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RESEARCH HIGHLIGHT

Still recovering or just remembering? To understand drought legacies, modelling choices matter

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A study by Anderegg et al. (2015) sparked renewed interest in understanding long-term impacts of drought on tree growth, as evidenced by the surge of papers in the past 7–8 years focused on quantifying 'drought legacies' in tree growth, including multiple reviews (Kannenberg et al., 2020; Peltier & Ogle, 2020). Others have raised the point that this term enjoyed broader use earlier in other ecosystem-centric contexts (Müller & Bahn, 2022; Vilonen et al., 2022). Without descending into a dispute over jargon and semantics, it is worth interrogating what we mean by 'drought legacy' and how we model and quantify such legacy effects. Unfortunately, a survey of the literature suggests there is little consensus on how to model or quantify such phenomena. Klesse et al. (2022) presents a very detailed and rigorous treatment of the statistical complexities of tree rings, and how such complexities can interfere with quantification of drought legacies. This study emphasizes the importance of interrogating our statistical models, demonstrating there is clear need for more nuanced treatment of tree growth, especially when using tree rings.

The Klesse et al. (2022) study provides a detailed analysis, using both observed and simulated data, that highlights properties of tree-ring time series that can impact conclusions about drought legacies. Inspired by this study, we see four major outcomes deserving wider attention in the community: (1) autocorrelation in tree-ring time series; (2) treatment of pre- and postdrought conditions; (3) individual tree idiosyncrasy; and (4) differentiating climate memory and legacies. Our reading of the literature suggests points (1)–(4) are accounted for inconsistently. While some of these issues are highlighted in Klesse et al. (2022), particularly (1), (3) and (4), we expand discussion of these themes to suggest a more nuanced treatment of tree-ring modelling, and highlight implications for our understanding of tree growth responses to drought.

First, the major message of the Klesse et al. (2022) study: how we account for and treat autocorrelation in tree-ring time series has major implications for our ability to quantify drought legacies. Attributing less temporal variation in tree-ring width to autocorrelation (or ignoring it) will result in the detection of apparently larger drought legacies. Idealized legacy effects from different modelling approaches are depicted in Figure 1, such as from Anderegg et al. (2015) and the results from Klesse et al. (2022), where explicit accounting for autocorrelation reduces the mean magnitude of drought legacies ('SEA with AR model'). We are more likely to find reduced growth in years after drought if growth is positively autocorrelated; that is, growth is often low (narrow rings) in the year of the drought, and with positive autocorrelation growth after drought is expected to be similarly low. What does this mean for our understanding of the long-term impacts of drought on tree growth? And, does this suggest long-term impacts of drought are small? We return to these questions later, but the treatment of autocorrelation has been inconsistent in previous work, making it challenging to compare results among past studies.

Second, treatment of pre- and postdrought climate is essential, where our definition of 'normal' has implications for how 'abnormal' postdrought growth appears. While not discussed in Klesse et al. (2022), we argue that analyses should account for the role of postdrought climate in recovery. This is because wetter years may lead to faster recovery, while drier years (perhaps more common in the western United States) may lead to prolonged impairment. The most common approach for quantifying drought legacies globally is

This manuscript is a comment on the recent article: "Legacy effects in radial tree growth are rarely significant after accounting for biological memory." By Stefan Klesse et al. (2022) in the *Journal of Ecology*.

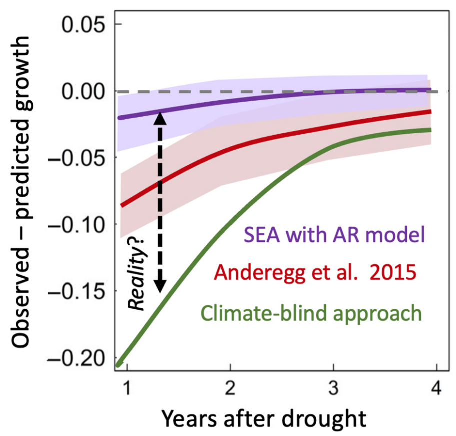

FIGURE 1 Many modelling approaches exist for analysing tree-ring time series, but detailed accounting for autocorrelation and memory reduces apparent magnitude of drought legacies. In this issue, Klesse et al. (2022) highlight statistical practices and properties that should be more considered by researchers quantifying drought legacies. In particular, detailed accounting for autocorrelation and incorporation of lagged climate effects reduces apparent legacies (purple) compared to previous approaches (red, green). But which line best approximates reality and what is the best approach? We suggest models can only teach us so much.

the Lloret et al. (2011) indices, which are simple, easy to interpret and very widely applied. However, these indices fail to account for the climate response, as they simply make comparisons of growth before, during and after a drought. We refer to this and similar approaches as 'climate blind', that is, they ignore postdrought (or postevent) climate and how that may enhance (or further impair) tree recovery. At large scales, where many events across many sites are analysed, such indices are useful. In such cases, a wide variety of postdrought climate conditions are included and so errors are 'averaged out'. However, if we are interested in quantifying responses of specific regions, sites or even trees, climate-blind approaches should be avoided.

Third, and related to the above issue, many studies have been conducted at very large spatial scale, drawing upon large datasets like the International Tree Ring Data Bank (ITRDB). While we might hope to learn about the response of individual trees to drought from these studies, individual idiosyncrasy means tree or even site-level legacy effects are extremely difficult to identify, observe and attribute (Peltier et al., 2021). Severe legacies have been observed in some cases, with the ultimate outcome being mortality several years after the instigating drought event (Bigler et al., 2007). But, on average, legacy effects are not large: taking the results of Anderegg et al. (2015), mean legacies were around −0.1, or a reduction in growth equivalent to 10% of mean ring width. Drought legacies in individual sites or trees are thus swamped by aspects of tree growth with greater influence, such as ontogeny, reproduction and everything else we might be tempted to call 'noise'. Many studies report some kind of 'uncertainty of the mean' or hierarchical uncertainty for this reason (rather than total uncertainty). Similarly, to quantify large-scale drought legacies, stand-level chronologies are often used, and tree-level variability is typically ignored or averaged over. We would suggest, however, that we have the most to learn about the potential existence, magnitude and underlying mechanisms of drought legacies if we focus on tree-level responses across broad spatial scales (Peltier et al., 2021). Exploring and quantifying the drivers of tree-level variability is a frontier for dendroecological research, where understanding the interactions among the numerous physiological and ecological processes influencing tree-ring time series is likely to greatly improve our ability to simulate future tree growth responses to climate change.

Finally, the results of the Klesse et al. (2022) suggest a broader need for research into climate memory of tree growth. When the authors relate ring widths to climate at increasing lags, they found that accounting for the effects of past climate reduces the strength or duration of estimated drought legacies. However, the climate covariate that they used is itself a drought metric (SPEI) that integrates over past time periods, raising the question of whether this is somewhat tautological: if we account for lagged effects of dryness, the lagged residual errors after drought events are reduced. We found limited evidence for similar effects in a previous study, where reducing the lag period from 5 to 2 years for climate covariates increases the apparent severity of drought legacies, though this is in a supplement (Peltier & Ogle, 2019). Regardless, these results raise the broader questions of how should we model tree growth responses to climate extremes? What should we wrap into 'memory' (i.e. 'normal' lagged responses to climate), and what should be considered a 'legacy' (i.e. transient perturbation to tree growth following an extreme event)? Is it even possible to separate these two things ('memory' and 'legacy') analytically?

We suggest conceptual definitions for distinguishing between memory and legacy effects (see Table 1), the key difference being legacies is specific to a transient, relatively extreme event. We further suggest climate memory effects are likely inherent to tree-growth–climate relationships, for many of the physiological reasons outlined in Klesse et al. (2022) and Peltier et al. (2021), and we concur with Klesse et al. (2022) that notable legacy effects of extreme climate events (e.g. droughts) may be less prevalent than suggested by recent, prior studies. Quantification of truly outstanding legacy effects, beyond inherent memory responses or autocorrelation, could be a useful goal for improving our representation of tree growth responses to drought. But if autocorrelation accounts for some portion of a drought legacy, does this imply that the observed declines in tree growth for multiple years after drought are inconsequential? As we asked earlier, what does the finding that drought legacy effects are partially explained by autocorrelation mean for our understanding of the long-term impacts of drought on tree growth?

Much of how we answer these questions hinges on what biological or physiological mechanisms we assume give rise to autocorrelation (Figure 2). Which physiological or ecological processes should be modelled or treated as simply 'autocorrelation', and which physiological or ecological processes should be modelled as memory, or as drought legacies? Is autocorrelation reflective

TABLE 1 Conceptual definitions for distinguishing climate legacies and memory.

Term	Usage	Definition
Autocorrelation	Positive autocorrelation	The empirical property of a time series (such as tree growth inferred from measured tree-ring widths) to be similar from 1 year to the next
Antecedent condition	Antecedent moisture or temperature	Past conditions, often in the context of environmental, climate or driving variables. The relevant 'past time period' (e.g. 2 days, 3 weeks, 1–2 years ago) depends on the response and the driving variable(s), and is often unknown, but can be estimated from data
Legacy	Drought legacy	Describes the lingering effect of a particular event (e.g. drought) on an ecological process (e.g. tree growth, GPP, NEE). For example, a drought in 1 year continues to impact productivity for multiple years after the drought event occurred. See Figure 1
Memory	Climatic memory	Describes the influence of antecedent conditions (e.g. moisture, temperature) on current or future responses (e.g. tree growth, GPP, NEE). If antecedent conditions (regardless of whether they include an extreme event) are important for predicting the response, this implies a 'memory' effect, which can include lags

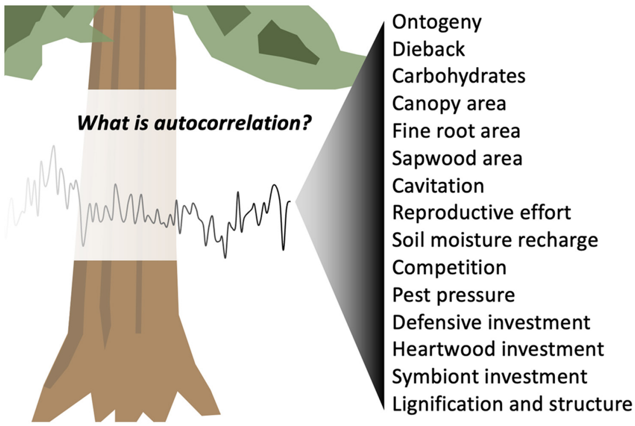

FIGURE 2 Many processes cause autocorrelation in tree-ring widths, how should we model them? Tree rings provide a powerful record of tree physiology and climate across timescales. They also exhibit autocorrelation, where our choices to account for such autocorrelation influence our ability to study processes of interest. Ultimately, we suggest modelling can only teach us so much without actual measurements of processes of interest.

of nonstructural carbohydrate dynamics? Hydraulic damage? Leaf area variations? Canopy dieback? Ontogeny? Multi-year soil moisture storage? Dendro-anatomical changes? Reproduction? Autoregressive models are just a simple way to account for processes we cannot model directly (e.g. for which we lack relevant covariate data or appropriate mechanistic understanding). If periodic cavitation produces autocorrelation, is that the best way to model cavitation effects on tree growth? Our own concept of climate memory (Table 1) is simply trying to account for as much of this autocorrelative process as possible by explicit relation to climate effects as an ultimate driver. But regardless of how much variation we ascribe to whichever nebulous statistical quantity in our regression model, we find the same thing: Tree growth is often reduced by drought for multiple years. There is strong evidence from experiments (Rehschuh et al., 2020) and suggestive results from theoretical models (Trugman et al., 2018) that reductions in tree growth following droughts are indicative of physiological damage. Lingering reductions in postdrought tree growth are so interesting because there is a diversity of potential physiological and ecological causes—that they are partially explained by autocorrelation does not imply they are not ecologically meaningful.

At some point, results across studies highlight that there is only so much we can learn from pulling apart a tree-ring time series into component processes with different periodicities and statistical treatments. Evidence for this statement may be taken from the very diverse potential mechanisms suggested by different authors. This is why we need experiments and improved physiological monitoring, as Klesse et al. (2022) so rightly conclude. For example, a manipulation of a key tree physiological metric (e.g. reduction in canopy area) followed by observation of radial growth for 3–5 years after the event to observe how long a legacy may persist. Coupling manipulations with observations of climate and physiology could inform discussion of what processes constitute true legacy effects, and which others are best thought of as climate memory or simply autocorrelation (Table 1). We suggest holistic monitoring of climate and physiological variables of individual trees over long time periods can improve our understanding of how tree growth functions. For example, eddy covariance techniques have revolutionized the study of forests, but can we imagine similarly long, high-resolution records of ecophysiological metrics coupled with tree rings? The data are becoming available to do such analyses as long-term records accumulate, and now is the time to leverage such data.

AUTHOR CONTRIBUTIONS

Drew M. P. Peltier wrote the first draft. All authors contributed to revisions.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

This paper uses no data.

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