

LETTER

Contemporary tree growth shows altered climate memory

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Abstract

Trees are long-lived organisms, exhibiting temporally complex growth arising from strong climatic “memory.” But conditions are becoming increasingly arid in the western USA. Using a century-long tree-ring network, we find altered climate memory across the entire range of a widespread western US conifer: growth is supported by precipitation falling further into the past (+15 months), while increasingly impacted by more recent temperature conditions (−8 months). Tree-ring datasets can be biased, so we confirm altered climate memory in a second, ecologically-sampled tree-ring network. Predicted drought responses show trees may have also become more sensitive to repeat drought. Finally, plots near sites with relatively longer precipitation memory and shorter temperature memory had significantly lower recent mortality rates ($R^2 = 0.61$). We argue that increased drought frequency has altered climate memory, demonstrate how non-stationarity may arise from failure to account for memory, and suggest memory length may be predictive of future tree mortality.

KEYWORDS

climate change, drought legacy, mortality, recovery, resilience

INTRODUCTION

Tree growth is fundamental to the structure and functioning of forested ecosystems, contributing to large terrestrial carbon storage (Bonan, 2008; Ellison et al., 2005). But climate change is impacting tree growth across the globe, bringing increased temperatures, vapour pressure deficits and soil moisture stress (Williams et al., 2013). This has led to longer, more extreme and more frequent droughts, particularly in the western USA (Williams et al., 2020). Major regional droughts occurring after the year 2000 spurred intense research into tree mortality (Breshears et al., 2005; McDowell et al., 2008), the mechanisms of which are still being refined (Adams et al., 2017). However, non-lethal impacts of climate warming on tree physiological processes may significantly impact the forest carbon cycle, namely via altered tree growth rates.

Increased drought stress may impact tree growth in numerous ways, but a key emerging framework—“drought legacies,” or slow recovery of tree growth following drought—shows these impacts to be long-lasting and widespread (Kannenberg et al., 2020). Drought

legacies also have important consequences for terrestrial carbon fluxes (Schwalm et al., 2017), which are not well captured by dynamic global vegetation models (Kolus et al., 2019). A question raised by recent syntheses is: how will increased drought frequency further impact tree growth, such as when repeat drought interrupts drought recovery (Schwalm et al., 2017)? This question has only been partly addressed by comparing tree growth responses to different numbers of short-return-interval droughts (Anderegg et al., 2020; Peltier & Ogle, 2019b; Serra-Maluquer et al., 2021).

Tree-ring syntheses suggest tree growth responses across most forests reflect greater recent moisture limitation (Babst et al., 2019), and there is limited evidence trees are becoming more sensitive (Keen et al., 2021) and less resilient to drought (e.g. Bose et al., 2020; Serra-Maluquer et al., 2018). However, because trees are long-lived organisms, tree growth is complex, exhibiting lagged responses to numerous climate variables (Bose et al., 2021), which are not well-captured by simple correlational approaches (Ogle et al., 2015). Trees integrate climate conditions across multiple years and seasons

through a poorly understood combination of interacting processes including carbon allocation to different organs, carbohydrate storage across multiple years, and hydraulic function and/or damage. We quantify this temporal integration through the concept of “climatic memory” of tree growth (Peltier et al., 2018). These complex temporal dynamics are being considered in terrestrial vegetation models (Guillemot et al., 2017). Temporal lags in growth, however, can sometimes be years longer than considered in models (e.g. Becker, 1989) and the impact of more frequent drought stress on climate memory is unclear. For example, how will the length of climate memory change as “normal” precipitation years become less frequent? Will trees tend to rely on precipitation delivered further in the past?

To quantify the impact of climate change on the climatic memory of tree growth, we leverage all two-needle piñon (*Pinus edulis*) tree-ring width observations in the International Tree Ring Data Bank (“ITRDB network”). *P. edulis* is a widespread, dominant western tree species (West, 1999) well-represented in the ITRDB (Figure 1). We applied a modified version of the stochastic antecedent model (Peltier et al., 2018) to these data. Within this modelling framework, the data are used to infer temporally weighted averages of antecedent precipitation and temperature, and drought conditions that reflect lagged conditions driving tree growth; including a temperature by precipitation interaction captured by the self-calibrating Palmer Drought Severity Index (Peltier & Ogle, 2019b). In a novel approach, we allow the weights to change linearly with time across the 115-year record (1899–2013). We hypothesise (H1) drought is a major driver of shifts in climate memory, and we tested how the response to and recovery from severe drought

has changed over the past century. We also hypothesise (H2) variation in memory length will be associated with mortality risk, and we assessed the mortality rates from nearby Forest Inventory and Analysis (FIA) plots. In line with growing recognition of the non-stationarity of tree growth to climate drivers (Anchukaitis et al., 2006; D'Arrigo et al., 2008; Peltier & Ogle, 2020; Wilmking et al., 2020), we demonstrate the temporal coherence between tree growth and climate is changing. Finally, we conduct a simple analysis demonstrating that non-stationarity may emerge from failure to account for long climate memory.

METHODS

Data sources and preparation

All *Pinus edulis* Engelm. (piñon) ring widths from the ITRDB (~250,000) were downloaded in late 2019 encompassing the entire range of this species (Utah, Arizona, Colorado, and New Mexico). Briefly, the raw ring widths were detrended for age effects via the R package `dpLR` (Bunn, 2008). As in past studies (Peltier & Ogle, 2019a), detrending was accomplished by dividing ring widths by a fitted curve—either modified negative exponential curves or, when this failed, flat lines—to remove age effects (and adjust the core-level mean to be equal to 1), producing ring-width indices (RWI). Alternative detrending approaches (e.g., splines) could have influenced our results, but the goal of this detrending was to preserve ecological variation, as well as low-frequency signals that may be related to climate change. Subsequently, we constructed site “growth” chronologies as the average

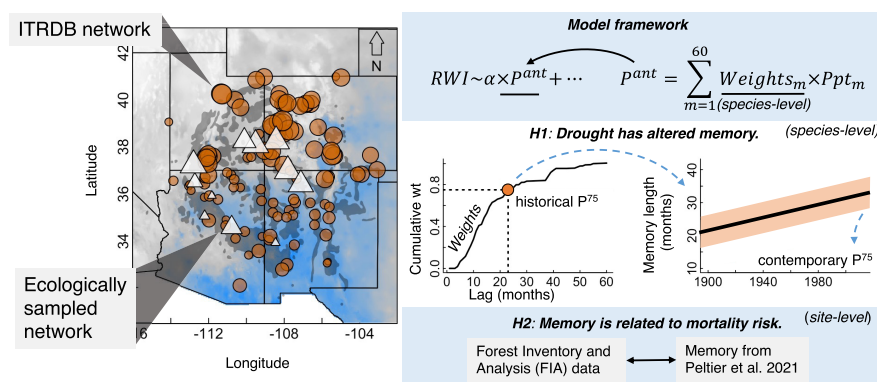


FIGURE 1 Tree-ring networks (left) and key concepts of the analytical framework illustrated for the effects of precipitation (right). We assessed shifts in climate memory in two tree-ring networks to address the hypotheses that (H1) drought has altered climate memory and (H2) memory is related to mortality risk in *Pinus edulis*. Model framework is simplified; see full description in Equations (1)–(3). Inset MAP: The range of *Pinus edulis* (dark grey shading) along with sites in the ITRDB network (orange circles, jittered) and a second ecologically sampled tree-ring network (white triangles) along with summer precipitation (Jul-Sep proportion of MAP, blue shading). Symbol size indicates chronology length, where the shortest ITRDB records end in the 1960s and the longest extend through 2013 (all but one chronology goes back to 1899). All records from the ecologically sampled network extend through 2016, with the shortest beginning in 1930. More details on chronology length are provided in Figure S1. Because we only estimate shifts in memory at the species-level, to address H2, we assess how spatial variation in memory quantified in a different study using the same data (Peltier et al., 2021) is related to mortality in the most recent survey at nearby Forest inventory and analysis (FIA) plots.

of all RWI values (i.e., across cores) in a given year, producing 109 age-detrended chronologies containing a total of 8714 annual ring-width indices. The period covered by this dataset is 1899–2013 (115 years); 11 chronologies include records after 2002.

To address differences in sample depth across time and concerns about over-representation of “sensitive” trees in the ITRDB (Klesse et al., 2018; Nehrbass-Ahles et al., 2014), we repeated our analysis (see *Model description*) with an “ecologically sampled” network of 11 piñon sites across the southwestern US (Peltier et al., 2021). Briefly, we sampled dominant and co-dominant trees of varying sizes and ages at 11 sites in Arizona, New Mexico, Colorado and Utah. Sites were co-located adjacent to FIA (Bechtold & Patterson, 2005) plots (themselves randomly located) to represent a range of landscape and topographical positions. Tree rings from FIA plots have been shown to be less sensitive to climate than ITRDB datasets (Klesse et al., 2018). Eight of the 11 sites include records before 1899; all include records from 1938–2016.

Monthly precipitation and mean monthly temperature (0.5° resolution) were obtained from the PRISM Climate Group (<http://prism.oregonstate.edu>, 2019). Self-calibrating Palmer drought severity index (hereafter, “PDSI,” 0.5° resolution) was obtained from the West Wide Drought Tracker (Abatzoglou et al., 2017). These datasets were downloaded subsequent to October 2019 updates to the PRISM dataset that addressed temporal inconsistency of temperature datasets.

Model description

Our application of the SAM model to tree growth chronologies was modified by Peltier et al. (2018). As in that study, annual growth—chronology-level annual ring-width index (RWI)—is modelled as a linear response to antecedent climate variables. As in previous applications, this is essentially a linear mixed effects approach, where the antecedent climate variables are constructed from weighted averages of monthly climate across the current and preceding 4 years (i.e., up to 4 years prior to the year of ring formation). The unknown “antecedent importance weights” are parameters estimated from the data, allowing for inference on climatic memory (Ogle et al., 2015).

Uniquely here, we allow antecedent weights to change linearly with time (year) across the 115-year record (1900–2013). This allows assessment of how memory, as determined from the weights, has changed during the last century. Because we are investigating changes in the temporal signature (memory) of tree ring width response to climate, rather than the magnitude of that response (sensitivity), changes in mean climate conditions across the record are unlikely to bias our results.

We assumed age-detrended RWI was normally distributed with mean, $\mu_{y,c}$, in year y for site c :

$$\mu_{y,c} = \alpha_{c,1} + \alpha_{c,2}P_{y,c}^{ant} + \alpha_{c,3}T_{y,c}^{ant} + \alpha_{c,4}D_{y,c}^{ant} + \alpha_{c,5}RWI_{y-1,c} \quad (1)$$

the α 's (considered temporally constant) include an intercept (base-line RWI under average climate conditions) and the main effects of three antecedent climate covariates—precipitation (P^{ant}), temperature (T^{ant}) and PDSI (D^{ant})—and a previous year RWI term ($RWI_{y-1,c}$), analogous to an AR(1) effect. PDSI represents an interaction between precipitation and (negative) temperature (Peltier & Ogle, 2019a), thus a $P^{ant} \times T^{ant}$ interaction was omitted.

The three antecedent climate variables are constructed across years y and sites c , where $X_{y-t,m}$ denotes the climate value at month m ($m = 1-12$; Jan-Dec), t years into the past ($t = 0-4$; year of ring formation up to 4 years prior) relative to year y . Because we allow the weights to vary linearly across the record, in relation to year y (see below), we denote the antecedent importance weights as $w_{t,m,y}$. Thus, the antecedent climate variables, $X_{y,c}^{ant}$, are calculated as:

$$X_{y,c}^{ant} = \sum_{t=0}^4 \sum_{m=1}^{12} w_{t,m,y} X_{y-t,m,c} \quad (2)$$

Equation (2) is applied to each site-specific climate variable (where $X^{ant} = P^{ant}$, T^{ant} or D^{ant} , for precipitation, temperature or PDSI); each climate variable gets its own set of weights, w .

Rather than estimating an independent set of importance weights, $w_{t,m,y}$, for each year, y , of the record, which would result in a heavily parameterized model, the weights are linearly interpolated between the first ($y = 1$ for year 1899) and last ($y = 115$ for year 2013) year of the record. Thus, we estimate an independent set of weights only for the first, $w_{t,m,1}$, and last year, $w_{t,m,115}$, of the record, while weights in intermediate years ($y = 2$ through 114) are interpolated as:

$$w_{t,m,y} = w_{t,m,1} + \frac{(w_{t,m,115} - w_{t,m,1})}{114}(y - 1) \quad (3)$$

These calculations are performed within the model and inform the likelihood of the RWI data. The values of the importance weights determine the overall fit of the model to the observed RWI data, and thus weights for the first and last year will be adjusted to produce intermediate-year weights that “best match” the observations. Non-linear interpolation approaches could also be considered in future work.

As in Peltier et al. (2018), we assume the model is unable to detect climate importance at the same resolution farther into the past relative to current climate, and so we estimate weights of increasingly “coarse” time blocks (blocks of months) further into the past (see Figure 2 in Peltier et al., 2018). Monthly weights are constrained between zero and one, and they sum

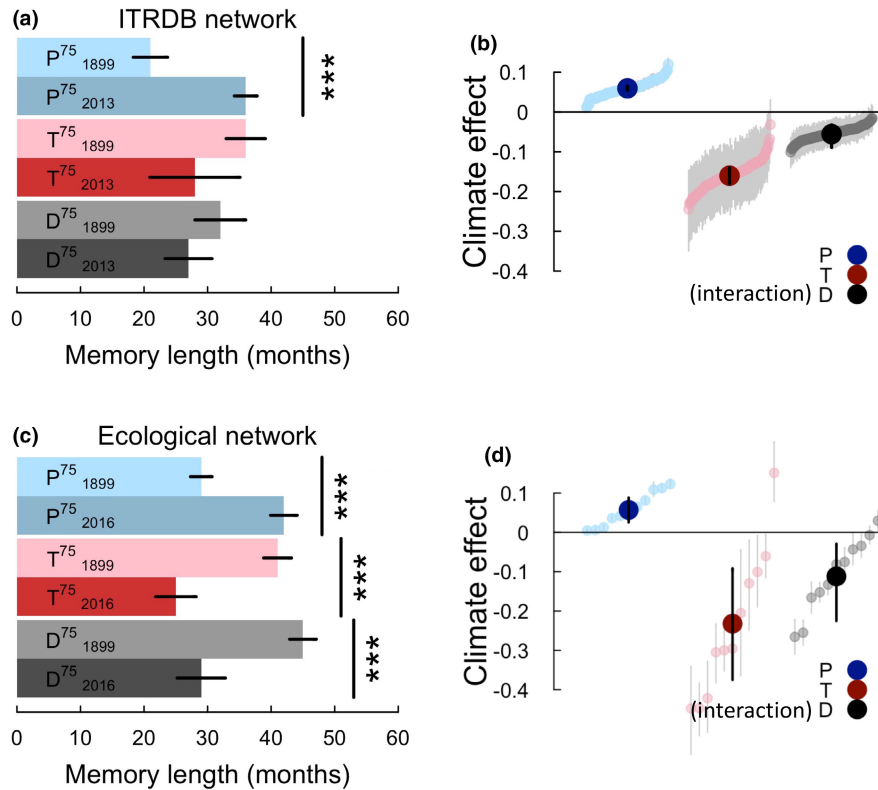


FIGURE 2 Memory of precipitation conditions has lengthened by more than a year in *P. edulis*, while temperature memory has shortened by 8–16 months. (a) Means \pm SD of tree growth memory of precipitation (P^{75} , blues), temperature (T^{75} , reds) and PDSI conditions (D^{75} , greys) at the start (1899, light colours) and end (2013, dark colours) of the 115-year ITRDB record. (b) These results are consistent with those found for a second, ecologically sampled tree-ring network. P^{75} , T^{75} and D^{75} are quantified as the time into the past (in months) at which 75% of the cumulative memory of precipitation, temperature or PDSI on growth is achieved (illustrated in Figure 1). “***” indicates significant changes ($p < 0.001$) in memory length between the beginning and end of the record for a given climatic covariate (P, T or D). (c, d) mean (large circles) and site-level (small circles) climate effects for (c) the ITRDB network and (d) the ecologically sampled network, where vertical lines denote 95% CI (intervals not including zero denote significant effects).

to one across lag years t and months m for each year y and climate variable v ; these constraints enable separation of the effects (α terms) and weights. Finally, annual weights, $W_{t,y}$, were computed by summing all 12 monthly weights within each lag year t for a given year and climate variable. Note a climate variable's weights (e.g., w or W) are meaningless in the absence of a significant associated effect ($\alpha_{c,2}$, $\alpha_{c,3}$ or $\alpha_{c,4}$ in Equation 1); we only interpret weights when associated effects are significant.

To understand how memory has changed, memory length indices P_{75} , T_{75} and D_{75} were defined as the number of months prior to the cessation of ring formation at which the cumulative weights exceed 75% of the total importance weight for precipitation (P), temperature (T) and their interaction (drought index, D). By this definition, only 25% of the impact of P, T or D on growth is driven by conditions preceding P_{75} , T_{75} or D_{75} (that is, further into the past). Thus, at P_{75} months into the past, 75% of the effect of precipitation on growth is achieved. We estimated these quantities at the beginning and end of the record,

including associated uncertainty, within the modelling framework (Figure 1).

Prior specification

The model defined in Equations (1)–(3) was implemented in a hierarchical Bayesian framework, with normal hierarchical priors for site-level effects (α terms) that vary around global means and variances for group of effects. Antecedent importance weights for the first and last year were assigned Dirichlet priors.

Implementation

The model was implemented using JAGS 4.3.0 (Plummer 2003) via the R 3.6.3 (R Core Team, 2021) package rjags (Plummer, 2013) according to standard methodology (3 chains, thinning to obtain ≥ 3000 relatively independent samples, chains assessed for convergence). See the supplement for full JAGS model code.

Analysis of drought recovery

To assess whether the response to severe drought has changed during the last century, ring-width indices (RWI) during 2002–2006 were predicted with fitted model parameters representing memory at the beginning (1899, “historical memory”) and end (2013, “contemporary memory”) of the study record. Thus, we predicted RWI using climate data from the years 2002–2006, using two sets of weights ($w_{t,m,y}$): those from the beginning of the record ($w_{t,m,1}$) reflecting historical climate memory, and those from the end of the record ($w_{t,m,115}$) reflecting contemporary memory. The years 2002–2006 encompass the most severe and warmest drought in the instrumental record for this region (2002, Breshears et al., 2005), plus a 4-year recovery period (average: Anderegg et al., 2015). A second major regional drought occurred in 2006, permitting inference on how the response to repeat drought may have changed.

Altered sensitivity or altered memory?

We also evaluated if altered climate sensitivity (non-stationarity) may emerge from incomplete accounting for altered memory. Thus, we monitored two key quantities in the model: (1) the antecedent temperature covariate (Equation 2), and (2) a “short” antecedent temperature covariate constructed identically to (1) except with a shorter integration period (24 months, compared to 60 months for (1)). For each of the 109 sites, we then regressed tree-growth (RWI) on “long” and “short” temperature covariates during 1899–1955 (first half) and 1956–2013 (second half). All sites have 57 years in the first half of the record (total $n = 6213$), and 31 ± 16 years in the second half of the record (total $n = 3381$). Finally, we compared the mean temperature sensitivities (across sites) between the two halves of the record with a paired t-test under both sets of assumptions about temperature memory (“long” vs. “short”).

Mortality risk assessment

Because the 11 *P. edulis* sites in the ecologically sampled network were collocated adjacent or near to FIA census plots, we used the FIA dataset (Gray et al., 2012; Woudenberg et al., 2010), and site-level, temporally static memory length estimates (e.g. P_{75}) from Peltier et al. (2021) to assess whether variation in memory length across sites was related to local mortality. We note assessing variation across sites in the model in Equations (1) and (2) would have resulted in an overparameterized model. We also assessed these relationships for P_{50} and T_{50} (time into the past at which 50% of P or T effect is reached), and P_{90} and T_{90} (time into the past at which 90% of effect is reached), which have been useful

in previous work (Peltier et al., 2021). We selected the nearest pinon site in the FIA dataset (Table S1, Venturas et al., 2021) with resurvey data and no recent fire (mean distance = 0.06 ± 0.07 degrees, roughly 5–6 km), and compared basal area normalised mortality rate at the first re-census to indices of precipitation and temperature memory length using linear regression in R. Note the model described in Equations (1)–(3) only quantifies shifts in memory at the species-level (average across all sites, Figure 1); a site-level model would be overparameterized. However, this analysis allows us to assess how variation in memory may be linked with mortality risk (H2).

RESULTS

Regression of predicted versus observed RWI yielded $R^2 = 0.65$ and a slope of 1.02, indicating low bias; model RMSE was 0.24.

Altered memory length

Contemporary tree growth shows longer memory of precipitation conditions and shorter memory of temperature conditions relative to historical tree growth. In the ITRDB network, precipitation memory length became on average 15 months longer, with shorter memory a century ago (e.g., $P_{75} = 21$ months) compared to contemporary memory ($P_{75} = 36$ months; Figure 2a; $p < 0.001$). In contrast, there was a trend for contemporary temperature memory to be about 8 months shorter (from $T_{75} = 36$ months to 28 months; Figure 2a; n.s.), which was 6 months shorter than the 2.5th percentile historical temperature memory (32 months). PDSI memory (D_{75}) changed little (Figure 2a), indicating that the interactive effect of precipitation and temperature was relatively stable across the century-long record (see also Figure 3c). Trees responded positively to precipitation and negatively to temperature, with a negative PDSI (interaction) effect (Figure 2b), consistent with Peltier et al. (2018). Consistent with ITRDB results, changes in memory were similar, or even greater in the ecologically sampled network, where P_{75} became 13 months longer ($p < 0.001$) and T_{75} became 16 months shorter ($p < 0.001$, Figure 2b). Effect signs and magnitudes (Figure 3c) were consistent with previous applications of similar models to *P. edulis* in the ITRDB (Figure S2, Peltier & Ogle, 2019a, Peltier et al., 2018) and in the ecological network (Peltier et al., 2021).

Unlike in the ITRDB network, PDSI memory in the ecological network became 16 months shorter ($p < 0.001$, Figure 2b). The PDSI effect can be interpreted as an interaction effect describing increased sensitivity to precipitation under warm conditions (PDSI product is derived from same PRISM dataset, Peltier & Ogle, 2019a). That

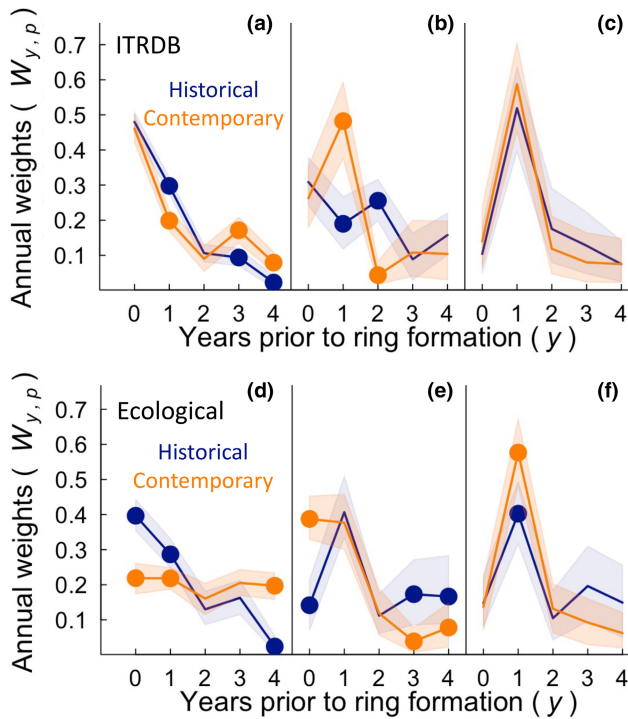


FIGURE 3 Significant shifts in annual importance weights reflect decreased reliance of contemporary tree growth on recent precipitation (left column), and enhanced detriment of more recent temperature conditions (middle column). Annual importance weights represent the relative importance of climate conditions occurring in different years towards the overall response of growth to a given climate covariate (note negative temperature effects; Figure 2c,d). Weights that significantly changed during the record are denoted by filled circles ($p < 0.05$); shading denotes 95% credible intervals. Weights are shown for (a, d) precipitation (P^{ant}), (b, e) temperature (T^{ant}) and (c, f) their interaction via PDSI (d^{ant}) at the beginning (1899, blue lines and symbols with blue shading) and end (2013, orange lines and symbols with orange shading) of the tree-ring record. Estimates are shown for trees from (a–c) the ITRDB network and (d–f) the ecologically sampled network (see Figure 1). Importance weights are estimated for 0, 1, 2, 3 and 4 years prior to ring formation, where 0 represents the year of ring formation.

is, if we interpreted the PDSI effect as simply the effect of drought, a negative effect (Figure 3c,d) is nonsensical, implying higher growth under warm-dry conditions (negative PDSI), and this ignores the direct effects of precipitation and temperature. Thus, consistent with past applications, the shift in memory of PDSI indicates increased sensitivity to past precipitation when more recent conditions are warmer—essentially, memory of this interactive effect tracks changes in temperature memory (Figure 2).

Altered memory pattern

Shifts in the temporal pattern of memory (Figure 3) highlight key time periods driving shifts in climate memory length. For example, in the ITRDB network, longer precipitation memory in contemporary tree

growth is driven by decreased importance of prior year precipitation, coupled with increased importance of precipitation falling 3–4 years prior to the growing season (Figure 3a). At the monthly resolution, we also found reduced importance of previous winter precipitation, and increased importance of pre-monsoon (spring) and fall temperature conditions (Figure S3). Similar but more extreme patterns were observed in the ecologically sampled network, where the response of contemporary tree growth to precipitation is muted, due to a large decrease in importance of current year precipitation (Figure 3d). For temperature, in the ITRDB network, we find increased importance of prior year temperature with decreased importance of 2 years prior temperature (Figure 3b). In the ecological network, we find increased importance of current year temperature and reductions in importance of 3 years prior temperature (Figure 3e). Increased importance of recent PDSI in the ecological network indicates a greater importance of moisture during hot periods, consistent with the increased importance of recent temperature conditions (Figure 3f).

Altered drought recovery

Shifts in memory length, while having no impact on drought-year growth, resulted in reduced predicted growth rates in the second and third years following the 2002 drought for most sites (Figure 4). Predicted RWI based on historical (1899) and contemporary (2013) tree growth parameters is nearly identical during the predicted drought year (Figure 4a,b). However, contemporary tree growth at >60% of ITRDB sites was predicted to be reduced in the second and third years after drought compared to historical tree growth (Figure 4c). Contemporary tree growth was also predicted to be lower (compared to historical tree growth) in response to repeat drought (2006 conditions) at more than half the ITRDB sites (Figure 4c). Thus, at a majority of sites, tree growth with contemporary climate memory was predicted to be reduced following drought events compared to growth with historical climate memory, and also result in greater growth reductions during subsequent repeat droughts (2006 was another drought event, Figure 4a,c).

Memory length and mortality risk

We also found spatial variation in memory length was associated with mortality risk. Mortality rates tended to be lower in FIA plots near sites in the ecological network with comparatively long precipitation memory and comparatively short temperature memory (Figure 5). We emphasize this analysis used mean memory lengths across the entire record estimated in Peltier et al. (2021) using an

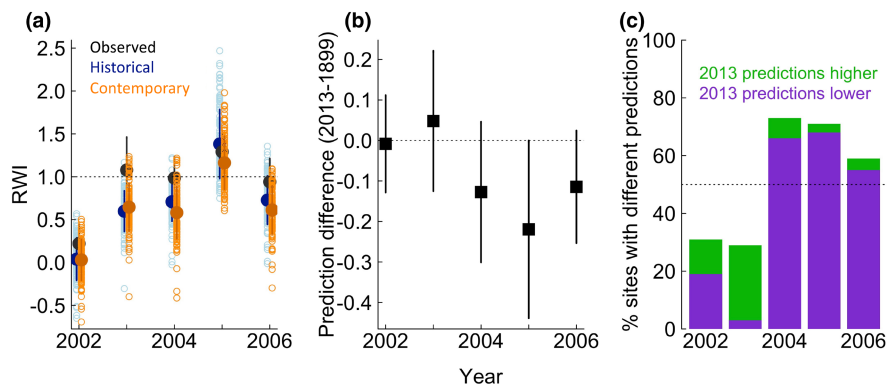


FIGURE 4 Reduction of predicted contemporary (2013) tree growth during recovery from drought at a majority of sites suggests drought legacies are more severe in contemporary *P. edulis*. (a) Predicted ring-width index (RWI) during and following the 2002 drought event using importance weights representative of historical (blue; parameters in 1899) and contemporary (orange; parameters in 2013) tree growth, based on estimates obtained by modelling the ITRDB tree-ring data. Predicted RWI during each year is overlaid with the observed RWI (dark grey). Predicted RWI is based on parameters that are informed by all data and chronologies from the ITRDB data, whereas the observed RWI only represents chronologies that extended to 2006 (6 of 114). (b) Differences between predictions (contemporary – Historical) for each year from 2002–2006. (c) Percentage of sites with higher (green) or lower (purple) predicted contemporary (2013) tree growth compared to historical (1899) tree growth.

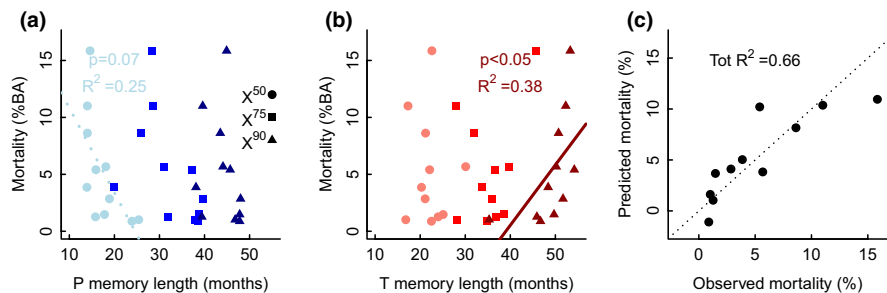


FIGURE 5 Long precipitation memory and short temperature memory are associated with lower mortality in nearby FIA plots. Different site-level memory length indices (circles: P^{50} and T^{50} ; squares: P^{75} and T^{75} ; triangles: P^{90} and T^{90}) for (a) precipitation and (b) temperature are shown for plots in the ecological tree-ring network (from Peltier et al., 2021). In (c), combined regression with P^{50} , T^{90} and their interaction explained 61% of the variation in mortality rate ($p < 0.05$ for all effects, $R^2 = 0.61$).

analogous (but temporally static) memory model. For example, 31% of the variation in FIA plot mortality was explained by P^{50} , where mortality declined with increasing memory length ($p < 0.05$, Figure 5a); the relationship with P^{75} was similar. In contrast, there was weak evidence for increasing FIA plot mortality rate with increasing T^{90} (Figure 5b). A combined model using the best two predictors (P^{50} , T^{90}) explained 61% of the variation in mortality (all effects significant, $p < 0.05$). The interaction term in this model was negative ($p < 0.05$), indicating that as temperature memory length (T^{90}) becomes shorter, the beneficial effect of precipitation memory length (P^{50}) on mortality rate becomes weaker.

Altered sensitivity only when memory is ignored

Temperature sensitivity of tree growth was only significantly different between time periods (1899–1955 vs 1956–2013) when long memory was ignored (Figure 6). In both scenarios, temperature sensitivity had a more

negative effect on tree growth in the latter half of the record (1956–2013). However, this change was only significant when a 24-month “short” temperature lag was considered (rather than the 60 months used in the full model).

DISCUSSION

Contemporary tree growth in *P. edulis* shows altered climate memory in two different tree-ring networks since the end of the 19th century. Tree growth sensitivity to climate is temporally variable (Peltier & Ogle, 2020; Wilmking et al., 2020), and syntheses show shifts in the response of tree growth to climate following disturbance such as severe drought (Anderegg et al., 2015; Peltier et al., 2016) or to changes in mean conditions at a given site (D'Arrigo et al., 2008). But climatic memory of tree growth has also been shown to be temporarily altered by more frequent drought (Peltier & Ogle, 2019b). This study expands upon these results by showing that

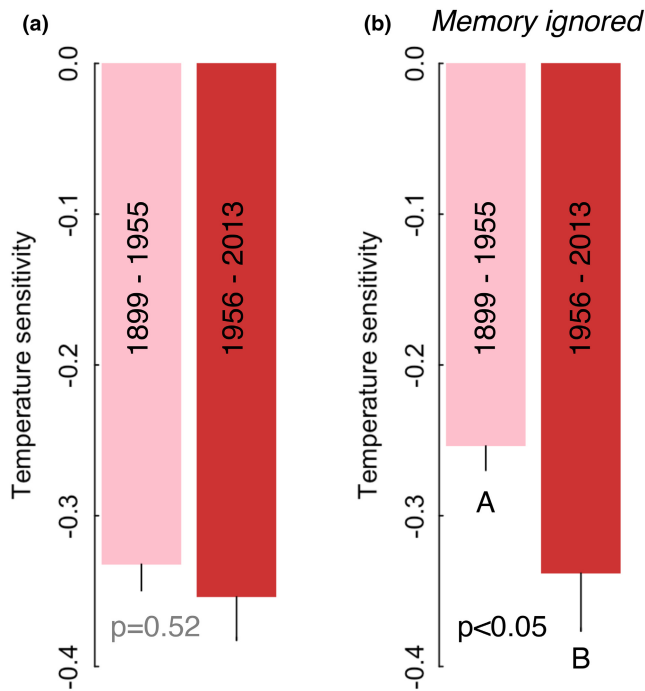


FIGURE 6 Ignoring long climate memory increases apparent changes in climate (temperature) sensitivity. We compared site-level effects of temperature on tree-ring width during the first and second halves of the 115-year record. In (a), we used the 60-month lag period applied in this study to produce antecedent climate covariates; in (b) we only used the preceding 24 months (2 years). Increased contemporary sensitivity to temperature only emerges because a 24-month integration period fails to capture the full historical temperature response in [Figure 3b](#).

climatic memory has undergone directional change in the southwestern USA, with 45–71% longer precipitation memory (P_{75}) and 22–39% shorter temperature memory since 1899 ([Figure 2](#)). Shifts to longer precipitation and shorter temperature memory may reduce mortality risk ([Figure 5](#)), depending upon the interactions of beneficial (e.g., NSC remobilisation) and detrimental (e.g., hydraulic damage) adjustments. As shifts in both precipitation and temperature memory length have compelling physiological interpretations (discussed below), these indices could potentially be useful metrics to assess future tree mortality risk.

Contemporary tree growth exhibits temporal patterns in memory that are characteristic of drought. For example, previous work has shown multiple conifer species in the western USA, including *P. edulis*, exhibit longer precipitation memory (e.g. [Figure 3a,d](#)) and shorter temperature memory (e.g. [Figure 3b,e](#)) during transient drought periods (Peltier & Ogle, 2019b, a). Here, contemporary tree growth is less reliant on recent winter precipitation ([Figure S3](#)), historically a key driver of growth in conifers in the western USA (Peltier et al., 2018) but now less reliable due to frequent regional drought. Contemporary tree growth is also more negatively impacted by warmer conditions during the pre-monsoon and late fall, compared to historical tree growth in the early 1900s

([Figure S3](#)). Decreased reliance on winter precipitation and increased negative impacts of pre-monsoon (Apr-Jun) and late fall temperature ([Figure S3](#)) are also both consistent with how trees respond to antecedent climate during drought periods in this region (Peltier & Ogle, 2019a, 2019b). Finally, increased importance of recent PDSI in the ecological network ([Figure 3f](#)) indicates a greater importance of moisture during hot periods (interactive effect is explained in Peltier & Ogle, 2019a, 2019b), consistent with the increased importance of recent temperature conditions.

Thus, contemporary tree growth shows a clear “fingerprint” of drought—altered climate memory over the last century is a symptom of increasingly arid climate conditions (Williams et al., 2013, 2020). Consistent with this interpretation, contemporary tree growth at most sites is predicted to be lower following single or repeat drought (larger drought legacies) compared to historical tree growth ([Figure 4a,c](#)). This might suggest altered memory is a symptom of physiological impairment, as reduced growth commonly precedes mortality in gymnosperms (Cailleret et al., 2017). However, sites with longer precipitation memory and shorter temperature memory across the entire record might have a lower mortality risk ([Figure 5](#)), consistent with previous work showing *P. edulis* trees most sensitive to climate (i.e., short memory) may be at higher risk of mortality (Ogle et al., 2000), suggesting these memory shifts could confer drought resilience. We suggest both of these interpretations can simultaneously be correct: shifts in memory are consistent with expectations from both beneficial physiological adjustments (carbon allocation changes) and physiological impairment (hydraulic damage). But even if these shifts confer short-term resilience, they may not be sufficient to prevent mortality under long-term increases in drought stress. For example, ongoing regional mortality in species previously considered to be extremely drought tolerant (*Juniperus* spp., Kannenberg et al., 2021) suggests the cumulative stress of increased drought frequency may yield future surprises.

Of the physiological mechanisms often posited to underlie climatic memory—long-term non-structural carbohydrate (NSC) storage (Carbone et al., 2013), lasting hydraulic damage (Trugman et al., 2018), access to water resources built up over multiple years (Rempe & Dietrich, 2018), or multi-year needle function (Peltier et al., 2016)—each would be influenced by more frequent drought stress. For example, more frequent drought would reduce NSC available to support subsequent growth, decrease functional sapwood area through increased xylem embolism, deplete deep soil moisture resources, and damage older, potentially hydraulically vulnerable needle cohorts. However, dry conditions are increasingly associated with unusually warm conditions (Williams et al., 2013), which would tend to compound these impacts through increased evaporative demand (Grossiord et al., 2020; McDowell

et al., 2016). Our results are consistent with these hypothesised impacts. For example, longer precipitation memory suggests greater reliance on older NSC reserves formed further into the past. Radiocarbon measurements of NSC have shown that trees mobilize increasingly older carbon reserves under severe or lethal stress (Muhr et al., 2018). Carbon and water status are ultimately linked, and high temperature and moisture stress would also lead to increased cavitation stress (Sevanto et al., 2014). Shortened temperature and/or PDSI memory is consistent with increased negative impacts of more frequent high-temperature stress under low precipitation conditions (e.g., increased cavitation events). Reduced canopy moisture supply following cavitation would tend to limit tree carbon assimilation in subsequent years (Trugman et al., 2018), reducing a tree's ability to take advantage of moisture pulses. Persistent declines in the amount of available soil moisture are also well supported by multi-year drawdowns of regional water reservoirs (Udall & Overpeck, 2017), comparisons with paleoclimate (Cook et al., 2004; Meko et al., 2007), and isotopic water sourcing in Southwest conifers (Szejner et al., 2020).

There are a number of potential explanations for altered climate memory, larger drought legacies and increased vulnerability to repeat drought in contemporary tree growth found here. First, only a subset of the chronologies extend through the 2000s droughts (Figure 1), indicating the potential for some trees to have died during the century long record, and it is not known how these trees would have responded to contemporary climate. However, because predictions are for all sites (not just those with observations extending into the 2000s), and because the ecologically sampled network showed consistent or more extreme changes in memory (all chronologies run through 2016, Figure 1), we consider our results robust to time-series length. Second, trees impacted by more frequent drought may have altered carbon allocation, for example, increased allocation to roots or canopy, or decreased respiration under more frequent drought stress (Hagedorn et al., 2016; Kannenberg et al., 2019). Altered carbon allocation may also emerge from drought-induced canopy dieback (i.e. Jump et al., 2017), but each of these carbon allocation changes might increase or decrease tree resilience to future drought. Third, absolute reduction of sapwood area due to cavitation would likely increase tree vulnerability to future drought events (Trugman et al., 2018). Fourth, changes in NSC dynamics, where trees reduce respiration rates and increasingly prioritise storage of NSC, or maintenance of older tissues (deeper sapwood) containing old NSC, could explain longer drought recoveries and longer precipitation memory. Finally, as these tree-ring datasets primarily comprise dominant or co-dominant trees, ontogeny or changes in tree size could explain increased vulnerability to drought in contemporary

trees (Bennett et al., 2015). Though older trees are likely to be more deeply rooted, older trees are likely most severely impacted by hydraulic damage due to reliance on narrower, more numerous tree rings to support the same relative sapwood area as younger trees (Trugman et al., 2018). We posit that reduction in sapwood area (via cavitation), changes in NSC storage and/or reliance on old NSC, and interactions with tree size are most plausible. We note these physiological mechanisms would tend to be amplified by management leading to higher density stands (e.g., grazing and fire exclusion, Margolis, 2014), effectively reducing available soil water (Heilman et al., 2022). There may also be unmeasured changes in stand density, perhaps due to past mortality, that might influence climate responses.

While tree growth is typically well explained by current and previous-year climate, if widespread and frequent droughts persist across the western USA, we may expect weaker correlation between tree-ring widths and previous-year precipitation at the regional scale. While past work has shown loss of correlation between variability in tree growth and temperature indices, that is, “divergence” (Carrer & Urbinati, 2006; D'Arrigo et al., 2008), or increased sensitivity to drought (Keen et al., 2021), our results show divergence in the temporal synchrony between growth and climate may also be widespread, likely due to warmer and drier conditions. Furthermore, we demonstrate altered sensitivity to climate conditions may be more evident in models that do not account for long climate memory (Figure 6), where shifts in importance to more recent temperature conditions (Figure 2b) manifest as increased sensitivity (Figure 6b). While non-stationarity likely arises from both changes in sensitivity and memory, this highlights that how we conceptualise tree growth has implications for our ability to capture responses to both transient events (e.g. drought legacies are reduced when accounting for memory: Peltier & Ogle, 2019b) and long-term climate change (Figure 6). Compared to other widespread or economically important USA conifers (e.g. *P. ponderosa* and *Pseudotsuga menziesii*), *P. edulis* is relatively adapted to dry conditions. Thus, this fingerprint of global climate change on the ring widths of trees from a single species across its entire range suggests these effects could be prevalent in other, more drought-sensitive western USA tree species (Stanke et al., 2021), and perhaps, in coniferous forests globally.

AUTHOR CONTRIBUTIONS

DP conceived the study, DP and KO wrote and implemented the model, and DP analysed the output. WRLA contributed to the FIA mortality analysis. JG contributed to the figure design. DP wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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DATA AVAILABILITY STATEMENT

This paper uses no new data. All data was obtained via the International Tree Ring Data Bank, PRISM climate group, the West Wide Drought Tracker, or The Forest Inventory and Analysis (FIA) Program of the U.S. Forest Service (FIA data reported in supplement). Tree-ring and climate datasets are archived on Zenodo, DOI: <https://doi.org/10.5281/zenodo.7117401>.

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REFERENCES

- Abatzoglou, J.T., McEvoy, D.J. & Redmond, K.T. (2017) The West wide drought tracker: drought monitoring at fine spatial scales. *Bulletin of the American Meteorological Society*, 98, 1815–1820.
- Adams, H.D., Zeppel, M.J., Anderegg, W.R., Hartmann, H., Landhäusser, S.M., Tissue, D.T. et al. (2017) A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nature ecology & evolution*, 1, 1285–1291.
- Anchukaitis, K.J., Evans, M.N., Kaplan, A., Vaganov, E.A., Hughes, M.K., Grissino-Mayer, H.D. et al. (2006) Forward modeling of regional scale tree-ring patterns in the southeastern United States and the recent influence of summer drought. *Geophysical Research Letters*, 33, 33.
- Anderegg, W.R., Trugman, A.T., Badgley, G., Konings, A.G. & Shaw, J. (2020) Divergent forest sensitivity to repeated extreme droughts. *Nature Climate Change*, 10, 1091–1095.
- Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M. et al. (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349, 528–532.
- Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P. & Frank, D.C. (2019) Twentieth century redistribution in climatic drivers of global tree growth. *Science Advances*, 5, eaat4313.
- Bechtold, W.A. & Patterson, P.L. (2005) *The enhanced forest inventory and analysis program—national sampling design and estimation procedures*. Asheville, North Carolina: USDA Forest Service, Southern Research Station.
- Becker, M. (1989) The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. *Canadian Journal of Forest Research*, 19, 1110–1117.
- Bennett, A.C., McDowell, N.G., Allen, C.D. & Anderson-Teixeira, K.J. (2015) Larger trees suffer most during drought in forests worldwide. *Nature Plants*, 1, 1–5.
- Bonan, G.B. (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, 320, 1444–1449.
- Bose, A.K., Gessler, A., Bolte, A., Bottero, A., Buras, A., Cailleret, M. et al. (2020) Growth and resilience responses of scots pine to extreme droughts across Europe depend on predrought growth conditions. *Global Change Biology*, 26, 4521–4537.
- Bose, A.K., Rigling, A., Gessler, A., Hagedorn, F., Brunner, I., Feichtinger, L. et al. (2021) Lessons learned from a long-term irrigation experiment in a dry scots pine forest: impacts on traits and functioning. *Ecological Monographs*, 92, e1507.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G. et al. (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*, 102, 15144–15148.
- Bunn, A.G. (2008) A dendrochronology program library in R (dplR). *Dendrochronologia*, 26, 115–124.
- Cailleret, M., Jansen, S., Robert, E.M., Desoto, L., Aakala, T., Antos, J.A. et al. (2017) A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology*, 23, 1675–1690.
- Carbone, M.S., Czimczik, C.I., Keenan, T.F., Murakami, P.F., Pederson, N., Schaberg, P.G. et al. (2013) Age, allocation and availability of nonstructural carbon in mature red maple trees. *New Phytologist*, 200, 1145–1155.
- Carrer, M. & Urbinati, C. (2006) Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*. *New Phytologist*, 170, 861–872.
- Cook, E.R., Woodhouse, C.A., Eakin, C.M., Meko, D.M. & Stahle, D.W. (2004) Long-term aridity changes in the western United States. *Science*, 306, 1015–1018.
- R Core Team (2021). R: a language and environment for statistical computing. R Foundation for Statistical Computing, 2015.
- D'Arrigo, R., Wilson, R., Liepert, B. & Cherubini, P. (2008) On the 'divergence problem' in northern forests: a review of the tree-ring evidence and possible causes. *Global and Planetary Change*, 60, 289–305.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R. et al. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, 3, 479–486.
- Gray, A.N., Brandeis, T.J., Shaw, J.D., McWilliams, W.H. & Miles, P. (2012) Forest inventory and analysis database of The United States of America (FIA). In: Dengler, J., Oldeland, J., Jansen, F., Chytrý, M., Ewald, J., Finckh, M. et al. (Eds.) *Vegetation databases for the 21st century. Biodiversity and ecology*, Vol. 4. Hamburg, Germany: Biodiversity, Evolution and Ecology of Plants, pp. 225–231.
- Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T. et al. (2020) Plant responses to rising vapor pressure deficit. *New Phytologist*, 226, 1550–1566.
- Guillemot, J., Francois, C., Hmimina, G., Dufrène, E., Martin-StPaul, N.K., Soudani, K. et al. (2017) Environmental control of carbon allocation matters for modelling forest growth. *New Phytologist*, 214, 180–193.
- Hagedorn, F., Joseph, J., Peter, M., Luster, J., Pritsch, K., Geppert, U. et al. (2016) Recovery of trees from drought depends on below-ground sink control. *Nature plants*, 2, 16111.
- Heilman, K.A., Dietze, M.C., Arizpe, A.A., Aragon, J., Gray, A., Shaw, J.D. et al. (2022) Ecological forecasting of tree growth: regional fusion of tree-ring and forest inventory data to quantify drivers and characterize uncertainty. *Global Change Biology*, 28, 2442–2460.

- Jump, A.S., Ruiz-Benito, P., Greenwood, S., Allen, C.D., Kitzberger, T., Fensham, R. et al. (2017) Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Global Change Biology*, 23, 3742–3757.
- Kannenberg, S.A., Driscoll, A.W., Malesky, D. & Anderegg, W.R. (2021) Rapid and surprising dieback of Utah juniper in the southwestern USA due to acute drought stress. *Forest Ecology and Management*, 480, 118639.
- Kannenberg, S.A., Novick, K.A., Alexander, M.R., Maxwell, J.T., Moore, D.J., Phillips, R.P. et al. (2019) Linking drought legacy effects across scales: from leaves to tree rings to ecosystems. *Global Change Biology*, 25, 2978–2992.
- Kannenberg, S.A., Schwalm, C.R. & Anderegg, W.R.L. (2020) Ghosts of the past: how drought legacy effects shape forest functioning and carbon cycling. *Ecology Letters*, 23, 891–901.
- Keen, R.M., Voelker, S.L., Wang, S.-Y.S., Bentz, B.J., Goulden, M.L., Dangerfield, C.R. et al. (2021) Changes in tree drought sensitivity provided early warning signals to the California drought and forest mortality event. *Global Change Biology*, 28, 1119–1132.
- Klesse, S., DeRose, R.J., Guiterman, C.H., Lynch, A.M., O'Connor, C.D., Shaw, J.D. et al. (2018) Sampling bias overestimates climate change impacts on forest growth in the southwestern United States. *Nature Communications*, 9, 1–9.
- Kolus, H.R., Huntzinger, D.N., Schwalm, C.R., Fisher, J.B., McKay, N., Fang, Y. et al. (2019) Land carbon models underestimate the severity and duration of drought's impact on plant productivity. *Scientific Reports*, 9, 2758.
- Margolis, E.Q. (2014) Fire regime shift linked to increased forest density in a piñon–juniper savanna landscape. *International Journal of Wildland Fire*, 23, 234–245.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T. et al. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719–739.
- McDowell, N.G., Williams, A.P., Xu, C., Pockman, W.T., Dickman, L.T., Sevanto, S. et al. (2016) Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nature Climate Change*, 6, 295–300.
- Meko, D.M., Woodhouse, C.A., Baisan, C.A., Knight, T., Lukas, J.J., Hughes, M.K. et al. (2007) Medieval drought in the upper Colorado River basin. *Geophysical Research Letters*, 34, L10705.
- Muhr, J., Trumbore, S., Higuchi, N. & Kunert, N. (2018) Living on borrowed time—Amazonian trees use decade-old storage carbon to survive for months after complete stem girdling. *New Phytologist*, 220, 111–120.
- Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R. et al. (2014) The influence of sampling design on tree-ring-based quantification of forest growth. *Global Change Biology*, 20, 2867–2885.
- Ogle, K., Barber, J.J., Barron-Gafford, G.A., Bentley, L.P., Cable, J.M., Huxman, T.E. et al. (2015) Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters*, 18, 221–235.
- Ogle, K., Whitham, T.G. & Cobb, N.S. (2000) Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology*, 81, 3237–3243.
- Peltier, D.M., Guo, J., Nguyen, P., Bangs, M., Wilson, M., Samuels-Crow, K. et al. (2021) Temperature memory and non-structural carbohydrates mediate legacies of a hot drought in trees across the southwestern US. *Tree Physiology*, 42, 71–85.
- Peltier, D.M. & Ogle, K. (2019a) Legacies of La Niña: north American monsoon can rescue trees from winter drought. *Global Change Biology*, 25, 121–133.
- Peltier, D.M. & Ogle, K. (2019b) Legacies of more frequent drought in ponderosa pine across the western United States. *Global Change Biology*, 25, 3803–3816.
- Peltier, D.M. & Ogle, K. (2020) Tree growth sensitivity to climate is temporally variable. *Ecology Letters*, 23, 1561–1572.
- Peltier, D.M.P., Barber, J.J. & Ogle, K. (2018) Quantifying antecedent climatic drivers of tree growth in the southwestern US. *Journal of Ecology*, 106, 613–624.
- Peltier, D.M.P., Fell, M. & Ogle, K. (2016) Legacy effects of drought in the southwestern United States: a multi-species synthesis. *Ecological Monographs*, 86, 312–326.
- Plummer, M. et al. (2003). JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: *Proceedings of the 3rd international workshop on distributed statistical computing*. Vienna, p. 125.
- Plummer, M. (2013). rjags: Bayesian graphical models using MCMC. R package version 3–10.
- Rempe, D.M. & Dietrich, W.E. (2018) Direct observations of rock moisture, a hidden component of the hydrologic cycle. *Proceedings of the National Academy of Sciences*, 115, 2664–2669.
- Schwalm, C.R., Anderegg, W.R., Michalak, A.M., Fisher, J.B., Biondi, F., Koch, G. et al. (2017) Global patterns of drought recovery. *Nature*, 548, 202–205.
- Serra-Maluquer, X., Granda, E., Camarero, J.J., Vilà-Cabrera, A., Jump, A.S., Sánchez-Salguero, R. et al. (2021) Impacts of recurrent dry and wet years alter long-term tree growth trajectories. *Journal of Ecology*, 109, 1561–1574.
- Serra-Maluquer, X., Mencuccini, M. & Martínez-Vilalta, J. (2018) Changes in tree resistance, recovery and resilience across three successive extreme droughts in the Northeast Iberian Peninsula. *Oecologia*, 187, 343–354.
- Sevanto, S., McDowell, N.G., Dickman, L.T., Pangle, R. & Pockman, W.T. (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment*, 37, 153–161.
- Stanke, H., Finley, A.O., Domke, G.M., Weed, A.S. & MacFarlane, D.W. (2021) Over half of western United States' most abundant tree species in decline. *Nature Communications*, 12, 1–11.
- Szejner, P., Belmecheri, S., Ehleringer, J.R. & Monson, R.K. (2020) Recent increases in drought frequency cause observed multi-year drought legacies in the tree rings of semi-arid forests. *Oecologia*, 192, 241–259.
- Trugman, A.T., Detto, M., Bartlett, M.K., Medvigy, D., Anderegg, W.R.L., Schwalm, C. et al. (2018) Tree carbon allocation explains forest drought-kill and recovery patterns. *Ecology Letters*, 21, 1552–1560.
- Udall, B. & Overpeck, J. (2017) The twenty-first century Colorado River hot drought and implications for the future. *Water Resources Research*, 53, 2404–2418.
- Venturas, M.D., Todd, H.N., Trugman, A.T. & Anderegg, W.R. (2021) Understanding and predicting forest mortality in the western United States using long-term forest inventory data and modeled hydraulic damage. *New Phytologist*, 230, 1896–1910.
- West, N.E. (1999) Distribution, composition, and classification of current juniper-pinyon woodlands and savannas across western North America. In: *Ecology and management of pinon–juniper communities within the interior West*. Ogden, UT: USDA, Forest Service, Rocky Mountain Research Station, pp. 20–23.
- Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M. et al. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, 3, 292–297.
- Williams, A.P., Cook, E.R., Smerdon, J.E., Cook, B.I., Abatzoglou, J.T., Bolles, K. et al. (2020) Large contribution from anthropogenic warming to an emerging north American megadrought. *Science*, 368, 314–318.
- Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C. et al. (2020) Global assessment of relationships between climate and tree growth. *Global Change Biology*, 26, 3212–3220.
- Woudenberg, S.W., Conkling, B.L., O'Connell, B.M., LaPoint, E.B., Turner, J.A. & Waddell, K.L. (2010) The Forest inventory and

analysis database: database description and users manual version 4.0 for phase 2. In: *Gen. Tech. Rep. RMRS-GTR-245*, Vol. 245. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station, p. 336.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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