Global Change Biology

Differences in species-level growth responses to hydroclimate extremes in eastern US forests: Implications for a changing region

Journal:	*Global Change Biology*
Manuscript ID	GCB-24-0776
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	15-Mar-2024
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	dominant, are more sensitive to drought than the xeric species such as oaks (Quercus) and hickory (Carya), especially the moderate and extreme drought intensities. Although more extreme droughts produce a larger annual growth reduction, mild droughts resulted in the largest cumulative growth decreases due to their more frequent occurrence. When using global climate model projections, all scenarios show drought frequency increasing substantially (3-9x more likely) by 2100. Thus, the ongoing demographic shift toward more mesic species in the eastern US combined with drier conditions results in larger drought-induced growth declines, suggesting that drought will have an even larger impact on aboveground carbon uptake in the future in the eastern US.

Title: Differences in species-level growth responses to hydroclimate extremes in eastern US forests: Implications for a changing region

Running Title: Species growth responses to climate extremes

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Abstract

Forests around the world are experiencing changes due to climate variability and human land use. How these changes interact and influence the vulnerability of forests are not well understood. In the eastern United States (US), well-documented anthropogenic disturbances and land-use decisions have influenced forest species assemblages, leading to a demographic shift from forests dominated by xeric species to those dominated by mesic species. Contemporarily, the climate has changed and is expected to continue to warm and produce higher evaporative demand, imposing stronger drought stress on the forests. Here, we use an extensive network of tree-ring records from common hardwood species across ~100 sites and ~1300 trees in the eastern US to examine the magnitude of growth response to both wet and dry climate extremes. We find that growth responds asymmetrically to drought, with the positive growth response to pluvials failing to outweigh reductions of growth during drought. Mesic species such as *Liriodendron tulipifera* and *Acer saccharum*, which are becoming more dominant, are more sensitive to drought than the xeric species such as oaks (*Quercus*) and hickory (*Carya*), especially the moderate and extreme drought intensities. Although more extreme droughts produce a larger annual growth reduction, mild droughts resulted in the largest cumulative growth decreases due to their more frequent occurrence. When using global climate model projections, all scenarios show drought frequency increasing substantially (3-9x more likely) by 2100. Thus, the ongoing demographic shift toward more mesic species in the eastern US combined with drier conditions results in larger drought-induced growth declines, suggesting that drought will have an even larger impact on aboveground carbon uptake in the future in the eastern US.

Keywords: Drought, Pluvial, demographic shift, tree rings, climate change

Introduction

Globally, forests are vulnerable to changes in climatic conditions (Breshears et al. 2005; McDowell et al. 2008; Allen et al. 2010) and from human land-use decisions (Hamrick 2004; McDowell et al. 2020). Forests in the eastern United States (US) are a classic example, with well-documented, frequent, and extensive anthropogenic and natural disturbances over the past *ca.* 200 years. Forest species composition across the eastern US have been strongly influenced by human land management, where frequent fire and thinning before the 1850s by indigenous groups prompted forests dominated by *Quercus* (oak) and *Carya* (hickory). European colonization was followed by massive deforestation and later reforestation coupled with fire suppression. Such practice resulted in a decline in the prevalence of *Quercus* and *Carya* species and allowed the establishment of other less fire tolerant species such as *Acer spp.* (maple), *Fagus grandifolia* (American beech)*,* and *Liriodendron tulipifera* (tuliptree) (Fei et al. 2011), which are now poised to replace the aging oaks and hickories (Novick et al. 2022).

The climate in the eastern US is also changing. Over the last several decades, an extended wet period (or pluvial) has been prevalent across large parts of the eastern US (Karl et al., 1996; Pederson et al., 2013; Ford 2014; Maxwell and Harley 2017). Further, the rate of temperature increase in the eastern US compared to other regions of the world has been muted, in a large part, due to reforestation (Barnes et al., 2024). Thus, the wetter and relatively cooler climate has reinforced and accelerated ongoing demographic shifts in eastern US forests, resulting in less drought and fire (McEwan et al., 2011). However, the rate of reforestation is likely to decrease, diminishing the temperature buffering effect (Barnes et al., 2024). Combined with the continued warming of global temperatures from anthropogenic emissions, hotter and drier conditions in the eastern US are likely to accelerate (Ficklin and Novick, 2017; Wehner et al., 2017).

The likelihood of a shift from an exceptionally wet climate to a more arid climate in eastern North America requires an understanding of the response of species and forest stands to climatic extremes (Costanza et al., 2023). The impact of climatic extremes on tree growth depends on the timing, context, duration and intensity of water stress (Schwarz et al., 2020), with trees experiencing greater growth reductions when drought occurs during the growing season (Delpierre et al., 2016; D'Orangeville et al., 2018; Hoffmann et al., 2018). Additionally, forest composition may play a role in drought response since tree species diversity may buffer the sensitivity of forests to climate extremes (Grossiord, 2020; Isbell et al., 2015; Anderegg et al., 2018). Less is known about forest responses to pluvial conditions (but see Jiang et al., 2019; Lockwood et al., 2023). Thus, characterizing the response of different species assemblages to climatic extremes is crucial for understanding forest dynamics and productivity under projected future scenarios. This understanding is especially important in the eastern US, where forests have historically sequestered ca. 40% of regional carbon emissions (Pan et al. 2011). The future fate of this sink is uncertain and hinges on tree- and stand-level responses to climate extremes.

While ecophysiological responses to droughts and pluvials, such as changes in gas exchange, are useful for examining species-specific responses, the short length of such records limits the number of extremes to examine species-specific responses. Using tree rings from mature, canopy-dominant trees extends the number of extreme wet and dry events that we can examine to see how growth responds to extreme climatic conditions. Further, growth is often decoupled from photosynthesis (Dow et al. 2022; Cabon et al. 2022), and this is exacerbated during drought (Kannenberg et al. 2022). Thus, examining growth directly can give insight into how droughts will impact long-term carbon storage in woody biomass and how ongoing demographic shifts could impact the response of eastern US forests to future climate change.

Here, we examine the magnitude of growth responses of several common eastern US hardwood tree species to both wet and dry climate extremes. We hypothesize that ongoing demographic shifts are producing forests that are more susceptible to deleterious drought impacts on growth, a change with negative impacts to carbon sequestration. To test the hypothesis, we leverage a broad and diverse network of ~100 tree-ring chronologies (~1300 trees), focusing on five of the most widespread species throughout the eastern US. We further examine how this demographic shift will impact future responses of eastern US forests by using climate model projections for a number of greenhouse-gas scenarios.

Methods

Study region/samples

The study region encompasses a large portion of the Eastern Deciduous Forest biome in North America (Figure 1). The climate over this area is humid continental with the southern portion of the study region having a humid sub-tropical climate. We targeted canopy-dominant trees from the most common species in this region, species that also employ a range of water-use strategies from aggressive (*i.e.* anisohydric; *Q. rubra and Q. alba*), intermediate (*C. ovata* and *A. saccharum*), and conservative (*i.e.* isohydric; *L. tulipifera*) (Roman et al. 2015; Yi et al., 2019; Novick et al. 2022).

Tree-ring processing

We collected tree-ring chronologies (published in: Pederson, 2005; Maxwell et al., 2020) across 36 forest stands for a total of 99 chronologies. All 36 sites had at least two co-occurring species, while 19 sites had three, and six sites had four or more. While each of the five species were not present at every site, sampling those that are growing in the same landscape position at each site decreases the confounding influence of site conditions and allows for a clearer comparison of species-specific growth response to extreme climate (Au et al. 2020, 2022a; Lockwood et al. 2023). Overall, we gathered a total of 18 chronologies for *Q. rubra,* 25 for *Q. alba,* 19 for *C. ovata,* 15 for *A. saccharum*, and 22 for *L. tulipifera* across the eastern deciduous forest (Figure 1).

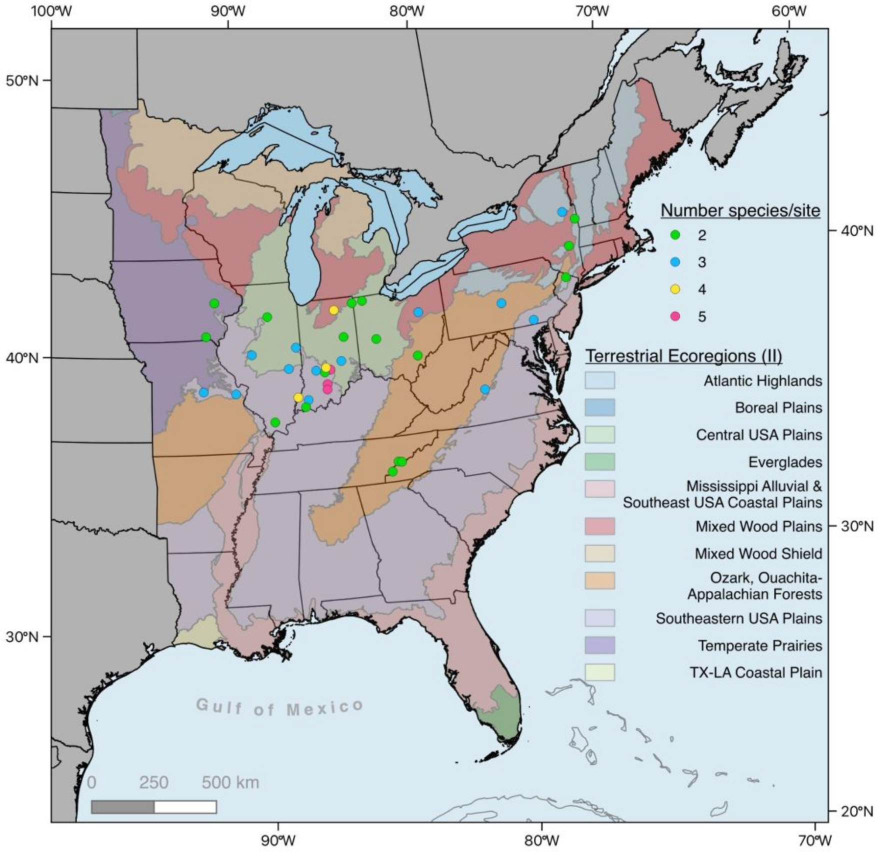

Figure 1: Tree-ring study sites across the Eastern Deciduous Forest biome. Map of tree-ring sites showing the number of species-specific chronologies per study site along with the level two terrestrial ecoregions as defined by Commission for Environmental Cooperation (http://www.cec.org/north-american-environmental-atlas/).

For each site, we created species-specific chronologies that were generated from 5 to 50 trees, giving us a total of 1,299 trees used in this study. We followed standard collection methods for dendrochronological studies. We targeted canopy-dominant trees and extracted two core samples per tree. Once the samples were prepared using progressively finer sandpaper, we visually crossdated the ring widths and used the program COFECHA (Holmes 1983) to statistically ensure accurate dating. We reduced growth related to non-climatic influences by standardizing each measurement series with a two-thirds spline (Cook and Peters 1981) and adjusting for endpoints (Bussberg et al. 2020) using the program ARSTAN (Cook 1985).

Sampling from canopy-dominant trees whilst not including information from the subcanopy can introduce a bias when examining species-specific responses to climate (Dye et al. 2016). Traditionally, canopy-dominant species were thought to be more sensitive to climate (Alexander et al. 2018) compared to subcanopy trees, but this may not be the case in more mesic forests, such as in the eastern US, where the sub-canopy trees could have a larger decrease in growth during hot periods (Rollinson et al. 2021). However, canopy-dominant trees sequester carbon for longer periods, account for more biomass and carbon reserve (Bennett et al. 2015), and have lived long enough to experience multiple droughts and pluvials of differing intensities. Thus, they are arguably a fundamental portion of the forest canopy for understanding drought impacts on growth and their consequences for carbon sequestration.

Climate Data

We gathered monthly standardized precipitation-evapotranspiration index (SPEI; Beguería et al. 2014) data for the nearest (0.5 °) grid point to each forest stand. The SPEI is standardized based on a probabilistic mapping of the precipitation (water supply) minus potential evapotranspiration (water demand) distribution onto a standard normal distribution, producing an index where 0 represents median conditions for a given location over the time period used for the fitting. This approach allows us to compare the influence of extreme dryness and wetness on tree growth across multiple sites that experience different climatic regimes. Because both water supply and water demand can influence tree growth, incorporating an index that includes both metrics is important (Williams et al. 2013, Novick et al. 2024). The SPEI is multiscalar, so it also allows us to evaluate how the duration of abnormal to extreme wet and dry conditions impact species-specific growth. We gathered SPEI for three temporal scales (1, 3, and 6 months) to represent short-term to growing season length anomalies in soil moisture. To capture climatic conditions that could influence the entire growing season, we examined conditions from March through August, using SPEI6 for August. To represent the peak of the growing season, we examined SPEI3 in July, which represents conditions from May through July. Lastly, for the short timescale (SPEI1), we gathered data for each month from May–August, which are the most important months for growth in eastern North America (D'Organville et al. 2018). We present the results from SPEI6 in the main text and provide the shorter timescale results, which all were similar to those from SPEI6, in the supplemental materials.

Drought and Pluvial effects

To determine how mild to extreme departures in water supply and demand impact species-specific growth, we calculated drought and pluvial effects for each species. We defined three, mutually exclusive drought thresholds, from mild (SPEI ±1.0, which probabilistically equates to one standard deviation from the mean) to moderate (SPEI ±1.5) and extreme (SPEI ±2.0). For each threshold, we calculated the percentage growth change during a drought or pluvial (i.e., drought and pluvial effects) by averaging the standardized ring width (SRW) for all years that were classified as a drought (SRWd) or pluvial (SRWp). We then calculated the averaged ring width for non-drought and non-pluvial years (SRWn). Drought effects were calculated as the difference between the averaged SRW during drought from the normal years then divided by averaged growth during normal years and multiplied by 100 to get a percentage change (Kannenberg et al. 2019; Au et al., 2020). Pluvial effects were calculated in the same manner except with the difference between the averaged growth during pluvial years and normal years.

$$Drought\ Effect = \frac{\underline{SRW}d - \underline{SRW}n}{\underline{SRW}n} X\ 100$$

where SRWd and SRWn are the average standardized growth for all drought years and normal years respectively.

$$Pluvial\ Effect = \frac{\underline{SRW}p - \underline{SRW}n}{\underline{SRW}n} X\ 100$$

where SRWp and SRWn are the average standardized growth for all pluvial years and normal years respectively.

We calculated drought and pluvial effects for each month from May–August for SPEI1, May-July average for SPEI3, and March-August average for SPEI6. To determine if the mean effects were significantly different across the species, we used one-way ANOVA with a Tukey HSD post hoc test.

To examine the lasting effects of extreme wet and dry conditions on SRW, we calculated the growth differential percentage (Lloret et al., 2011) where we formed the ratio of the mean SRW during the two years following the extreme year (Kannenberg et al., 2019) subtracted from the growth during the extreme year in the numerator and the mean of SRW during the five years preceding the extreme year (Au et al. 2022b) in the denominator:

$$Growth\ Differential\ = \frac{\underline{SRW}post1-2\ -\ \underline{SRW}e}{\underline{SRW}pre1-5} X\ 100$$

where *e* represents the year of an extreme event.

We excluded extreme years that occurred within five years following or two years prior to another event. We chose to examine only the two years following an extreme event since previous research has found that legacies longer than two years are relatively rare in Eastern Deciduous Forests (Kannenberg et al. 2019). When examining the growth differential percentage from pluvials, the resulting index typically will be negative, while recovering from droughts will result in a positive growth differential percentage. In addition to drought and pluvial effect size, we compared the overall response to climate for each species (i.e., between the SRW and SPEI during the period of overlap, 1901 to 2015) using both a linear and a quadratic regression model. We then used both the Akaike Information Criterion (AIC) and adjusted R^2 to evaluate model performance and fit, finding AIC to be lower and adjusted R^2 to be higher for the quadratic model for all species (Supplemental Table 1).

Future projections

To examine how future climate change could impact species-specific responses to extreme wet and dry conditions, we extracted climate projections from 12 global climate models (GCMs) from the Coupled Model Intercomparison Project – Phase 6 (CMIP6; Eyring et al., 2016) listed in Supplemental Table 2 and for four Shared Socio-economic Pathways (SSP) that include low (SSP1-2.6), moderate-low (2-4.5), moderate-high (3-7.0), and high (5-8.5) emission pathways (O’Neill et al., 2016). For each GCM, we extracted average monthly air temperature, precipitation, and the variables needed to estimate reference evapotranspiration (Allen et al., 2006), which include maximum air temperature, minimum air temperature, wind speed, relative humidity (used to estimate vapor pressure deficit), and incoming solar radiation (used to estimate net solar radiation). After bi-linearly interpolating each GCM to a common 1.5° grid, climate data for the nearest GCM grid node to each forest stand was extracted.

We used the ensemble mean of the monthly mean precipitation along with reference evapotranspiration (Allen et al., 2006) averaged across the growing season months (March-August), to calculate SPEI using the "SPEI" package in R (Beguería et al., 2014; Vicente-Serrano et al., 2010). The parameters of the log-logistic distribution used to estimate SPEI were calculated using the instrumental period (1901-2015). Because the ensemble mean of the future climate conditions has muted interannual variance compared to the instrumentally recorded data, we bias-corrected the projected SPEI after fitting the SPEI distribution using the climate model outputs. The time series of SPEI had both positive and negative biases across its cumulative probability distribution, thus we used quantile mapping to bias correct the projected SPEI for each site (Ficklin et al. 2016; Robeson et al. 2020) with the "RQUANT" method in the "QMAP" package in R (Gudmundsson et al. 2012).

Scaling for forest response

To examine how our results using 36 forest stands may scale to larger spatial scales, we used a community-weighted mean approach based on composition estimates of the canopy from the Forest Inventory and Analysis (FIA) for the eastern US. Because our study sites cover a large area and species composition varies dramatically over space, we calculated multiple forest response scenarios based on species compositions found throughout the eastern US including: 1) a xeric species (*Quercus* and *Carya*) dominated forest with *Quercus* making up 40%, *Carya* 40%, *Acer* 10%, and *Liriodendron* 10%; 2) a mesic species dominated forest where *Acer* makes up 40%, *Liriodendron* 40%, *Quercus* 10%, and *Carya* 10%; and 3) a mixed forest, where

Quercus, *Carya*, *Liriodendron*, and *Acer* each make up 25% of the forest. In the FIA data, we did not see an *Acer* or *Liriodendron* dominated forest and thus did not create one for this analysis. Similarly, there were other assemblages like “beech-maple” (*Fagus-Acer*) or “maple-hemlock” (*Acer-Tsuga*) that were common in the FIA data, but we did not have the species well-replicated in our co-occurring tree-ring network and thus, we did not examine these species combinations.

Lastly, to evaluate the cumulative effect of droughts and pluvials for each forest type, we multiplied the magnitude of the drought and pluvial effects using 75th, 50th, and 25th percentiles (shown in Figure 2) of the range of effects sizes across the sites for each species with the number of occurrences over the observed period (1901-2015). We then scaled those cumulative effects across the different forest types. For future conditions, we conducted the same calculation using future climate projections for each climate scenario, where we used the same effect sizes but then multiplied by the number of occurrences of extreme events for each threshold for the future period (2016-2100). To make the comparison over the same number of years across the observed and the future projections, we shorten the observed record to 1932-2016.

Results

Drought and Pluvial Effects

Of the five species examined, the growth of *L. tulipifera* was most sensitive to drought, with a median drought effect ranging from a 19% decrease in growth during mild droughts to a 53% decrease during extreme droughts. During mild droughts (using the seasonal August SPEI6 = -1.0), all species had a similar growth decrease (Figure 2). As the drought intensity threshold increased, drought response differences across species expanded in effect size and *L. tulipifera* was significantly ($p<0.05$) different from *C. ovata, Q. alba,* and *Q. rubra* (Figure 2). The average drought effect of *L. tulipifera* and *A. saccharum* was two times greater than for the *Quercus* and *Carya* species during extreme droughts, while the difference is only 1.25 times greater during mild droughts. The same pattern existed when examining shorter drought durations (i.e., SPEI1 and SPEI3), where all species experienced similar growth decreases during mild droughts but as drought increased, *L. tulipifera* consistently experienced significantly greater decreases in growth during drought while *A. saccharum* had an intermediate response, and *C. ovata* and the *Quercus* species had smaller growth decreases (Supplemental Figure 1 and 2).

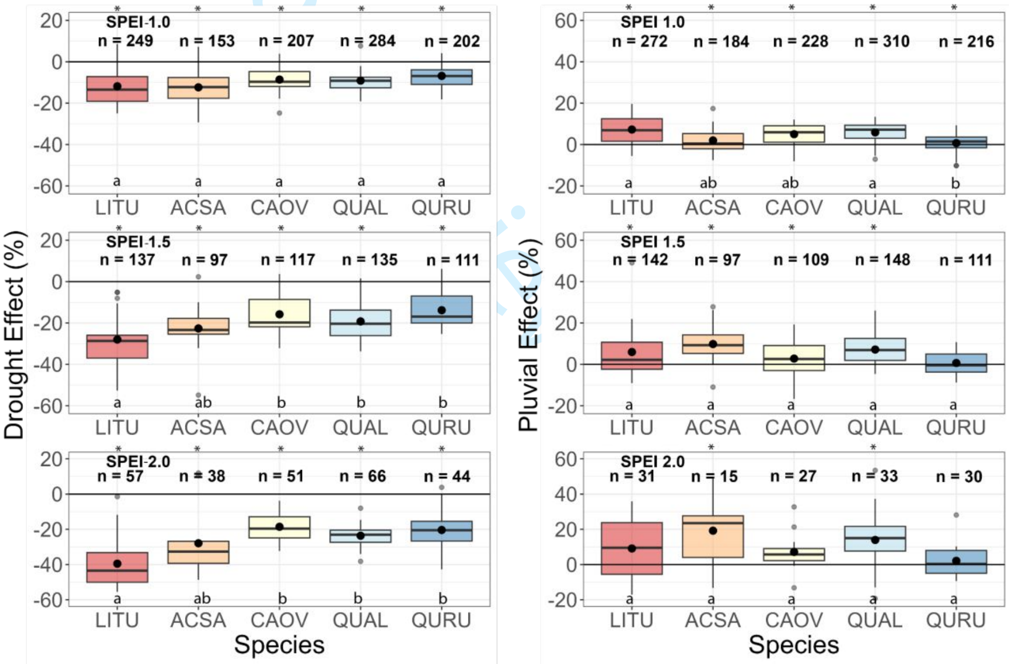

Figure 2: Species-level responses to hydroclimate extremes in eastern US forests. Effects of species growth to drought (left) and pluvial (right) conditions for seasonal (March-August average; August SPEI6) hydroclimate conditions for mild (SPEI6=±1.0; top), moderate (SPEI6=±1.5; middle), and extreme (SPEI6 = ±2.0; bottom) events. Lower-case lettering represents statistical significance differences in effect size between species via an ANOVA analysis Tukey HSD post hoc test. Asterisks represent the mean is significantly ($p \leq 0.05$) different from zero using a one-sample t-test. The sample size of the number of extremes experienced by each species is denoted. LITU=*L. tulipifera;* ACSA=*A. saccharum;* CAOV=*C. ovata;* QUAL= *Q. alba;* QURU=*Q. rubra.*

The pluvial effects were relatively smaller in magnitude (all less than 20% increases in growth) than drought responses, and there were few differences in pluvial response among species (Figure 2). As pluvial intensity increased, growth generally remained the same or marginally increased (Figure 2). Further, the lack of species-specific response remained as pluvial intensity increased, although the variance of the response increased to the point that only *A. saccharum and Q. alba* had responses significantly different than zero (Figure 2). This same pattern occurred during shorter pluvial durations (SPEI1 and SPEI3), with increased variance in the pluvial response with increased intensity and a lack of a species-specific response (Supplemental Figures 3 and 4). In all cases, the pluvial response was smaller than the drought response.

Sensitivity to climatic extremes

When examining the slope of the non-linear relationship between growth and the full spectrum of growing season SPEI (not just the extremes), we find similar species-specific responses (Figure 3, Supplemental Table 1). *Liriodendron tulipifera* has the steepest slope followed by *A. saccharum, Q. alba*, *C. ovata,* and *Q. rubra* during drought conditions (Figure 3). Slopes during pluvial conditions were marginally positive or flat during mild wet conditions and shifted to more negative slopes when pluvial conditions increased in intensity for all species (Figure 3).

The growth differential percentage indicates that *L. tulipifera* growth post drought is the closest to the pre-drought level (Figure 4) across the two lower drought intensity thresholds, however *A. saccharum* has a higher growth after the most extreme droughts. Interestingly, we see species-specific patterns in growth after drought throughout the various drought intensities (Figure 4). However, for more intense droughts, species-specific responses become more pronounced with the general pattern that growth from *L. tulipifera* and *A. saccharum* is closer to pre-drought conditions, while *C. ovata, Q. alba,* and *Q. rubra* have less growth compared to pre-drought conditions (Figure 4). When examining how growth returns to normal from wet events (Supplemental Figure 5), the growth differential percentage has generally lower negative percentages (i.e., above the pre-pluvial growth conditions) with few differences among species. As conditions get wetter, we see a weaker growth differential percentage with only *Q. alba* having a growth differential percentage different from zero during the most extreme pluvials.

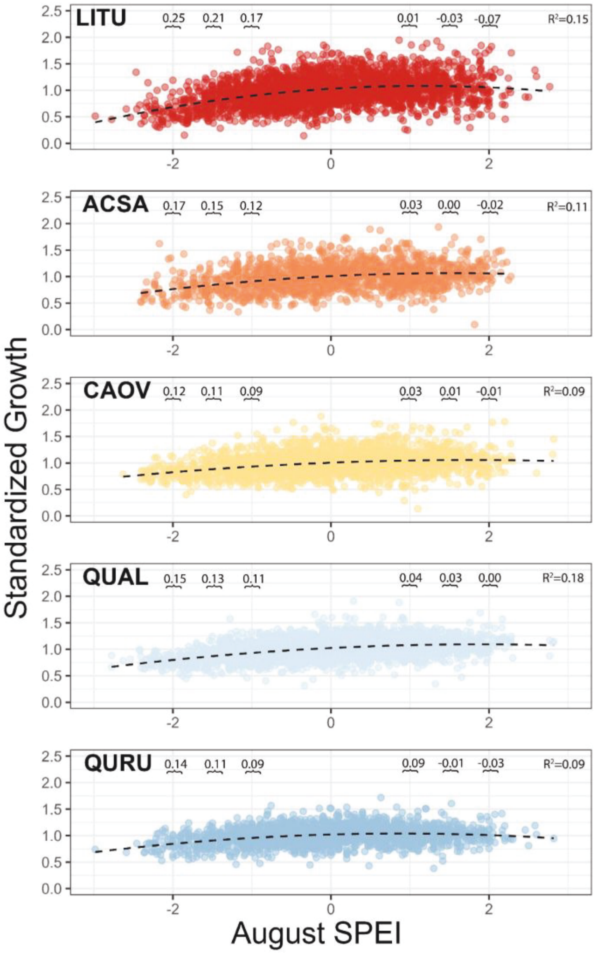

Figure 3: The relationship between standardized growth and March-August SPEI (August SPEI6) values for each species. Dashed line is the ordinary least-squares quadratic regression whose slope (SRW/ SPEI) at SPEI values of -2.0, -1.5, -1.0, 1.0, 1.5, and 2.0 along with R^2 are given in each panel.

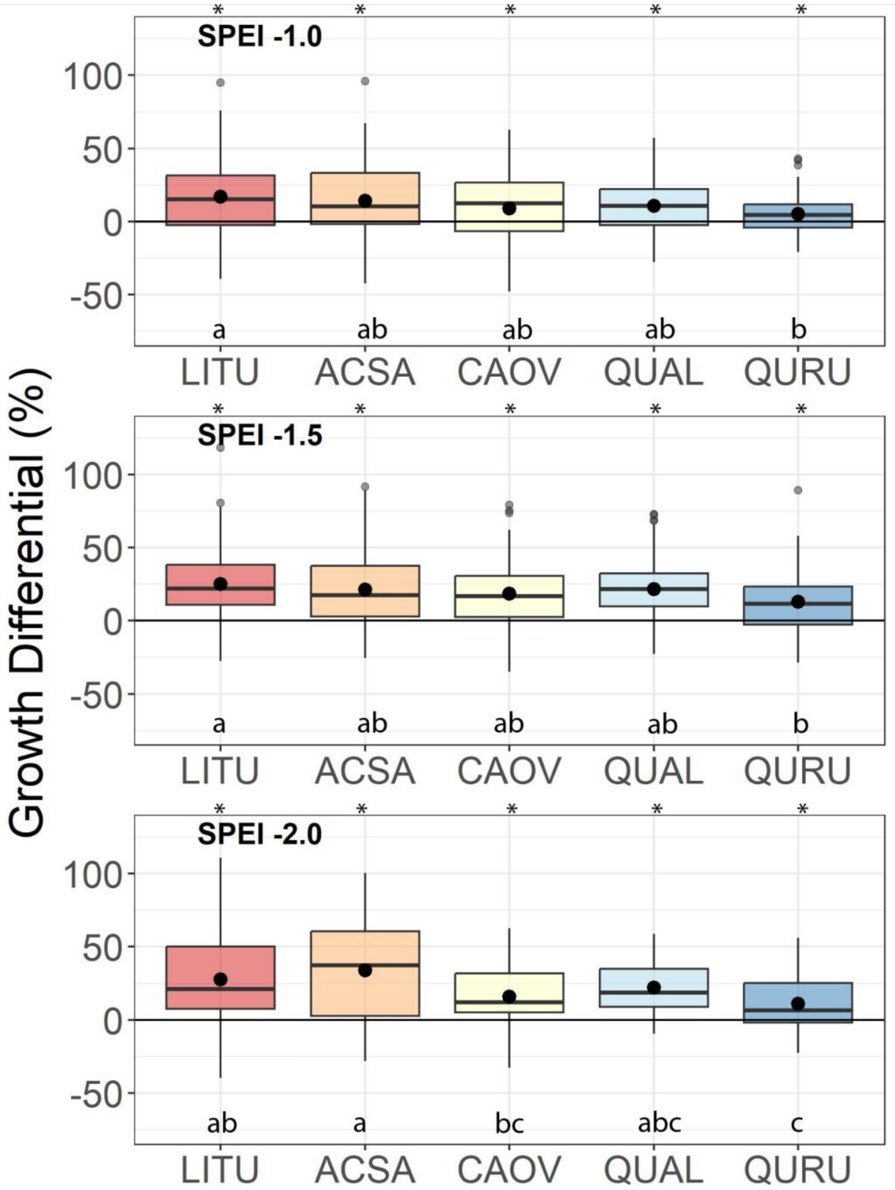

Figure 4: Growth differential percentage from drought index for each species. The growth differential percentage is averaged from the two years after drought and accounts for the weighting of drought impacts on growth. A higher mean growth differential percentage indicates growth closer to the pre-drought conditions. Lettering represents statistical significance differences in effect size between species via an ANOVA analysis Tukey HSD post hoc test. Asterisks represent the mean is significantly higher than zero using a one-sample t-test.

Forest Response

When scaled to represent various species compositions of canopy-dominant trees throughout the eastern US, we found that the xeric species makeup (80% *Quercus*-*Carya*) had the smallest mean growth reduction (14.5%) to drought compared to the other forest compositions (15.9-18.7%) across drought intensities for the growing season (August SPEI6) (Figure 5). The mesic species makeup (80% *Acer-Liriodendron*) had the highest mean growth reduction at 18.7%. Thus, more intense droughts have a larger (up to 8% total) impact on growth for mesic dominant forests compared to xeric (Figure 5). For pluvials, we see that xeric forests have the smallest increase in growth and mesic forests have the largest increases. In all cases, the increases in growth from pluvials are smaller than the decreases during drought (Figure 5). In terms of growth differential percentage, forests composed of mesic species have higher growth differential percentages than xeric forests, particularly for extreme droughts (Figure 5). The return to normal growth from pluvial conditions is modest with large errors, independent of the intensity of the pluvial event (Figure 5).

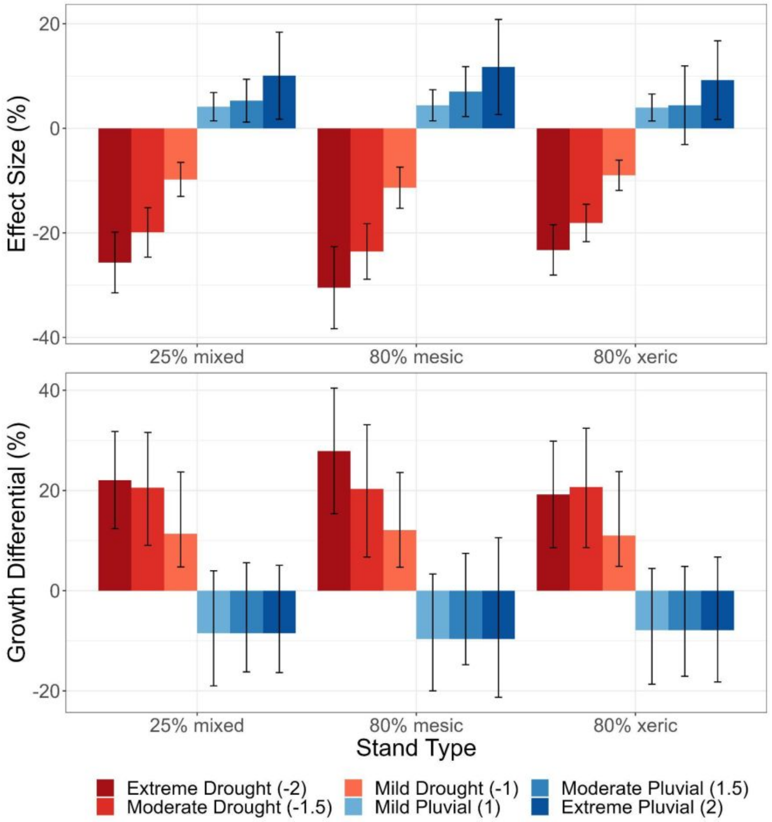

Figure 5: Effect size and growth differential percentage for Eastern Deciduous Forest species under hydroclimate extremes. Top) Pluvial and drought effect sizes for scaled canopy dominant species composition scenarios across intensity thresholds, with error bars. Bottom) Growth differential percentage percentages for scaled canopy dominant species composition scenarios across intensity thresholds, with error bars. Xeric = 80% of canopy dominant trees are *Qurcus* and *Carya*; Mesic = 80% of trees are *Acer* and *Liriodendron*; Mixed = *Quercus, Carya, Liriodendron,* and *Acer* each make up 25% of the forest.

Future Climate

The ensemble of the climate models projects a drier climate in the future (2016-2100) for all scenarios across the 37 sites, ranging from a mean decrease of –0.38 (SSPI -2.6) to –1.00 (SSP5-8.5) in August SPEI6 (Supplemental Figure 6). In addition to a shift in mean conditions, the distribution of SPEI values changes depending on concentration scenario and drought or pluvial category (Supplemental Figure 6). On the wet tail of the distribution, we see very little change across scenarios and only marginal changes from the observed period, although the mildly wet SPEI values become much less frequent (2-5 times less frequent depending on the scenario) compared to the observed period (Supplemental Table 3). On the drier side of the distribution, we see dramatic shifts in occurrence for mild, moderate, and extreme droughts (SPEI = –1.0, –1.5, and –2.0 respectively). Regardless of the scenario, all droughts are projected to be much more frequent. The likelihood ratio for the mild droughts result in a 3-20 times increase in occurrence (Supplemental Table 3), depending on the scenario of warming, while the moderate and extreme droughts see dramatic increases but to a lesser extent (3-9 times and 3-5 times more likely, respectively) (Supplemental Table 3). Thus, the largest, most likely changes are decreases in mild wet events and increases in all dry events, especially mild droughts.

While the effect size is an important feature, the frequency of occurrence of an extreme event is also critical when thinking about the overall impact of extremes over time. Due to their higher frequency during the observed period, mild droughts have a much larger cumulative effect on growth than do more extreme droughts (Figure 6A). Similarly, mild pluvials lead to a larger cumulative effect on growth due the increased frequency of occurrence, albeit a smaller overall effect compared to drought decreases. Of the various forest types, mesic forests are the most affected by changes in extremes with drought having a larger impact than pluvials (Figure 6A and 6B).

Increased frequencies of hydroclimatic extremes in the future increase the cumulative effect that drought has on growth (Figure 6C and 6D). All climate scenarios indicate an increase in frequency of all drought categories (Supplemental Figure 6), thus we see increases in the cumulative effect of drought across all scenarios with increasing cumulative effects as warming increases. Conversely, more warming leads to less frequent pluvials (likely driven by water demand), thus we see larger effects in the lower warming scenarios (SSP1-2.6 and SSP2-4.5), but in all cases the effect is smaller than in the observed period. Further, the overall effect size is substantially smaller than the drought cumulative effect (Figure 6).

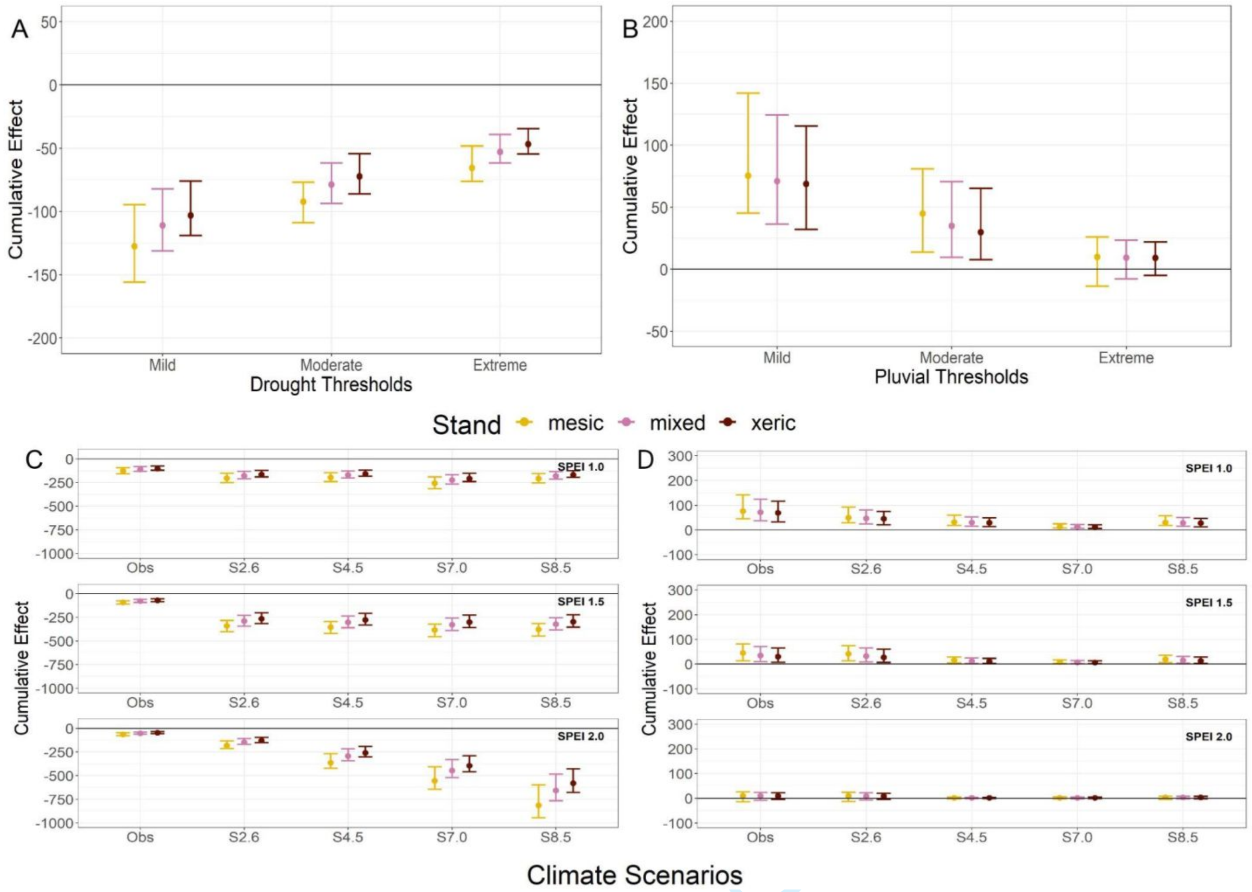

Figure 6: Cumulative effects (effect size multiplied by the number of events) of hydroclimate extremes on species growth for the observed (1901-2016) across each drought (A) and pluvial (B) thresholds and for each future (2016-2100) climate scenario of the 75th, 50th, and 25th quantities for droughts (C) and pluvials (D).

Discussion

We found that the impacts of drought on growth are larger than the pluvial effects (Figures 2 and 6), supporting assertions that nonlinear climate-growth responses are predominant in forests (Dannenberg et al. 2019) including in the eastern US (Rollinson et al. 2021; Anderson-Teixeira et al. 2022). If we assumed a linear relationship, the drought response would have been underestimated (by two-three times), and the pluvial response would have been overestimated compared to the nonlinearly estimated responses (Supplemental Table 1). These findings highlight the importance of accurately modeling the asymmetric climate-growth responses of trees, with implications for estimating impacts to carbon sequestration. Such asymmetric responses across the five studied species indicate that carbon lost from drought-induced radial growth declines is not compensated by increases in growth during wet periods in the eastern US (Figures 2 and 6).

The magnitude of the growth response to drought reveals species-specific responses for all drought intensities. The effect size and the difference of the mean effect size between species increased with drought intensity (Figure 2). Previous research on species-specific growth responses to drought demonstrates mixed results. Some studies found little to no difference in growth responses to drought among species in eastern US forests (e.g., LeBlanc and Terrell 2011; Martin-Benito and Pederson 2015). These studies often used correlation analyses and compared species from different sites. The sensitivity of growth to drought from a given species is dependent on the site climate, with individuals growing in the wettest portion of the range being more sensitive (Heilmayr et al. 2023). Thus, comparing responses between species situated across various locations of their respective range can confound analysis of their drought sensitivity. Other studies that focused on the magnitude of the growth response and examined species that were located in the same landscape positions found that species-specific growth responses to drought depended on water-use strategy, with those being more conservative (isohydric) having greater growth sensitivity to drought (Brzostek et al. 2014; Elliot et al. 2015; Au et al. 2020; Novick et al. 2022; Lockwood et al. 2023). While others have hypothesized that species-specific differences in growth response to drought intensity would increase in a warming climate (e.g., Elliot et al. 2015), little to no evidence has been presented to support that hypothesis. Here, we find support for this hypothesis, finding that species-specific responses increase with drought intensity, likely due to changes in the water table (Brzostek et al. 2014). During mild droughts, all trees have some access to water and thus have smaller growth decreases. During extreme droughts, all species are impacted but those with shallow roots, such as *L. tulipifera* and *A. saccharum* (Bzrostek et al. 2014), have an even larger decrease in growth (Figure 2).

While species-specific responses are prevalent in the moderate and extreme drought intensities, the cumulative impact of mild droughts on growth are larger due to their greater frequency (Figure 6). Eastern US forests are composed of several species that employ various water-use strategies, thus drought conditions can impact certain forest types more than others. Forest stands that have a larger component of mesic species, such as *A. saccharum* and *L. tulipifera*, have larger growth reductions during moderate and extreme droughts compared to those stands with larger proportions of xeric species, such as those in the *Quercus* and *Carya* genera (Figure 6). However, we found the growth differential percentage from the mesic species is higher and thus growth after drought is closer to the pre-drought growth compared to xeric species (Figure 4). This is in part because all species returned close to pre-drought growth after one year, resulting in larger growth differential from the mesic species because they had larger drought effects. Nevertheless, drought will have a larger impact on growth in forests with mesic species but with shorter drought legacies in the years following drought. These nonlinear and species-specific growth responses are important to include in vegetation models to increase our ability to predict how climate will impact forests in the future.

Climate models project a drier climate with more frequent drought in the future in eastern US forests across all scenarios (Supplemental Figure 6), even those with aggressive mitigation (e.g., SSP1-2.6). Given that even moderate droughts have a large impact on species-specific growth responses, the future is very likely to see an increase in differential responses of forest growth to drought, making understanding species responses to climate even more important in the future. In the higher emissions scenarios (SSP3-7.0 and SSP5-8.5), increases in the frequency of extreme drought could have a cumulative effect ~five-times greater than that of the observed period. Depending on the emission scenario of the future, the relative growth after extremes could also see more species-specific responses (Figure 5). The higher emissions scenarios show mesic species returning to pre-drought growth better than the xeric species. Thus, future warming will impact both the growth response during and after extremes, but the intensity of future droughts will determine the degree of species-specific impacts from drought and thus the impact to forest stands with various species composition. We note that this study does not account for any acclimation/adaptation of a given species or new species compositions, something important to consider as we try to better understand how forests will respond to ongoing climate change.

Stem growth is the main above-ground carbon pool (Fahey et al. 2010) and thus, tree-ring responses to climate have large carbon implications (Babst et al. 2014). Compared to variations in photosynthetic processes, drought has a much larger impact on growth (Cabon et al. 2022; Dow et al. 2022) and mortality (Martinez-Vilalta et al. 2019), so drought particularly affects long residence carbon stored from growth and has the potential to reduce the residence time of carbon and impact the amount of carbon that forests sequester (Kannenberg et al. 2022). Our results indicate that as the demographic shift from xeric to mesic species continues throughout large portions of the eastern US (Abrams 2003; McEwan et al. 2011; Novick et al. 2022), drought will have a larger impact on growth and thus carbon storage. While drought induced mortality is relatively less common in the mesic eastern US, mortality remains an important component of the carbon budget. However, mortality tends to be uncorrelated with drought-driven growth reductions (Novick et al. 2022). The need to better understand the role of mortality in the overall above-ground carbon budget is critical to get a more complete picture of how climate impacts carbon pools in mesic forests.

Conclusions

Across deciduous forests of the eastern US, we found that mesic species such as *L. tulipifera* and *A. saccharum* were more sensitive to drought across all drought intensities. Further, growth responded asymmetrically to drought, with the positive growth response to pluvials failing to outweigh reductions of growth during drought. When accounting for forest species composition, forests dominated by mesic species show greater reductions in growth during drought but also higher growth differential percentages. Thus, the ongoing increase in mesic species in eastern US forests in combination with the likely increase in drought conditions, suggest that drought will likely have a larger impact on the carbon uptake in the future in the eastern US. However, these same forests showed higher growth differential percentages following droughts compared to those that are dominated by xeric species. Even with the higher growth after drought, a warmer future with more frequent droughts along with more mesic species will result in more drought-induced carbon losses from a forest that is a tremendous carbon sink.

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Acknowledgements

We thank Josh Bregy, James Dickens, James McGee, Josh Oliver, Karly Schmidt-Simard, Brynn Taylor, Brandon Strange, Michael Thornton, Senna Robeson, Matt Wenzel, and Luke Wylie for assistance in the field and lab. We also would like to acknowledge the following funding: USDA Agriculture and Food Research Initiative grant 2017-67013-26191, National Science Foundation, P2C2 Program AGS-1805617 and AGS-1805276, the Harvard Forest Bullard Fellowship, Harvard University, and Indiana University Vice Provost for Research Faculty Research Program.

Author contribution: Justin T. Maxwell, Tsun Fung Au, Steven A. Kannenberg, and Neil Pederson conceived the ideas and designed methodology; Justin T. Maxwell, Grant L. Harley

Tsun Fung Au, Benjamin Lockwood, Matthew P. Dannenberg, and Neil Pederson collected the data; Justin T. Maxwell, Grant L. Harley, Darren L. Ficklin, and Neil Pederson organized and analyzed the data; Justin T. Maxwell led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

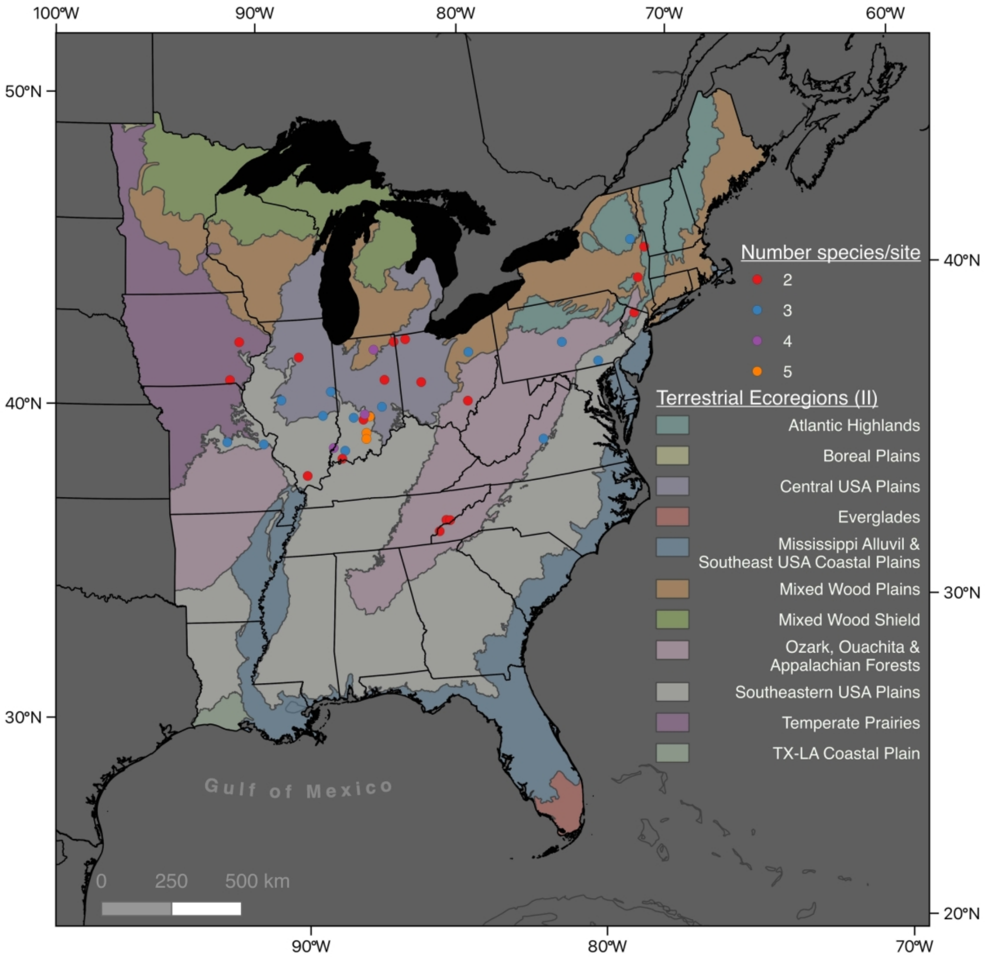

Figure 1: Tree-ring study sites across the Eastern Deciduous Forest biome. Map of tree-ring sites showing the number of species-specific chronologies per study site along with the level two terrestrial ecoregions as defined by Commission for Environmental Cooperation (http://www.cec.org/north-american-environmental-atlas/).

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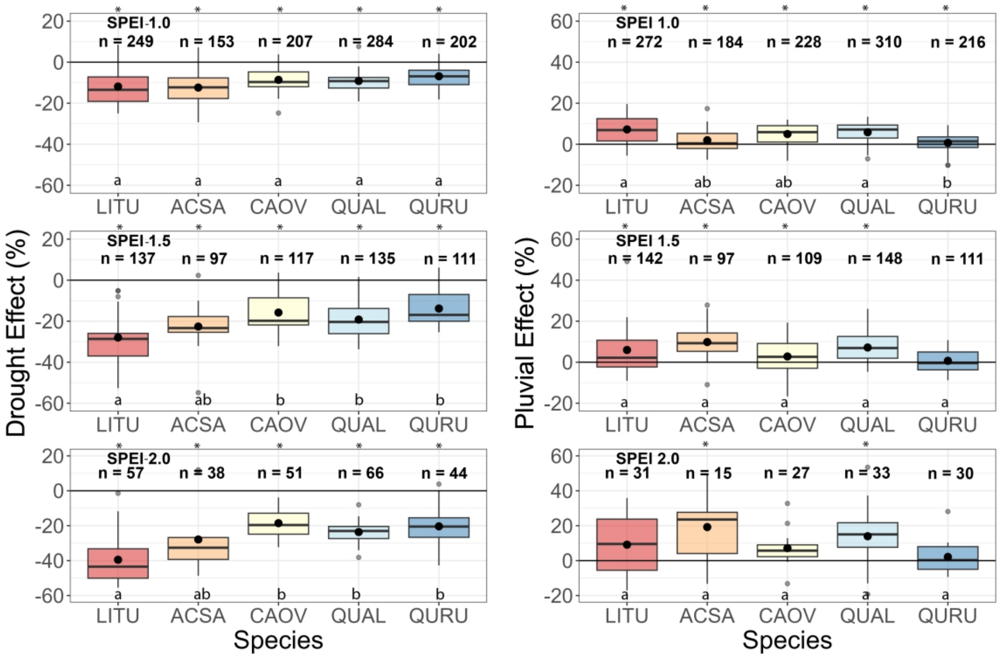

Figure 2: Species-level responses to hydroclimate extremes in eastern US forests. Effects of species growth to drought (left) and pluvial (right) conditions for seasonal (March-August average; August SPEI6) hydroclimate conditions for mild (SPEI6=±1.0; top), moderate (SPEI6=±1.5; middle), and extreme (SPEI6 = ±2.0; bottom) events. Lower-case lettering represents statistical significance differences in effect size between species via an ANOVA analysis Tukey HSD post hoc test. Asterisks represent the mean is significantly ($p \leq 0.05$) different from zero using a one-sample t-test. The sample size of the number of extremes experienced by each species is denoted. LITU=L. tulipifera; ACSA=A. saccharum; CAOV=C. ovata; QUAL= Q. alba; QURU=Q. rubra.

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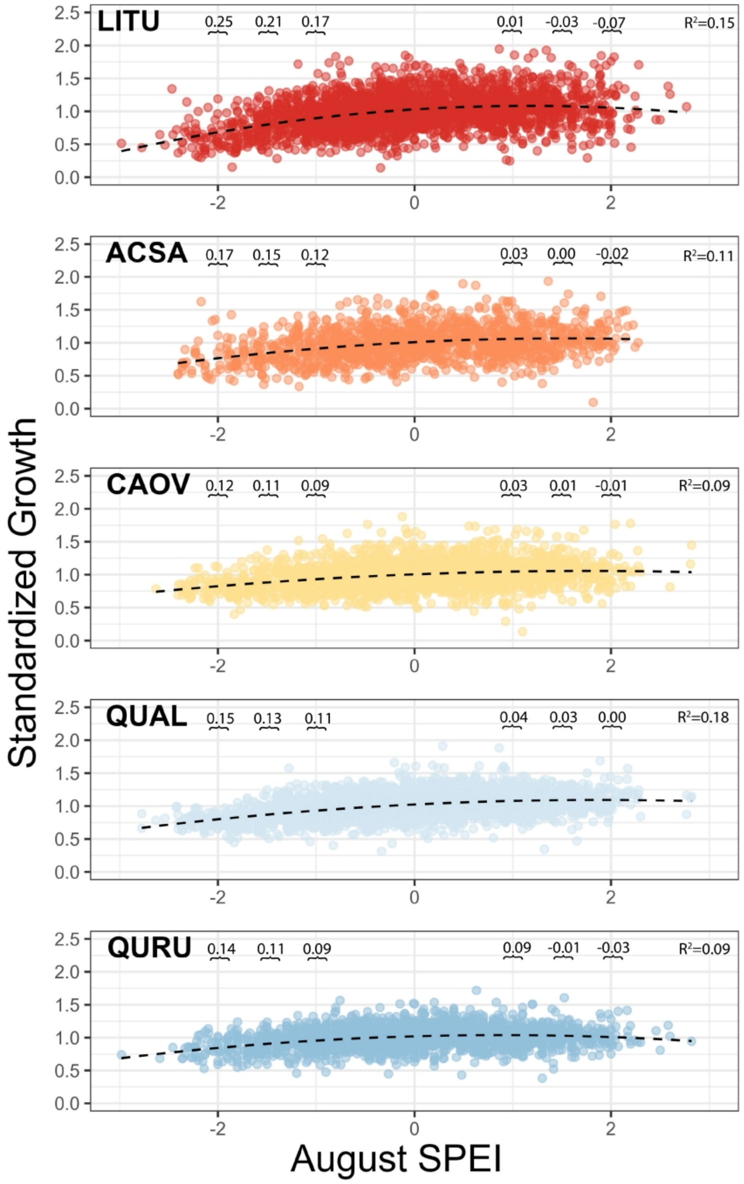

Figure 3: The relationship between standardized growth and March-August SPEI (August SPEI6) values for each species. Dashed line is the ordinary least-squares quadratic regression whose slope (��SRW/��SPEI) at SPEI values of -2.0, -1.5, -1.0, 1.0, 1.5, and 2.0 along with R2 are given in each panel.

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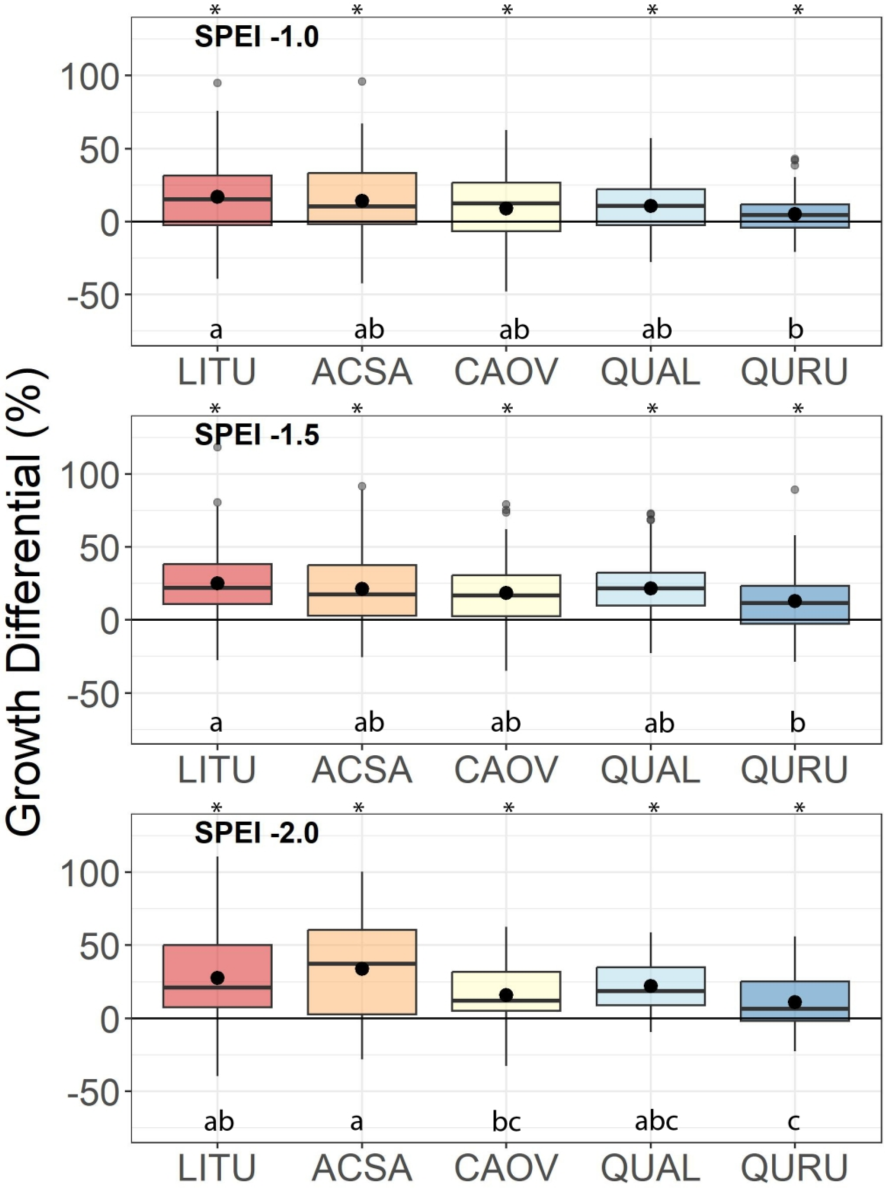

Figure 4: Growth differential percentage from drought index for each species. The growth differential percentage is averaged from the two years after drought and accounts for the weighting of drought impacts on growth. A higher mean growth differential percentage indicates growth closer to the pre-drought conditions. Lettering represents statistical significance differences in effect size between species via an ANOVA analysis Tukey HSD post hoc test. Asterisks represent the mean is significantly higher than zero using a one-sample t-test.

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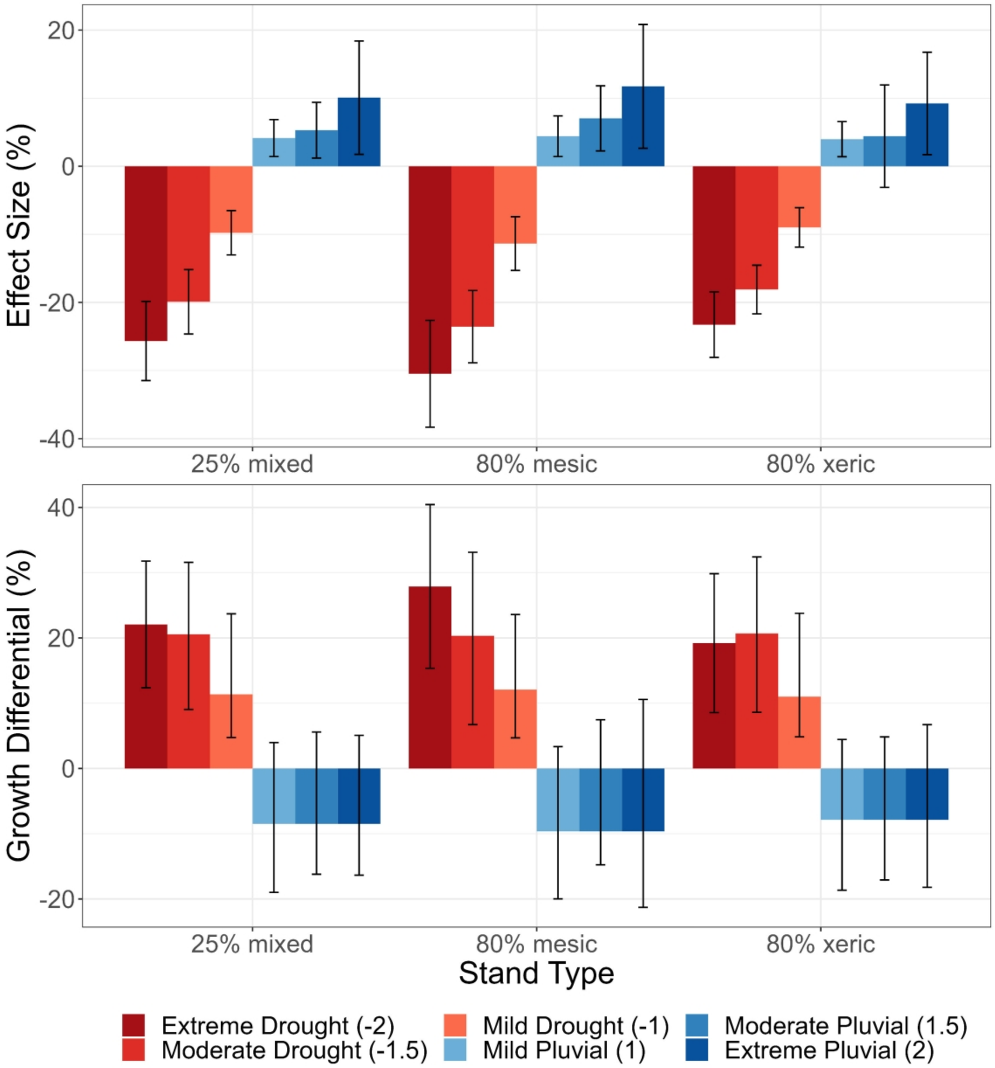

Figure 5: Effect size and growth differential percentage for Eastern Deciduous Forest species under hydroclimate extremes. Top) Pluvial and drought effect sizes for scaled canopy dominant species composition scenarios across intensity thresholds, with error bars. Bottom) Growth differential percentage percentages for scaled canopy dominant species composition scenarios across intensity thresholds, with error bars. Xeric = 80% of canopy dominant trees are Qurcus and Carya; Mesic = 80% of trees are Acer and Liriodendron; Mixed = Quercus, Carya, Liriodendron, and Acer each make up 25% of the forest.

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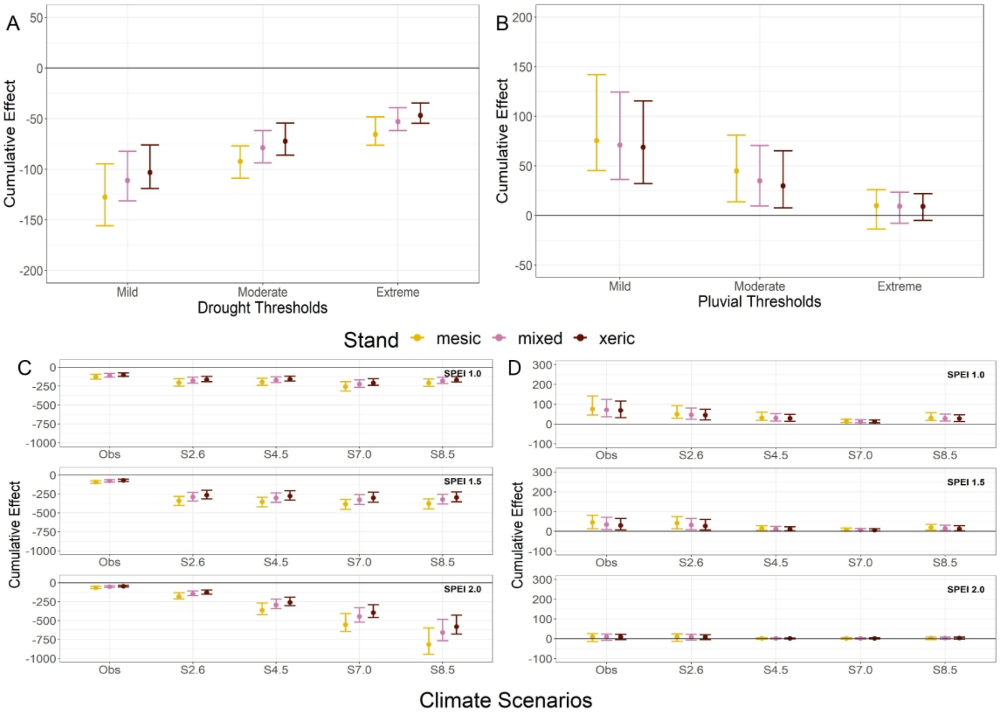

Figure 6: Cumulative effects (effect size multiplied by the number of events) of hydroclimate extremes on species growth for the observed (1901-2016) across each drought (A) and pluvial (B) thresholds and for each future (2016-2100) climate scenario of the 75th, 50th, and 25th quantities for droughts (C) and pluvials (D).

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