states of Colorado, New Mexico, Arizona, and Utah (southwest US), and darker colors indicate greater amounts of tree die-off in each pixel. Total area affected was estimated by multiplying the size of each polygon by the middle estimate of each ADS severity class. Panel B is zoomed to the extent of tree die-off observations in the study area. Tree-die off in 2019 was not spatially widespread across the area and was only present in 2.7% of the areas surveyed by ADS.

Table 1. Descriptions of four drought metrics and the hypothesized thresholds of piñon pine die-off.

| Metric | Description | Threshold |
|--------|-------------|-----------|
| FDSI<sup>a</sup> | Mean FDSI of the current year and the year prior. FDSI is calculated as the combination of winter PPT (November–March), early summer VPD of the current year (May–July), and late summer VPD (August–October) of the year prior. FDSI is standardized by applying a ratio of the current conditions to the long-term mean. | −1.41 |
| SPEI<sup>b</sup> | Negative SPEI values for the 11 month period of September (during the year prior) through July (of the current year). SPEI is calculated as difference between PPT and potential evapotranspiration, standardized to the long-term mean. | −1.64 |
| PPT<sup>c</sup> | Total PPT of the current water year (previous September–current October) and the year prior. | <600 mm |
| VPD<sup>c</sup> | Mean warm-season (May–August) VPD, averaged over the current year and the year prior. | >17 hPa |

<sup>a</sup>Williams et al (2013).
<sup>b</sup>Huang et al (2015).
<sup>c</sup>Clifford et al (2013).

in each pixel to visualize the spatial patterns of mortality across the region.

2.3. Quantifying drought intensity—climatic thresholds
We compared thresholds derived from four drought metrics that were hypothesized to predict regional conifer die-off in the southwestern US (reviewed in Breshears et al 2018, table 1; figure 3): the FDSI (Williams et al 2013), the SPEI (developed by Vicente-Serrano et al 2010, threshold proposed by Huang et al 2015), and absolute PPT and VPD (described by Clifford et al 2013). Gridded 4 km monthly climate data from PRISM (PRISM Climate Group 2020) were used to calculate all metrics across the study area. Detailed descriptions of the drought metrics, and how each threshold was calculated, can be found in the supplementary material (Supplementary appendix 1).

2.4. Agreement between climatic thresholds and tree die-off
We extracted continuous values of the drought metrics for each pixel with and without observations of tree die-off, and then plotted the distribution of all pixels for each individual metric in relation to their proposed threshold to visualize the skill of the threshold in discriminating areas that experienced die-off. Climate data were transformed to binary variables (0—below threshold, or 1—beyond threshold)
Figure 3. Spatial patterns of the climate thresholds hypothesized to be predictors of tree die-off during the 2018 hotter drought across the range of piñon pine that was surveyed by aerial detection surveys in 2019. Gridded climate data were classified as either beyond (red colors) or below (blue colors) the mortality thresholds. The proportion of area above or below mortality thresholds are included in parentheses.

and compared to presence/absence maps of tree die-off with confusion matrices using in the caret package in R (Kuhn 2021). We evaluated metrics based on their sensitivity (i.e. true positive rate, or the proportion of correct predictions containing tree die-off), specificity (i.e. true negative rate, or the proportion of correct predictions not containing tree die-off), and the AUC (a metric of overall predictive power that balances the trade-off between sensitivity and specificity using a receiver’s operating characteristic curve, Marzban 2004). Values are constrained from 0 to 1, with values of 0.5 indicating predictions no better than chance, and higher values indicating a higher proportion of correct predictions (both presence and absence).

3. Results

3.1. Can empirically derived thresholds predict the spatial patterns of tree die-off?
Tree die-off was not spatially extensive across the study area (figure 2). We estimate that between 5621.1 and 10,950.4 ha (middle estimate = 8285.9 ha) were directly affected by tree die-off (i.e. tree mortality >10%) in 2019. The area of mortality observations (n = 313) ranged from 0.4 to 2354.4 ha, with a median polygon area of 5.2 ha. Simple comparisons of the total area beyond the climate threshold relative to the total area that experienced tree die-off would suggest that overall, these metrics tended to overestimate the amount of tree die-off anticipated in 2019 (ranging from 13.1% to 46.1% of the study area predicted to experience die-off, figure 3).

The FDSI threshold was the most sensitive (sensitivity = 86.9%) indicating that this metric was highly skilled at correctly predicting locations where tree mortality was most likely to occur across the landscape (figure 4). However, the FDSI threshold also had the lowest specificity (15.8%), indicating that a substantial amount of mortality occurred in areas that FDSI predicted it would not. Overall, the FDSI threshold had the lowest AUC score (51%), indicating a lack of skill in discriminating between areas with and without tree die-off (figure 4). The absolute PPT threshold better balanced predictions of both presence and absence, with the highest AUC score (71%), highest true negative rate (specificity = 73.2%) and the second highest true positive rate (sensitivity = 68.6%; figure 4). Based on visual assessments, the value of the VPD threshold was roughly consistent
Figure 4. Results of confusion matrices classifying the agreement between areas surveyed by ADS in 2019 within the distribution of piñon pine that experienced tree die-off (>10% mortality) and those areas that exceeded threshold values of the studied drought metrics. Sensitivity is the true positive rate, specificity is the true negative rate, and AUC balances the overall proportion of correct predictions (accounting for both sensitivity and specificity).

Figure 5. Distribution of the 2018 drought metric values for areas surveyed by ADS in 2019 that either had evidence of tree die-off (yellow) or had no tree die off (blue). Distribution of drought metric values for the entire study are plotted on the x axis, and the location of the threshold is shown by a vertical dashed line. The y axis shows the cumulative density of all pixels in each category. Drought stress increases from right to left along the x axis of each panel, denoted by direction of red arrows.

with the location proposed by Clifford et al (2013; figure 5); however, the VPD threshold was less specific than the PPT threshold, (sensitivity = 64.3%, specificity = 57.9%, AUC = 61.1%; figures 4 and 5). Observations of tree-die off were skewed towards the hotter and drier side of SPEI values, indicating relatively low specificity (figure 5). The SPEI threshold also predicted the most amount of tree die-off relative to the other metrics (46.4% of all pixels were expected to contain die-off, figure 3) and classification accuracy metrics hovered near 54% (sensitivity = 54.3%, specificity = 54% and AUC = 54.6%).

4. Discussion

This study was a key first step in advancing future forecast models of tree die-off. By field-testing multiple pre-existing mortality thresholds (specifically those which can be easily calculated from readily
available climate data), we can begin to evaluate our understanding of regional-scale tree die-off, refine future predictions under repeat drought events, highlight areas of potential uncertainty, and point to areas of growing confidence where these results may be translated into action. In the southwest US, droughts are projected to increase in frequency, intensity, and duration in step with a warmer climate, portending continued tree die-off events that will have major impacts on society and ecosystems alike (Williams et al 2013, 2020, McDowell et al 2016, Overpeck and Udall 2020, Chiang et al 2021). Yet significant uncertainties remain about when and where these droughts will ultimately occur, and which trees are the most likely to die following drought. Thus, managing for forest and woodland persistence in a hotter future will require the capacity to respond to extreme climate events as they are developing, and to rapidly implement targeted interventions that increase ecosystem resiliency to drought or aid in the recovery of ecosystems following droughts (Bradford et al 2018, 2020a, Redmond et al 2019).

Tree mortality is notoriously difficult to accurately predict (Trugman et al 2021). Recent research has used hydraulic data, forest inventories, remote sensing, and climate data to predict tree mortality in many different species with mixed success (Das et al 2013, Preisler et al 2017, Rogers et al 2018, Venturas et al 2021). Ecophysiological approaches to understanding drought-driven mortality may provide a mechanistic understanding of the processes that proximately lead to tree death (McDowell et al 2013). Yet individual-level factors can confound hydraulic predictions, and such models often contain many parameters that vary continually and can be difficult to estimate precisely. In this study, we bypass the variability in drought responses at the individual level and instead take a top-down approach to predicting tree mortality at regional scales. Our results suggest that simple metrics derived from readily available climate data may provide broadly useful generalizations about the spatial patterns of tree mortality across large spatial extents and lay the groundwork for refining future forecasts of drought-driven tree die-off. Such information can help rapidly identify areas of priority for implementing adaptive management decisions, including managing for understory vegetation responses, future fire risk, public fuelwood sources, wildlife habitat, and the provisioning of other ecosystem services.

4.1. Tree die-off following repeat hotter drought events

Following the 2018 drought, tree die-off was less severe compared to the 2002 drought. Though the estimates are not directly comparable, Hicke et al (2020) estimated that across approximately 300 000 ha impacted by hotter drought and piñon Ips beetles (Ips confusus), 400 million trees died following the 2002 hotter drought. For comparison, these estimates are an order of magnitude greater than what we estimate died following the 2018 event (middle estimate of tree die-off = 8,286 ha). We also estimate that the highest severity class of tree die-off (i.e. >50% mortality) accounted for only 20% of the total area experiencing die-off in 2019 (middle estimate = 1643 ha, minimum estimate = 1095.5 ha, maximum estimate = 2191 ha, figure S1). A lack of highly susceptible trees following the 2002 hotter drought could explain the discrepancy in die-off severity between droughts. Many of the regions affected during the 2018 hotter drought were also affected by the 2002 event (Meddens et al 2015, Hicke et al 2020). Though ADS data does not characterize size and age distributions of surveyed forests, the absence of widespread and severe mortality may reflect the lack of large and old trees remaining on these landscapes (Floyd et al 2015), which are preferred hosts of piñon Ips beetles (Negrón and Wilson 2003).

Repeat tree die-off events may also increase the relative abundance of drought adapted genotypes in surviving populations, which can shape the susceptibility of populations to future drought at the landscape level (Kuperinnen et al 2010). Trees likely exhibit some capacity to adapt to repeated exposure to drought, possibly through temporarily reducing structural growth or the remobilization of stored carbon (Ovenden et al 2021, Peltier et al 2021), though damage incurred from past droughts can also influence mortality responses in subsequent droughts (Macalady and Bugmann 2014, Trugman et al 2018). It remains unclear whether any such adaptive capacity or phenotypic plasticity will maintain pace with the velocity of climate change (Jump and Peñuelas 2005, Kuperinnen et al 2010).

The 2002 drought also followed several decades of cool and wet weather, particularly during the 1970s and 1980s, which may have promoted structural overshoot of canopy growth (Jump et al 2017, Zhang et al 2021) or facilitated establishment of trees into marginal microsites, i.e. areas that can support young trees during cool and wet periods but lack the buffer from drought to support older trees during hot and dry periods (Greenwood and Weisberg 2008). The 16 year period between 2002 and 2018 was notably much drier and hotter than the long-term average (Park et al 2022), and since piñon pine can take decades to reach maturity, there have been few opportunities for episodic recruitment or structural overshoot during the historically dry conditions that have characterized the early 21st century (Floyd et al 2015). The 2002 drought lasted several years—notably longer than the 2018 drought, which was also punctuated by a small number of heavy summer rainfall events in part of the region, relieving short-term drought stress in a field experiment (Redmond et al 2019). The reduced regional mortality response of piñon pine to subsequent hotter drought events may
have important implications for forecasting and may bias these thresholds towards overpredicting mortality across the landscape.

4.2. Differences among drought metrics

While some of these metrics showed promise in predicting tree die-off, they varied in their predictive power and the context when each may be most useful. The FDSI mortality threshold was the most sensitive of the four metrics, correctly predicting the areas that experienced tree die-off more than 85% of the time. This suggests that the FDSI mortality threshold could be most useful for identifying locations that are the most likely to experience mortality during drought. For example, in situations where resources may be limited, managers or scientists may choose to selectively target only a subset of the areas likely to experience future mortality, and FDSI could be used to prioritize those locations. However, the low specificity of FDSI may limit its ability to accurately capture more detailed, spatial patterns of tree die-off at regional extents. The FDSI metric was initially developed as a region-wide indicator of annualized forest drought stress as measured by tree rings. In other words, widespread tree die-off is only predicted to occur in years when region-wide FDSI reaches below −1.41 (Williams et al. 2013), which was not achieved in 2018 (figure S2). For this reason, the authors of this index have argued that it may not be appropriate as a point-based metric (e.g. McDowell et al. 2016), because FDSI at any given point may not be indicative of FDSI across the entire southwest. This may explain the poor specificity of the metric in discriminating tree die-off from tree survival at point locations. Nevertheless, our study suggests that FDSI may still retain a high degree of sensitivity as a point-based metric and in some cases may be useful in identifying priority areas for targeted actions.

The PPT mortality threshold proposed by Clifford et al. (2013) was better able to discriminate both true-positives and true-negatives, providing a more balanced picture of tree die-off at the regional level. This was somewhat surprising, given the wide range of mean annual PPT across the study area relative to the extent this mortality threshold was originally developed at (i.e. 100 km transect in central New Mexico, Clifford et al. 2013), but also because responses to reduced PPT are implicitly constrained by temperature (i.e. VPD; Adams et al. 2009, Williams et al. 2013). Yet its simplicity provides significant practical value to land managers concerned about tree die-off in the face of increasing hot drought. Absolute PPT totals do not require data transformation (like FDSI) or software packages (like SPEI) to calculate, and PPT is widely and easily monitored by numerous individuals and agencies. Clear paths to refining this relationship include the use of weather station data and real time monitoring of tree die-off events. Furthermore, understanding how this relationship varies across individuals of different size and age classes, along topographic and climatic gradients, and in the presence and absence of pathogens and other biotic agents of tree mortality, will greatly improve future forecasting efforts as well.

Differences in predictive power among these metrics may arise from the different extents and scales that these metrics were originally developed at (i.e. range-wide extent for FDSI and SPEI, regional-extent for PPT and VPD), or the different data sources originally used to parameterize these thresholds. It should be noted here that the grain-size of our climate data (4 km²) did not always align with the mortality observations (ranging in size from 0.4 to 2354.4 ha or approximately 20 km²), and uncertainty in our relatively coarse-grained maps of pinon presence could also introduce error in these analyses. Within the relatively coarse-grained resolution of this climate data, there are many fine-scale biophysical attributes that likely also modulate mortality responses, including stand density, topographic exposure, and soil depth and texture (Trugman et al. 2021). Tree mortality often arises from cross-scale phenomena among these drivers (i.e. individual-level resistance, stand- or landscape-level vulnerability, and regional-scale climate drivers), and thus accounting for these different variables and their interactions in future models will be a key to producing more accurate forecasts of tree mortality.

Near term ecological forecasting requires a learn-by-doing approach, with close collaboration between scientists and managers to supply an iterative cycle of adaptive management (Dietze et al. 2018). We show that empirically derived thresholds show promise in predicting the spatial patterns of tree die-off in the future, although such relationships must continue to be tested, validated, and refined to develop accurate forecasts. Nevertheless, regional-scale forecasts of tree die-off, similar to semi-seasonal forecasts of fire activity or extreme weather, may soon be within reach for this species and other species at risk from hotter drought.

5. Conclusion

By building the capacity to forecast future tree die-off, we can inform efforts to manage and restore forested ecosystems following hotter droughts. This research highlights areas of both agreement and uncertainty in our predictive understanding of tree die-off from drought, and we suggest that simple forecasts using readily available climate data may soon be within reach for this widely studied conifer species. Yet numerous avenues remain to improve these predictions of tree die-off, including accounting for biophysical characteristics like stand density, soil properties, tree size, and topographic exposure, which are known to influence mortality in many species. The thresholds evaluated here should continue to be
tested in a forward-facing manner, including with independent field observations and local weather station data, to further refine our predictive understanding of tree survival and die-off in an increasingly hotter world.

**Data availability statement**

Data for replicating analyses will be made available on data dryad following acceptance.

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.5061/dryad.t76hf15.

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**Author Contributions**

A W curated the data, led the analysis and draft writing. M D R, D D B, and N C proposed this research, acquired funding, supervised the research, and provided critical input on text, figures, and analyses. S H, N M, and D L also provided critical input on the text, analyses, and figures.

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