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LETTER

Drought legacies are dependent on water table depth, wood anatomy and drought timing across the eastern US

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Abstract

Severe droughts can impart long-lasting legacies on forest ecosystems through lagged effects that hinder tree recovery and suppress whole-forest carbon uptake. However, the local climatic and edaphic factors that interact to affect drought legacies in temperate forests remain unknown. Here, we pair a dataset of 143 tree ring chronologies across the mesic forests of the eastern US with historical climate and local soil properties. We found legacy effects to be widespread, the magnitude of which increased markedly in diffuse porous species, sites with deep water tables, and in response to late-season droughts (August–September). Using an ensemble of downscaled climate projections, we additionally show that our sites are projected to drastically increase in water deficit and drought frequency by the end of the century, potentially increasing the size of legacy effects by up to 65% and acting as a significant process shaping forest composition, carbon uptake and mortality.

Keywords

Climate change, forests, legacy effects, tree rings.

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INTRODUCTION

Forests play a crucial role in regulating global carbon (C) and water fluxes (Bonan 2008), yet forest responses to drought remain one of the largest uncertainties in the C cycle (Reichstein *et al.* 2013). As the biosphere undergoes an intensification of the hydrological cycle, with increasing frequency and severity of drought events (Giorgi *et al.* 2011; Dai 2013; Cook *et al.* 2015), there exists the potential for water stress to markedly reduce the substantial C storage, timber production and other ecosystem services that forests provide (Bonan 2008; Reichstein *et al.* 2013; Vose *et al.* 2016). In addition to impacting C assimilation and growth during drought conditions, the physiological changes trees undergo during water stress can also hinder recovery. Such 'drought legacy effects' (hereafter, 'legacy effects') occur in all terrestrial ecosystems on earth (Schwalm *et al.* 2017), and can be consequential for global C cycling given their predominance in forests (Anderegg *et al.* 2015; Peltier *et al.* 2016; Gazol *et al.* 2017). As such, there is a need to better characterise the factors that modulate the magnitude of legacy effects as a first step towards developing predictive models of their impacts at local, regional and global scales (Anderegg *et al.* 2015; Berdanier & Clark 2016).

The impacts of drought on tree growth responses have been most studied in arid ecosystems. However, recent investigations of more mesic forests have highlighted their susceptibility to current and future water stress (Allen *et al.* 2010; Pederson *et al.* 2014; Martin-Benito & Pederson 2015; Millar & Stephenson 2015). In the temperate zone, mesic forests provide crucial ecosystem services, sequestering more C than arid systems and partially offsetting the effects of anthropogenic C emissions on atmospheric CO_2 concentrations (Pan *et al.* 2011; Xiao *et al.* 2011). These forests are diverse, varying significantly in species composition, site climate and edaphic factors – all processes that are likely to influence a tree's response to, and recovery from, drought. Indeed, local site characteristics such as soil texture and water table depth are known to play a role in determining drought responses (Phillips *et al.* 2016), underscoring the value of site-specific factors to assist in explaining variation in tree drought sensitivities (D'Orangeville *et al.* 2018). However, most previous investigations of legacy effects have been global in scale and span vast climate gradients (Anderegg *et al.* 2015; Schwalm *et al.* 2017; Wu *et al.* 2017), precluding any inference about the local factors that shape a species' legacy effect within biodiverse forests that are more mesic in climate.

In this study, we sought to characterise the ability of temperate forests to recover from water stress, uncover the factors that modulate the size of legacy effects, and to project the implications of this phenomenon in a warm and water stressed future. To do so, we amassed a dataset of 143 detrended tree ring chronologies across the midwestern and eastern US that spans 94 sites, includes 17 common tree species, and contains 15 476 growth rings. These site chronologies were paired with high resolution gridded climate data, estimates of various soil characteristics, and future climate projections for our sites in an attempt to understand the potential for climatic shifts to alter the frequency and severity of legacy effects by the end of the

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century. Specifically, we asked: (a) how large are legacy effects in eastern temperate forests and how long do they last, (b) what site factors (i.e. climatic and edaphic) influence drought responses and legacy effects, and (c) how might future climatic change impact the size of legacy effects across the eastern US? By investigating these questions, we hoped to gain an understanding of the local-scale factors that control variation in legacy effect size and assist in predicting when and where drought impacts on tree recovery will be largest in response to future droughts.

METHODS

Study area

Our study area spanned the mesic temperate forests of the midwestern and eastern US, encompassing 31°–55° N and −92° to −70° W (Fig. S1). Site climate was generally mesic, with mean total June–August precipitation varying between 290 and 450 mm and mean June–August temperature between 15 and 27 °C. All sites were mature forests with chronology lengths ranging from 85 to 226 years.

Tree ring data

A total of 143 chronologies were amassed across the study area, representing 94 individual sites and spanning 17 common tree species in this region (Table S1). All sampled trees were canopy dominant and selected to examine climate sensitivity (i.e. no visible damage, full foliage, not located on irregular topography). At each site, at least eight trees of each species were cored, processed, measured according to standard dendrochronological methods (Stokes & Smiley 1999; Voorhess 2000), and visually crossdated (Yamaguchi 1991). Crossdating was statistically confirmed with COFECHA (Holmes 1983) and chronologies were detrended using a 2/3 series length spline (Cook & Peters 1981). Site level chronologies were then constructed via bi-weight average using the dplR package in R (Bunn 2008). Standardized ring widths (SRW) outside the range of 1901–2015 were excluded in order to match the temporal coverage of our climate data. In order to evaluate the statistical quality of our dataset, we calculated the expressed population signal (EPS) of each chronology (Wigley *et al.* 1984; see Table S1). Of our 143 chronologies, only 12 had an EPS of < 0.8. Excluding these chronologies did not qualitatively alter our results and were therefore retained in our dataset to avoid overestimating the effects of drought on tree ring widths. Furthermore, EPS is not meant to reflect the suitability of an individual chronology (Buras 2017), and thus we chose not to apply an arbitrary EPS cutoff to our dataset.

Climate data

Gridded 0.5° monthly precipitation (P), potential evaporation (PET), vapour pressure deficit (VPD) and temperature (T) data were obtained from the CRU TS 3.24.01 dataset (Harris *et al.* 2014) for 1901–2015. Climatic water deficits (CWD) were calculated as the difference between P and PET. We then calculated annual growing season CWD by summing monthly June–August CWD. In order to analyse the effects of drought timing, CWD sums were also calculated for individual months of the growing season (May–September).

Soil data

Soil data – including sand/silt/clay content, bulk density, % organic matter and water table depth – were obtained from the SSURGO database using site coordinates (websoilsurvey.sc.usda.gov). Soil texture data represent weighted averages over the first meter of soil depth. The SSURGO database contains soil information collected at scales ranging from 1 : 12 000 to 1 : 63 360 by the National Cooperative Soil Survey. In the cases where multiple soil types were observed within the 1-ha square plot centred on our sites, a weighted average for all data was computed given the relative proportion of that entry in the database. It is important to note that water table depth data in the SSURGO database is set to 200 cm when the water table is deeper than observed. Since water table depth is not known with any certainty for these values, these data were cut for our analysis ($n = 54$). Including these values did not alter the statistical significance of any of our models.

Drought and legacy effect calculations

'Drought years' were identified as a 1 standard deviation (SD) anomaly in a given site's mean June-August CWD (see supplementary material for results using different drought year cutoffs). Reductions in SRW due to drought (i.e. 'drought effects') were calculated for each chronology as the difference between average drought year SRW and average non-drought year SRW. We then predicted what SRW should be (in the absence of legacy effects) by creating a site-specific linear model between CWD and SRW and applying that model in the years following a drought year. Legacy effects were then quantified as the average difference between SRW predicted by our model and observed SRW (see supplementary methods, Fig. S4, and Fig. S5 for alternate legacy effect calculations and drought year criteria). Our results were not significantly different when considering only chronologies where SRW was strongly related to climate (see supplementary material).

Climate, drought effect, and legacy effect projections

Daily projections of P and PET were obtained for 1950–2099 from the output of 18 General Circulation Models included in the Coupled Model Intercomparison Project – Phase 5 at each of our sites (Taylor *et al.* 2012). Downscaled model output (4 km^2 grid cell size) was obtained from the Multivariate Adaptive Constructed Analogs data warehouse (Abatzoglou & Brown 2012, climate.northwestknowledge.net/maca) with the RCP8.5 emissions scenario forcing. PET was calculated from daily model ensemble means using the Penman-Monteith method driven with minimum/maximum temperature, minimum/maximum relative humidity, precipitation, downward solar radiation and wind speed. Downscaled, daily time series

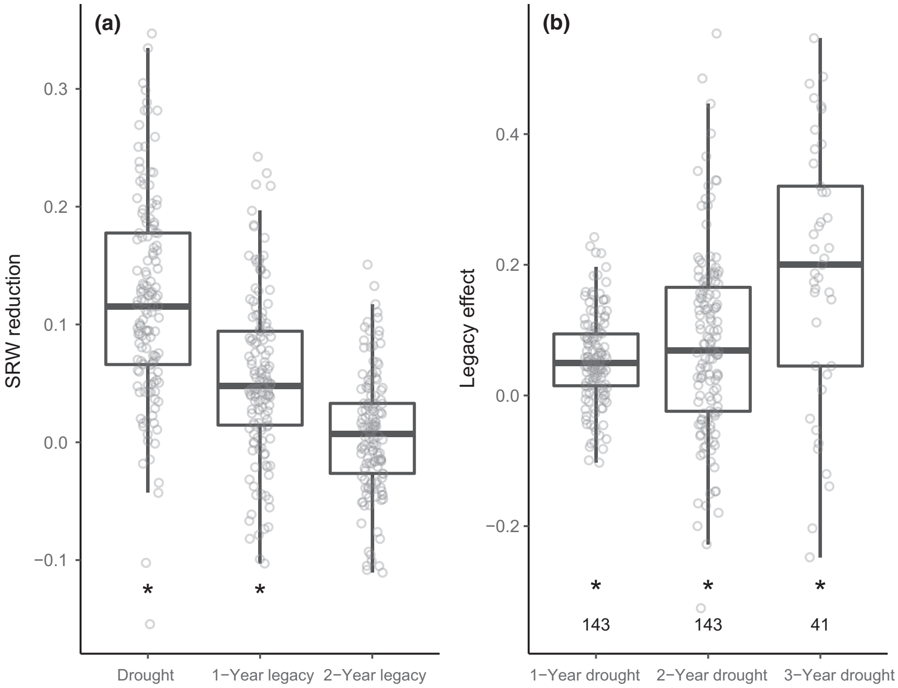

Figure 1 Panel (a) represents standardised ring width (SRW) reductions averaged across all sites during drought years and 1–2 years post-drought. Drought effects ($t(140) = 145.6$, $P < 0.001$) and 1 year legacy effects ($t(140) = 9.47$, $P < 0.001$) were significantly different from zero while 2 year legacy effects ($t(140) = 1.62$, $P = 0.107$) were not. Panel (b) represents legacy effects following droughts of 1–3 years in length. Legacy effects after multi-year droughts were significantly different from zero across all sites ($\alpha = 0.05$). Numbers at the base of the boxplot in panel (b) represent the number of site chronologies that experienced a drought of that length (i.e. sample size). Asterisks indicate effects that are statistically larger than zero ($\alpha = 0.05$).

data were then converted into CWD and summed for the June–August time period to get annual values of growing season CWD. To quantify site-specific changes in climate, we calculated raw shifts and % change in projected annual CWD between the 2079–2099 and 1995–2015 time periods. We estimated how legacy effects may change in the future using projected, site-specific CWD to calculate 1-SD drought year criteria for the 2079–2099 and 1995–2015 time periods. These new projected 1-SD cutoffs were then applied to our dataset and legacy effects were calculated as above, albeit with the new drought year cutoffs.

Statistical analysis

The statistical significance of drought effects and legacy effects across species and years was assessed using one-sample and two-sample Welch's *t*-tests, as appropriate. The changes in drought effects and legacy effects due to wood anatomy and drought timing were assessed via one-sample Welch's *t*-tests and ANOVA with Tukey's HSD for pairwise comparisons. Relationships between drought effects, legacy effects, site climate, and soil characteristics were assessed using linear models. Linear mixed models were also used to investigate the factors that influence legacy effects while controlling for species-specific responses. Only one soil texture variable (% sand) was included as a predictor in this model as soil textures are highly collinear and including additional soil texture variables did not improve the model fit. Linear mixed models were created with the lme4 R package (Bates *et al.* 2015), significance of model predictors was determined through Wald tests, and marginal and conditional r^2 were calculated via the method of Nakagawa & Schielzeth (2013), implemented with the MuMIn R package (Kamil 2016).

RESULTS

We found that legacy effects in mesic midwestern and eastern US forests typically last for 1 year (Fig. 1a; $t(140) = 9.47$, $P < 0.001$) and reduce SRW by *c.* 5%, which is *c.* 40% of the reduction in SRW experienced by trees during a drought. However, multi-year droughts (sequential 1-SD dry anomalies) markedly increased the size of legacy effects, such that legacy effects after a 3 year drought reduced wood growth by 19%, thereby exceeding the drought effects that occurred in response to a 1 year drought (Fig. 1b). Legacy effects were significantly positively related to ring width reduction during drought (Fig. S2, $r^2 = 0.26$, $P < 0.001$), indicating large drought effects usually were followed by large legacy effects. We observed a weak but significant relationship between mean site CWD and legacy effect size (Fig. S3b, $r^2 = 0.03$, $P = 0.037$). Drought effects, however, were more strongly related to mean site CWD (Fig. S3a, $r^2 = 0.17$, $P < 0.001$).

The magnitude of legacy effects across sites was largely controlled by tree species identity and edaphic factors. Species varied greatly in their observed legacy effects, with post-drought reductions in tree ring width of over 16% in *Betula lenta*, while *Pinus palustris* showed negative legacy effects

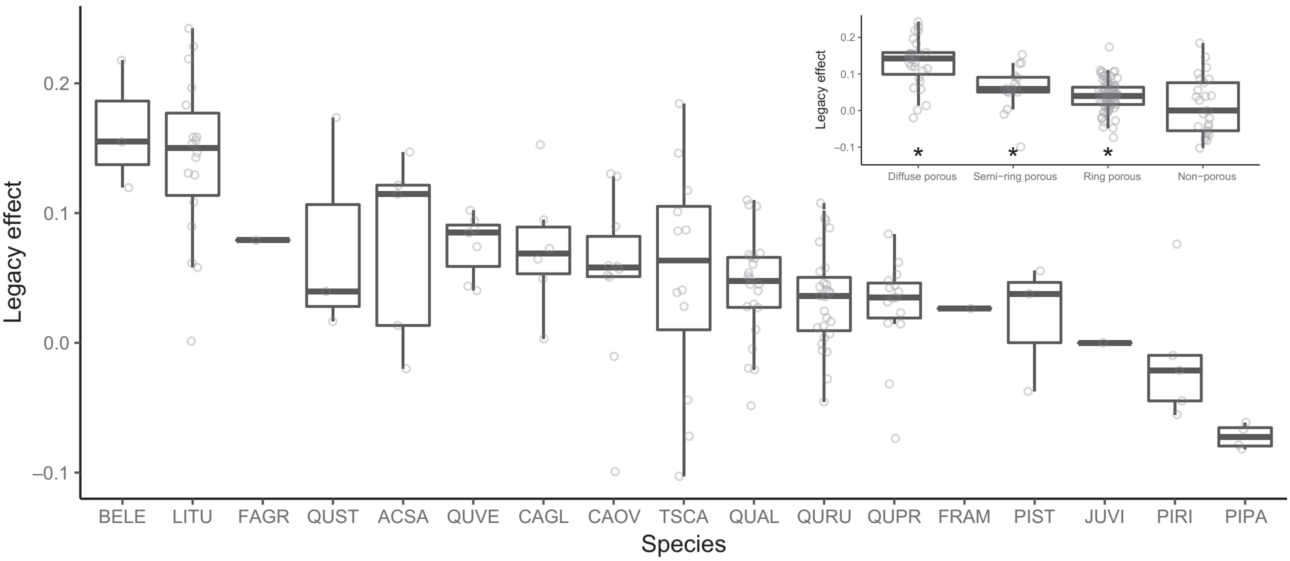

Figure 2 Legacy effect size across all 17 species. Species codes are defined in Table S2. Inset represents legacy effect sizes across various wood anatomies. All species' legacy effects were significantly different from zero (where $n > 1$, $\alpha = 0.05$). Diffuse porous species had larger legacy effects than all other wood anatomies, while all other wood anatomy categories were statistically indistinguishable. All species' legacy effects were significantly greater than zero (where $n > 1$) except for *Pinus rigida* and *Pinus palustris*. Asterisks in panel (b) indicate legacy effects that are statistically larger than zero ($\alpha = 0.05$).

(larger observed than predicted post-drought SRW, Table S2). All species' legacy effects were significantly larger than zero, with the exception of *Pinus rigida* and *Pinus palustris*. Additionally, *Fagus grandifolia*, *Fraxinus americana* and *Juniperus virginiana* were only represented once in our dataset, precluding any comparative analysis of their legacy effects. Among tree species, much of the variation related to interspecific differences in wood anatomy (Fig. 2). Diffuse porous species had the largest legacy effects (13%), whereas non-porous species (i.e. conifers) exhibited legacy effects that were not significantly different from zero. Among the edaphic and hydrological factors, water table depth was a primary determinant of legacy effects (Fig. 3h, $r^2 = 0.18$, $P = 0.002$). Notably, factors that controlled drought effects (such as soil texture; Fig. 3a–c) were less important in controlling legacy effects (Fig. 3e–g). We constructed a linear mixed model to predict the size of legacy effects, with mean site CWD, % sand and water table depth included as predictors and both species and site as random effects (marginal $r^2 = 0.10$, conditional $r^2 = 0.58$, $P < 0.001$ for all predictors except mean site CWD, which was non-significant). The marginal r^2 is associated with fixed effects only and the conditional r^2 incorporates random effects (Nakagawa & Schielzeth 2013). Our model indicates that while most of the variation in legacy effects can be explained by interspecific differences, soil texture and site hydrology also play a role irrespective of species- and site-specific factors.

In addition to tree species identity and edaphic factors, drought timing was a key factor regulating the size of both drought effects and legacy effects, as current year SRW reductions were largest when a drought occurred the months of May, June, or July (Fig. 4). Conversely, August drought produced the largest legacy effects in the year after the drought (Fig. 4). Drought effects and legacy effects were significantly larger than 0 ($\alpha = 0.05$) in response to all drought timings, except for September drought effects ($t(142) = 0.41$, $P = 0.684$).

In order to understand the potential importance of legacy effects in the face of climate shifts, we projected future CWD for our sites using a suite of 18 general circulation models downscaled to a grid cell size of 4 km^2. Mean ensemble June–August CWD across all sites is expected to decrease from the 1995–2015 average of −159 mm to −268 mm by the 2079–2099 time period (Figs 5 and 6), increasing the frequency of years below −223.9 mm CWD (the 1-SD drought year cutoff for the 1995–2015 baseline) from 16% to 71%. By pairing the historical climate responses derived from our tree ring dataset with site-specific, future 1-SD climate anomaly projections, we estimate that future dry anomalies could give rise to increases in legacy effects of up to 65% across our midwestern and eastern US sites (Fig. 5, Fig. 6).

DISCUSSION

Understanding the legacies of extreme events is one of the fundamental challenges for predictive biology (Frank *et al.* 2015), and is necessary for quantifying ecosystem feedbacks to global change. To date, most of what is known about legacy effects comes from arid regions, and the strong climatic control on legacy effects in that region has resulted in a prevailing notion that legacy effects in mesic regions are less consequential. Our results counter this narrative by providing evidence that large legacy effects are widespread across forests of the midwestern and eastern US. Moreover, our results show that the magnitude of legacy effects in mesic forests may be predictable based on species- and site-specific factors. While previous investigations have shown that the size of legacy effects can increase with site aridity across biomes (Anderegg *et al.* 2015; Schwalm *et al.* 2017), our results suggest that climate

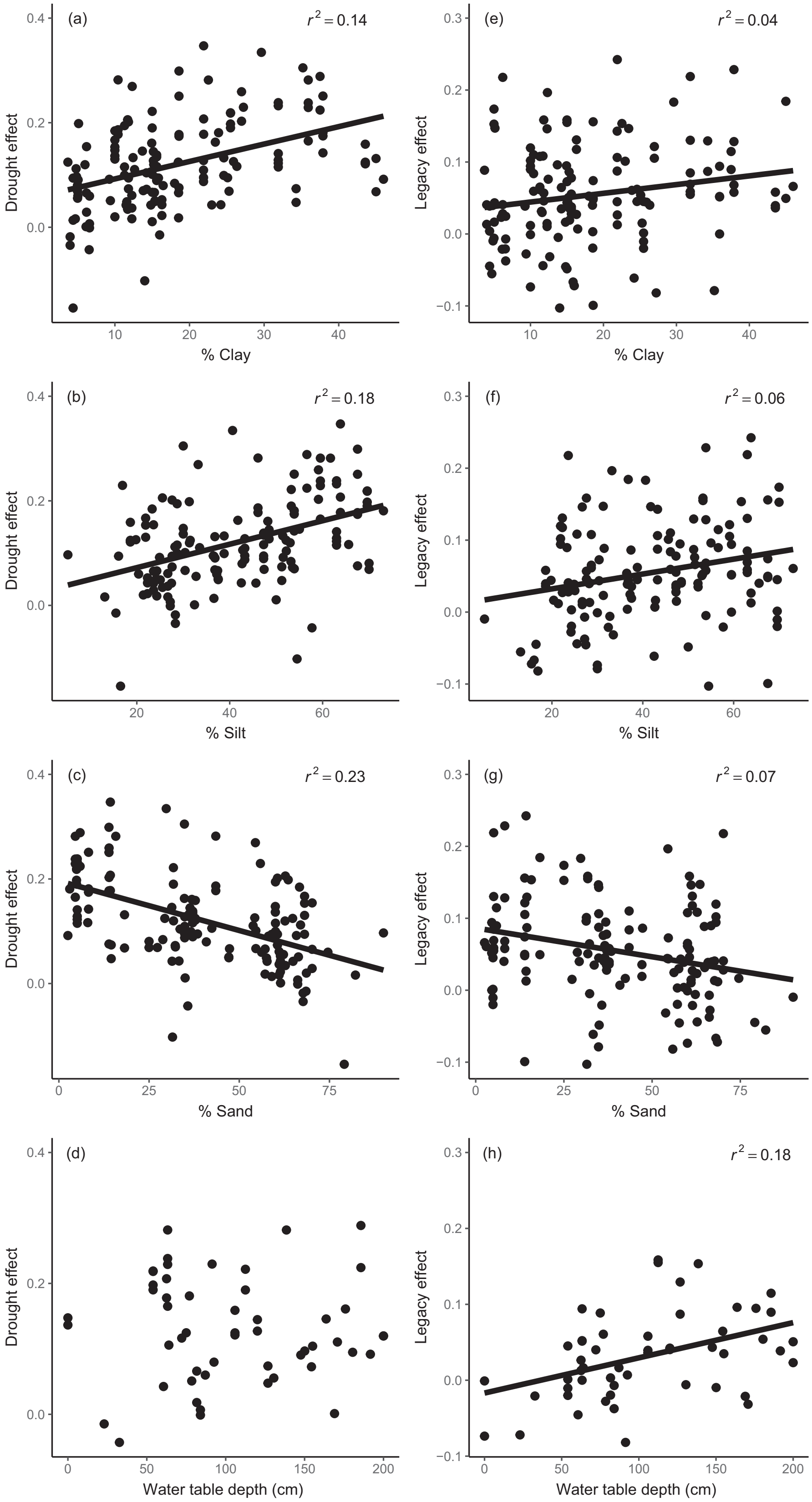

Figure 3 Relationships between soil texture variables and drought effect size (a, b and c), water table depth and drought effect size (d), soil texture variables and legacy effect size (e, f and g), and water table depth and legacy effect size (h) at each site. All linear model slopes are statistically significant ($\alpha = 0.05$) except panel (d). All other data in our soil characteristic database (e.g. bulk density and organic matter concentration) were unrelated to drought effects or legacy effects.

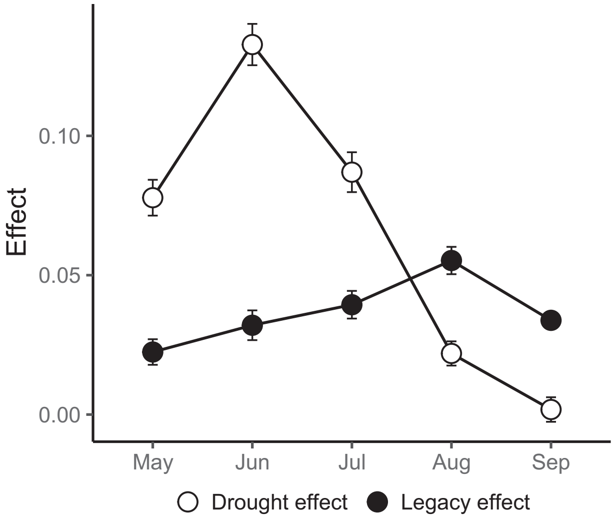

Figure 4 Effect of drought timing on drought effects and legacy effects. Each monthly time point represents the mean drought effect and legacy effect for a 1-SD CWD anomaly drought event in each month across all sites. All drought effects and legacy effects across all time bins were significantly larger than 0 ($\alpha = 0.05$), except for September drought effects ($t(142) = 0.41$, $P = 0.684$). Error bars represent ± standard error.

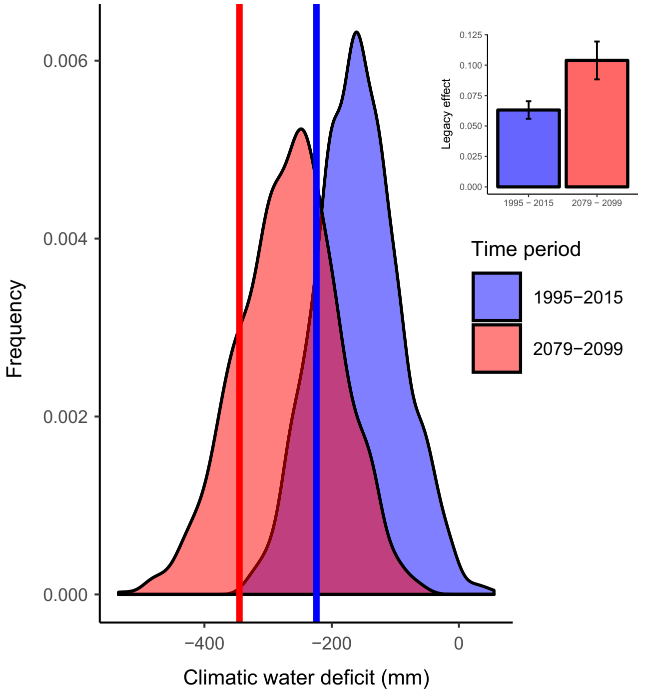

Figure 5 Projections of growing season CWD for all sites by the end of the century. The main graph represents a smoothed frequency distribution of ensemble mean June–August CWD for each site in the current (1995–2015) and future (2079–2099) time periods. The vertical blue line represents a 1-SD anomaly (our criterion for a drought year) for the 1995–2015 baseline period, while the red vertical line represents a 1-SD anomaly for the 2079–2099 period. The inset graph shows legacy effect magnitude when using current (1995–2015) and future (2079–2099) 1-SD climate anomalies as our drought year criterion. Altering the drought year cutoff to 2079–2099 projections resulted in a reduced number of our sites that have experienced a drought year of that magnitude, therefore reducing sample size ($n = 84$).

may play a minor role within temperate forests. Rather, tree species identity, edaphic characteristics and drought timing were the primary determinants of the size of legacy effects. Collectively, these results should improve our capacity to predict ecosystem sensitivity to drought (both during and after the event) across a region that is expected to experience increasing water stress in the coming decades (Dai 2013).

Of the four factors that influenced legacy effects (species identity, soil texture, water table depth and drought timing), tree species' wood anatomy controlled the most variation. These results add to current evidence indicating that diffuse porous species are more susceptible to water stress than species with different wood anatomy (Elliott *et al.* 2015). Our results also indicate that species that are more affected by the drought (i.e. have larger drought effects) face an additional stress in that they may also take longer to recover. This was true for nearly all species, as shown by the positive relationship between drought effects and legacy effects across all sites (Fig. S3). The link between wood anatomy and legacy effects may be mediated by the phenology of wood formation, as the majority of ring porous species' hydraulic transport occurs in the large, current year, earlywood vessels, while diffuse porous species transport water through the last few years of new xylem (Zimmerman 1983). Therefore, in the year following drought, ring porous species can recover by developing new xylem, while diffuse porous species either have to repair drought-induced hydraulic damage or experience growth declines due to losses in hydraulic conductivity. Legacy effects are likely controlled by a number of interactions between a species' physiology and its environment, necessitating further work into the species-specific and wood anatomical factors that give rise to lags in drought recovery.

Edaphic factors were also important for understanding the effects of drought on tree ring width. In particular, trees growing on sites with higher clay and silt content were more affected by drought (Fig. 3a–c), likely due to the low water potentials these soils can reach during drought and the limited ability of roots to extract water from soils with low water potential (Jackson *et al.* 2000; Sperry *et al.* 2016). Likewise, legacy effects were similarly related to soil texture. This relationship likely did not arise due to any *a priori* mechanism and instead emerged due to the relationships between drought effects and soil texture, and the positive relationship between drought effects and legacy effects. Therefore, any factor that causes ring width reductions during drought could potentially spillove and suppress wood growth in the year after drought.

Previous work has documented the role of site climate and soil texture in controlling drought effects on ring width (D'Orangeville *et al.* 2018). Here, we find that legacy effects were less affected by these factors, and instead were larger at sites with a deep water table. Legacy effects have been hypothesised to arise from lagged physiological consequences of water stress such as C depletion, bud damage or other losses of leaf area, persistent hydraulic damage, or pest/pathogen infection (Hacke *et al.* 2001; Bréda *et al.* 2006; van der Molen *et al.* 2011; Anderegg *et al.* 2013). While our data do

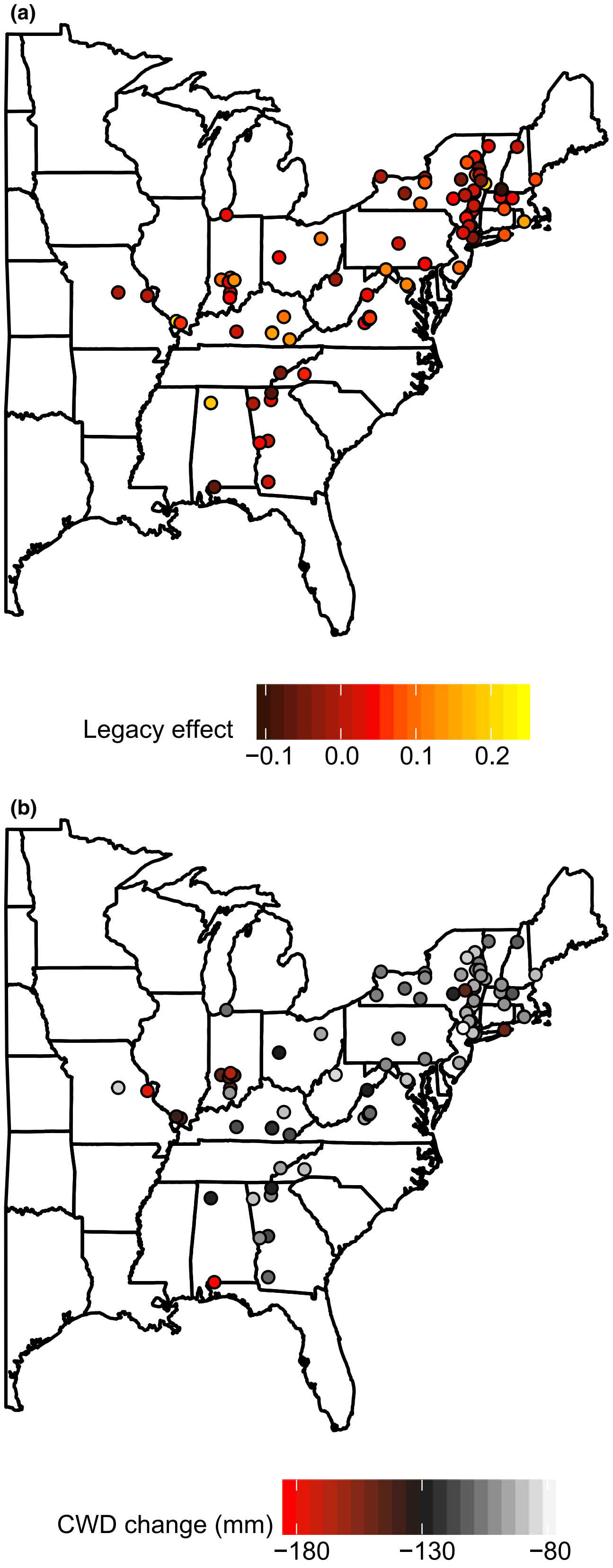

Figure 6 Maps of legacy effect magnitude (a) and the raw change in projected mean site CWD between 2079-2099 and 1995-2015 (b) across all sites.

not resolve this debate, our observation of a positive relationship between drought effects and legacy effects supports the role of drought-induced physiological damage in delaying tree recovery. Moreover, our data indicate that water table depletion may induce 'hydrological legacy effects'. Given the prevalence of relatively deep water tables (e.g. > 150 cm) across much of the US (Fan *et al.* 2013), the large percentage of a tree's C that is stored in wood (Pan *et al.* 2011), and the amount of C stored annually in US forests (Xiao *et al.* 2011), the ecological ramifications of legacy effects may be consequential for regional climate. Nevertheless, future work investigating the interactions between soil texture, water table fluctuations, rooting depth and drought responses is clearly needed (Phillips *et al.* 2016; Fan *et al.* 2017; Wu *et al.* 2017; Johnson *et al.* 2018).

The effects of drought on forests depend not just on species and site factors, but on how the timing of drought overlaps with tree phenology (Čufar *et al.* 2008; D'Orangeville *et al.* 2018). We found that drought timing had contrasting impacts on drought effects and legacy effects, as early season droughts primarily reduced current year ring width while late season droughts reduced the next year's ring width (Fig. 4). This observation is intuitive as an early season drought affects trees at their peak of biomass accumulation (Čufar *et al.* 2008; Duchesne *et al.* 2012; Delpierre *et al.* 2016; D'Orangeville *et al.* 2018), creating large drought effects apparent in ring width. In contrast, late season droughts likely do not give trees adequate time to recover lost foliage, rebuild C stores, or repair embolism before senescence, affecting their ability to leaf out and grow in the following spring (Bréda *et al.* 2006). Lagged effects of climatological extremes on tree ring width that are dependent on seasonal timing could have important implications for the fields of dendroecology and dendroclimatology.

Given the role that drought severity and length play in producing large legacy effects, shifts towards drier and more frequent drought events are likely to be an important factor governing forest functioning in the future. In order to project the effects of future climate on drought and legacy effects, we took advantage of the fact that, while legacy effects were only weakly related to mean site aridity, they were still strongly controlled by the severity of climate anomalies within a given site. By pairing our observed legacy effects with end of century climate projections for all of our sites, we have shown that legacy effects have the potential to increase markedly in the coming decades. While these coarse predictions do not account for the demographic processes, range shifts and mortality that play a large role in determining whole-forest responses to water stress (Clark *et al.* 2016), they do indicate a decreasing ability to tolerate and recover from drought in many temperate species as forests dry.

Our approach – using tree rings to study the lagged consequences of drought – has many strengths but also some caveats. This study relied on dendrochronological, climatic and edaphic observations to investigate factors that modulate legacy effect size across the eastern US. As such, critical insights as to the physiological underpinnings of legacy effects could not be determined, nor does our study account for interacting stressors (e.g. co-occurring pest or pathogen damage of drought-stressed trees). However, previous experimental studies on the physiology of legacy effects, while valuable mechanistically, omit the edaphic and climatic factors that we have shown to be important to a tree's drought recovery. Thus, a key research priority is to pair forest-based drought experiments (e.g. passive rain-out shelters or roofs) with dendrochronological measurements. The pairing of experiments with observations should greatly improve our understanding of the importance of legacy effects in mesic forests. Furthermore, since only living trees were cored our data do not allow investigation of perhaps the most significant legacy of drought, mortality. However, recent studies indicate that trees that experience the largest reductions in post-drought growth are also more prone to mortality (Berdanier & Clark 2016). Thus, the legacy effects we observed are likely conservative estimates for the total impact of drought on forest recovery in that they do not consider the fact that some percentage of trees may die.

This work represents a previously unrecognised aspect of the susceptibility of temperate forests to legacy effects and presents novel evidence that drought timing, soil characteristics and species traits such as wood anatomy are crucial factors controlling variation in drought responses and recovery processes. Linking local hydrological factors such as rooting depth and water table depth to demographic processes such as mortality (Chitra-Tarak *et al.* 2017) could provide context for the importance of legacy effects in broader scale forest C cycling. In the face of a drier climate, legacy effects are likely to increase in importance as a driver of forest function by suppressing wood biomass accumulation, reducing tree vitality over time (Camarero *et al.* 2018), and increasing the likelihood of mortality (Berdanier & Clark 2016) – thereby reducing forest C uptake in the short term (Anderegg *et al.* 2016) and impacting the species composition shifts that are already underway in eastern US forests (Clark *et al.* 2016; Fei *et al.* 2017; Zhang *et al.* 2018). If more frequent and severe legacy effects accumulate to impact plant function, future climate changes are likely to spur trees from these regions to adapt, shift ranges, or die.

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DATA AVAILABILITY

Soil characteristic data are available online via the United States Department of Agriculture National Resources Conservation Service Web Soil Survey data portal (sdmdataaccess.sc.egov.usda.gov). Gridded historical climate data are available on the Climatic Research Unit site (crudata.uea.ac.uk/cru/data/hrg/), and climate projections are also available online via the Multivariate Adaptive Constructed Analogs data warehouse (climate.northwestknowledge.net/maca). Tree ring chronology data, site metadata, and analytical code are available at datadryad.org/resource/doi:10.5061/dryad.4272kh0.

AUTHOR CONTRIBUTIONS

SAK designed the study and methodology, with input from JTM and RPP. SAK, JTM and NP collected and provided tree ring data, LD'O provided soil characteristic data and DLF provided future climate projection data. SAK conducted data analysis and drafted the manuscript, with subsequent feedback from all co-authors.

REFERENCES

Abatzoglou, J. & Brown, T. (2012). A comparison of statistical downscaling methods suited for wildfire applications. *Int. J. Climatol.*, 32, 772–780.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M. *et al.* (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.*, 259, 660–684.

Anderegg, W.R.L., Plavcová, L., Anderegg, L.D.L., Hacke, U.G., Berry, J.A. & Field, C.B. (2013). Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Glob. Chang. Biol.*, 19, 1188–1196.

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.

Anderegg, W.R.L., Martinez-Vilalta, J., Cailleret, M., Camarero, J.J., Ewers, B.E., Galbraith, D. *et al.* (2016). When a tree dies in the forest: scaling climate-driven tree mortality to ecosystem water and carbon fluxes. *Ecosystems*, 19, 1133–1147.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, 67, 1–48.

Berdanier, A.B. & Clark, J.S. (2016). Multi-year drought-induced morbidity preceding tree death in southeastern US forests. *Ecology*, 26, 17–23.

Bonan, G.B. (2008). Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, 320, 1444–1449.

Bréda, N., Huc, R., Granier, A. & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann. For. Sci.*, 63, 625–644.

Bunn, A.G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, 26, 115–124.

Buras, A. (2017). A comment on the expressed population signal. *Dendrochronologia*, 44, 130–132.

Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Cantero, A., Sánchez-Salguero, R., Sánchez-Miranda, A. *et al.* (2018). Forest growth responses to drought at short- and long-term scales in Spain: squeezing the stress memory from tree rings. *Front. Ecol. Evol.*, 6, 1–11.

Chitra-Tarak, R., Ruiz, L., Dattaraja, H.S., Kumar, M.S.M., Riotte, J., Suresh, H.S. *et al.* (2017). The roots of the drought: hydrology and water uptake strategies mediate forest-wide demographic response to precipitation. *J. Ecol.*, 12, 3218–3221.

Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C. *et al.* (2016). The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Glob. Chang. Biol.*, 22, 2329–2352.

Cook, E.R. & Peters, K. (1981). The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-ring Bull*., 41, 45–53.

Cook, B.I., Ault, T.R. & Smerdon, J.E. (2015). Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Sci. Adv*., 1, e1400082.

Čufar, K., Prislan, P., De Luis, M. & Gričar, J. (2008). Tree-ring variation, wood formation and phenology of beech (*Fagus sylvatica*) from a representative site in Slovenia, SE Central Europe. *Trees*, 22, 749–758.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nat. Clim. Chang*., 3, 52–58.

Delpierre, N., Berveiller, D., Granda, E. & Dufrêne, E. (2016). Wood phenology, not carbon input, controls the interannual variability of wood growth in a temperate oak forest. *New Phytol*., 210, 459–470.

D'Orangeville, L., Maxwell, J., Kneeshaw, D., Pederson, N., Duchesne, L., Logan, T. *et al*. (2018). Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. *Glob. Chang. Biol*., 24, 2339–2351.

Duchesne, L., Houle, D. & D'Orangeville, L. (2012). Influence of climate on seasonal patterns of stem increment of balsam fir in a boreal forest of Québec. *Canada. Agric. For. Meteorol*., 162–163, 108–114.

Elliott, K.J., Miniat, C.F., Pederson, N. & Laseter, S.H. (2015). Forest tree growth response to hydroclimate variability in the southern Appalachians. *Glob. Chang. Biol*., 21, 4627–4641.

Fan, Y., Li, H. & Miguez-Macho, G. (2013). Global patterns of groundwater depth. *Science*, 339, 940–943.

Fan, Y., Miguez-Macho, G., Jobbágy, E.G., Jackson, R.B. & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proc. Natl Acad. Sci*., 114, 10572–10577.

Fei, S., Desprez, J.M., Potter, K.M., Jo, I., Knott, J.A. & Oswalt, C.M. (2017). Divergence of species responses to climate change. *Sci. Adv*., 3, e1603055.

Frank, D., Reichstein, M., Bahn, M., Thonicke, K., Frank, D., Mahecha, M.D. *et al*. (2015). Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. *Glob. Chang. Biol*., 21, 2861–2880.

Gazol, A., Camarero, J.J., Anderegg, W.R.L. & Vicente-Serrano, S.M. (2017). Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Glob. Ecol. Biogeogr*., 26, 166–176.

Giorgi, F., Im, E., Coppola, E., Diffenbaugh, N., Gao, X., Mariotti, L. *et al*. (2011). Higher hydroclimatic intensity with global warming. *J. Clim*., 24, 5309–5324.

Hacke, U.G., Stiller, V., Sperry, J.S., Pittermann, J. & McCulloh, K.A. (2001). Cavitation fatigue. Embolism and refilling cycles can weaken the cavitation resistance of Xylem. *Plant Physiol*., 125, 779–786.

Harris, I., Jones, P.D., Osborn, T.J. & Lister, D.H. (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *Int. J. Climatol*., 34, 623–642.

Holmes, R. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull*., 43, 69–78.

Jackson, R., Sperry, J. & Dawson, T. (2000). Root water uptake and transport: using physiological processes in global predictions. *Trends Plant Sci*., 5, 1350–1385.

Johnson, D.M., Domec, J.-C., Berry, Z.C., Schwantes, A.M., Woodruff, D.R., McCulloh, K.A. *et al*. (2018). Co-occurring woody species have diverse hydraulic strategies and mortality rates during an extreme drought. *Plant, Cell Environ*., 41, 576–588.

Kamil, B. (2016) MuMIn: Multi-Model Inference. R package version 1.15

Martin-Benito, D. & Pederson, N. (2015). Convergence in drought stress, but a divergence of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. *J. Biogeogr*., 42, 925–937.

Millar, C.I. & Stephenson, N.L. (2015). Temperate forest health in an era of emerging megadisturbance. *Science*, 349, 823–826.

van der Molen, M.K., Dolman, A.J., Ciais, P., Eglin, T., Gobron, N., Law, B.E. *et al*. (2011). Drought and ecosystem carbon cycling. *Agric. For. Meteorol*., 151, 765–773.

Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol*., 4, 133–142.

Pan, Y., Birdey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A. *et al*. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333, 988–993.

Pederson, N., Dyer, J.M., Mcewan, R.W., Hessl, A.E., Mock, C.J., Orwig, D.A. *et al*. (2014). The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecol. Monogr*., 84, 599–620.

Peltier, D.M.P., Fell, M. & Ogle, K. (2016). Legacy effects of drought in the southwestern United States: a multi-species synthesis. *Ecol. Monogr*., 86, 312–326.

Phillips, R.P., Ibáñez, I., D'Orangeville, L., Hanson, P.J., Ryan, M.G. & McDowell, N.G. (2016). A belowground perspective on the drought sensitivity of forests: towards improved understanding and simulation. *For. Ecol. Manage*., 380, 309–320.

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M.D., Seneviratne, S.I. *et al*. (2013). Climate extremes and the carbon cycle. *Nature*, 500, 287–295.

Schwalm, C.R., Anderegg, W.R.L., Michalak, A.M., Fisher, J.B., Biondi, F., Koch, G. *et al*. (2017). Global patterns of drought recovery. *Nature*, 548, 202–205.

Sperry, J.S., Wang, Y., Wolfe, B.T., Mackay, D.S., Anderegg, W.R.L., McDowell, N.G. *et al*. (2016). Pragmatic hydraulic theory predicts stomatal responses to climatic water deficits. *New Phytol*., 212, 577–589.

Stokes, M.A. & Smiley, T.L. (1999). *An Introduction to Tree-Ring Dating*. University of Arizona Press, Tucson, AZ.

Taylor, K.E., Stouffer, R.J. & Meehl, G.A. (2012). An overview of CMIP5 and the experiment design. *Bull. Am. Meteorol. Soc*., 93, 485–498.

Voorhess, N. (2000). Project J2X V 5.0 software.

Vose, J.M., Clark, J.S., Luce, C.H. & Patel-Weynand, T. (2016). Effects of drought on forests and rangelands in the United States: a comprehensive science synthesis. *U.S. Dept Agric. Gen. Tech. Rep*., WO-93a, 302.

Wigley, T.M.L., Briffa, K.R. & Jones, P.D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Clim. Appl. Meteorol*., 23, 201–213.

Wu, X., Liu, H., Ciais, P., Flurin, B., Guo, W., Zhang, C. *et al*. (2017). Differentiating drought legacy effects on vegetation growth over the temperate Northern hemisphere. *Glob. Chang. Biol*., 24, 504–516.

Xiao, J., Zhuang, Q., Law, B.E., Baldocchi, D.D., Chen, J., Richardson, A.D. *et al*. (2011). Assessing net ecosystem carbon exchange of U. S. terrestrial ecosystems by integrating eddy covariance flux measurements and satellite observations. *Agric. For. Meteorol*., 151, 60–69.

Yamaguchi, D. (1991). A simple method for cross-dating increment cores from living trees. *Can. J. For. Res*., 21, 414–416.

Zhang, T., Niinemets, Ü., Sheffield, J. & Lichstein, J.W. (2018). Shifts in tree functional composition amplify the response of forest biomass to climate. *Nature*, 556, 99–102.

Zimmerman, M. (1983). *Xylem Structure and the Ascent of Sap*. Springer-Verlag, Berlin.

SUPPORTING INFORMATION

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

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