Divergent forest sensitivity to repeated extreme droughts

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Climate change-driven increases in drought frequency and severity could compromise forest ecosystems and the terrestrial carbon sink[1–3]. While the impacts of single droughts on forests have been widely studied[4–6], understanding whether forests acclimate to or become more vulnerable to sequential droughts remains largely unknown and is crucial for predicting future forest health. We combine cross-biome datasets of tree growth, tree mortality, and ecosystem water content to quantify the effects of multiple droughts at a range of scales from individual trees to the globe from 1900-2018. We find that subsequent droughts generally have a more deleterious impact than initial droughts, but this effect differs enormously by clade and ecosystem, with gymnosperms and conifer-dominated ecosystems more often exhibiting increased vulnerability to multiple droughts. The differential impacts of multiple droughts across clades and biomes indicate that drought frequency changes may have fundamentally different ecological and carbon cycle consequences across ecosystems.

One sentence summary: Differing ecosystem sensitivity to repeated droughts

Main text

Climate extremes have major impacts on the terrestrial carbon cycle[1–3]. Climate models project increases in the frequency and severity of prominent climate extremes such as drought[3,7,8]. Thus, the response of ecosystems to climate extremes represents an important uncertainty in carbon cycle feedbacks and may have the potential to alter terrestrial ecosystems from a net sink to a carbon source over the 21st century[2,3,9,10]. Severe droughts are one of the most consequential types of climate extremes when considering carbon cycle impacts[11] and can have reverberating societal impacts. The effects of single extreme droughts have been widely studied, such as for severe droughts in Europe[1], North America[4], and the Amazon[5]. By contrast, the ecosystem impacts of repeated extremes remains poorly understood. We remain unable to predict whether, after a severe drought, an ecosystem emerges more or less vulnerable to the next drought[12–14]. Thus, understanding ecosystem response to multiple, repeated droughts is crucial for predicting long-term climate change impacts on ecosystems and the subsequent carbon cycle feedbacks.

Ecosystem resilience to extreme droughts is an integrated combination of i) the capacity of the ecosystem to persist and maintain its state and function during the disturbance, often called 'sensitivity' or 'resistance', and ii) the recovery trajectory following the disturbance[15–17]. Multiple resilience-increasing and resilience-decreasing mechanisms exist at both organism- (e.g. tree) and ecosystem-scales. The net impact of repeated droughts on Earth's forests will depend on their balance. At a tree scale, adjustments in functional traits such as wood density or leaf turgor loss thresholds or in allometric patterns such as increased root or sapwood areas and decreased leaf area can improve tree resilience to future stress[18,19]. By contrast, lingering drought-driven physiological damage such as embolism of the xylem, decreased reserves or defenses, or pest/pathogen attacks and infections, among other mechanisms, may decrease tree resilience to subsequent droughts[20,21]. At an ecosystem scale, forest density changes that lead to lower community-level water loss or changes in species composition that result in a more drought-tolerant community may increase resilience[6,22–24]. By contrast, microclimate feedbacks that drive hotter and drier canopy microenvironments, or landscape-scale pest or pathogen population dynamics triggered by an initial drought that lead to higher pest pressures on communities, could decrease resilience[25–27]. Determining which of these mechanisms dominate under which circumstances and in which forest systems will be fundamental to predicting the future of Earth's forests and their carbon cycle feedbacks.

Here, we examine the drought sensitivity (i.e. inverse of resistance) of forests to repeated droughts based on growth increment at the tree level, mortality at the forest level, and water content at the ecosystem level. When multiple droughts strike a forest, we predict that a system that exhibited increased sensitivity would experience larger growth declines, higher mortality rates, and larger declines in canopy water content during a subsequent drought due to accumulated physiological damage from the initial drought. We leverage a cross-biome tree ring dataset, long-term forest monitoring plots, satellite measurements of canopy water content, and global drought datasets to quantify the effects of repeated droughts across scales. We quantify drought severity here from a climate perspective of the statistical distribution of drought metrics. We ask: 1) Are tree growth and mortality more, less, or similarly sensitive to a subsequent drought compared to an initial drought? 2) Do changes in tree-level drought sensitivity differ by clade, biome, or region? 3) Does drought sensitivity scale from the tree to ecosystem-level and how does this vary by biome and region? We analyze all ecological datasets at multiple levels of drought severity and use a number of approaches to control for potential confounding factors like differences in drought severity (see Methods).

We first examined tree growth patterns using a dataset of 1,208 stand growth chronologies spanning 1900-2015 from the International Tree Ring DataBank. Tree growth decline was larger in a subsequent drought at severe drought values ($p_{SPEI<-2} < 0.001$) and then converged to initial drought levels at more moderate drought values ($p_{SPEI(-1.5,-1.2]} = 0.33$) (Fig. 1A; Extended Data Fig. 1). This suggests a critical role of drought severity whereby an initial severe drought was associated with higher vulnerability to a subsequent severe drought, perhaps due to residual physiological damage. We next examined tree mortality patterns using the extensive U.S. Forest Inventory and Analysis dataset spanning >100,000 forested plots from 2000-2018. In contrast to the growth findings, we found that mortality was relatively similar between initial and subsequent droughts with no significant differences (e.g. $p_{SPEI<-2}$=0.13) (Fig. 1B). Drought severity between the initial and subsequent droughts was not significantly different and thus did not drive these patterns (Extended Data Fig. 2A-B). Tree-level drought sensitivity patterns held when accounting for differences in tree-ring analysis methods (Extended Data Fig. 3), multiple drought metrics (Extended Data Fig. 4), and spatial autocorrelation (Extended Data Fig. 5).

We then examined what factors mediated growth and mortality responses to multiple droughts. Clade (angiosperm-gymnosperm) and family were important predictors of tree ring-based growth sensitivity differences to severe droughts (p_{clade}=0.0009, ANOVA: p_{family}=0.01) with gymnosperms and pine species (Pinaceae) exhibiting the highest sensitivity to subsequent droughts (Fig. 2A-B, Extended Data Fig. 1B). By contrast, angiosperms and oak species (Fagaceae) showed an ‘acclimation-type’ response where growth was less sensitive to subsequent drought than the initial drought ($p=0.03$) (Fig 2A-B). Increased time between the initial and subsequent droughts was associated with smaller growth decline differences, although this effect was modest ($R^2=0.01$, $p=0.02$). When examining mortality from forest inventory data in response to repeated droughts, angiosperms and gymnosperms sensitivities diverged at moderate drought severities ($p_{(-2,-1.8]}=0.03$, $p_{(-1.8,-1.5]}=0.01$). Gymnosperms appeared to show slightly elevated mortality in the initial drought at severe drought levels (e.g. $p_{<-2}=0.02$), whereas angiosperms exhibited higher mortality rates to subsequent droughts at more moderate drought levels ($p_{(-1.8,-1.5]}=0.004$) (Fig. 2C). These contrasting clade patterns may explain the relatively muted mortality signal on the full dataset (Fig. 1B). We hypothesize that higher gymnosperm mortality during initial droughts may be due a "culling of the weak" effect where death of the most vulnerable trees in a population results in less vulnerable trees on average during subsequent droughts, potentially associated with differences in biotic agent attack differences between droughts (e.g. higher beetle attack prevalence in initial droughts).

Both decreases in growth and increases in mortality are likely to negatively impact ecosystem resilience and carbon sequestration over the long-term. Tree bole growth provides a key ecosystem function of carbon storage in a pool with a long residence time (decades to centuries), although extrapolation of tree-rings to whole forest carbon is often challenging, and low growth can be a warning signal preceding large-scale mortality[28,29]. Elevated mortality due to drought will have manifold ecological and carbon cycle consequences, including changes in community composition and carbon sequestration[23]. The higher mortality rate in subsequent droughts for angiosperms during moderate droughts (Fig. 2C) could be due to accumulated physiological damage[20] or because of "structural overshoot" whereby these species might allocate too much carbon to leaf area during non-drought conditions, leading them to experience elevated mortality when drought strikes[30]. We note, however, that the coarse temporal nature of inventory data adds uncertainty and is a caveat in our mortality rate analyses (see Methods).

We further examined ecosystem-scale responses to multiple droughts via remotely-sensed vegetation optical depth (VOD), which captures dynamics of canopy water content and ecosystem drought stress[31,32]. Ecosystem-scale responses showed generally greater magnitudes and similar patterns to tree-level responses, with larger VOD declines in the subsequent drought that were most prominent at severe drought levels ($p_{SPEI<-2}<0.0001$; $p_{SPEI(-1.5,-1.2]}<0.001$) (Fig. 3A). In this dataset alone, we detected slight differences in drought severity between initial and subsequent droughts at severe drought levels (SPEI<-2; Extended Data Fig. 2C) and thus implemented multiple models to account for these differences (see Methods). All of our patterns were robust when accounting for drought severity differences and drought legacy effects (Extended Data Fig. 6; Extended Data Fig. 7). At biome scales, temperate conifer forests and wet tropical forests showed the largest drought-severity-normalized increase in sensitivity in the second drought ($p<0.001$ for both) (Fig 3B; Fig 4). The decrease in drought sensitivity in boreal forests and Mediterranean-type woodlands is intriguing and may be due to community turnover favoring more drought-tolerance species[33]. The Amazonian rainforest stands out as a region of increased sensitivity, which is highly relevant because the Amazon experienced two very severe droughts in 2005 and 2010, which had widely-documented effects on growth, mortality, and carbon cycling in the region[5,34]. Given the importance of the Amazon in the global carbon cycle[35], and that climate projections indicate increased vapor pressure deficit (atmospheric dryness) and in some cases rainfall reductions in this region[36], increased sensitivity to repeated droughts is of critical concern (Fig. 4).

While forests on average showed increasing sensitivity to a subsequent drought, forests diverged enormously and with several broad patterns that were revealed across diverse datasets spanning a wide range of spatial and temporal scales. Angiosperm trees and angiosperm-dominated forests tended to show more acclimation (decreased sensitivity) responses. In contrast, gymnosperms tended to exhibit more stress accumulation (increased sensitivity) responses, except for mortality. These patterns are consistent with anatomical and physiological differences between these two clades. Angiosperms have much higher anatomical flexibility than gymnosperms, for example in terms of xylem anatomy, parenchyma fractions, and whole-plant allocation patterns, that allows angiosperms far more plastic responses when faced with drought[37,38]. Our results are broadly consistent with a recent study[39] that found differences in gymnosperms' and angiosperms' growth responses to drought were linked to subsequent mortality risk, although our analyses examine a greater number of sites and diversity of biomes and include ecosystem-level assessments of multiple drought impacts as well. Changes in competition, light environment, and pest/pathogen dynamics – for example, co-occurring drought and beetle outbreaks have been widely observed in western US gymnosperm species and could drive high mortality levels in initial droughts when stand densities are higher – are other potential mechanisms that might give rise to these responses. One notable exception to the broad clade patterns, however, was the strong increases in sensitivity observed in canopy water content in the Amazon between two severe and closely-timed droughts, which might indicate that drought severity and timing overwhelmed the acclimation responses. Further detailed and long-term studies on tree physiology and forest demography are greatly needed to elucidate and test the various mechanisms that might underlie these patterns.

Current vegetation and Earth system models largely do not contain the major potential mechanisms, such as accumulated physiological damage or pest/pathogen infections, that might generate the patterns observed here. However, representations of physiological processes of drought stress, such as plant hydraulics and forest demography are major priorities in Earth system model development[24,40,41]. These advances hold substantial promise for improving Earth system model simulation of the response of forests to single severe droughts[24,42]. Our results highlight that we must also consider including mechanisms that might mediate changes in forest responses to repeated droughts. For example, trait plasticity and allocation changes based on mechanistic understanding are currently possible to include in large-scale models[43,44] and may enable capturing the responses documented here. We hypothesize that both trait plasticity and clade-specific limits to plasticity have potential to capture the differential responses documented here. Our results further indicate that broad functional-type categories may be useful in setting the limits and directions of changes in acclimation and plasticity.

We have shown both at an individual tree scale and at an ecosystem scale that the response to repeated droughts can diverge from that of a single drought. While there are a few cases of similar or decreasing sensitivity to a subsequent drought, we generally see increased vulnerability to a subsequent drought. These responses were strongly mediated by the clade and family, with gymnosperms broadly showing much higher vulnerability to subsequent droughts. Given projected increases in drought frequency in the 21st century in many regions, our findings point towards decreasing ecosystem resilience, in the near term at least, that may portend ill news for the land carbon sink and Earth's forests in future climates.

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Figures

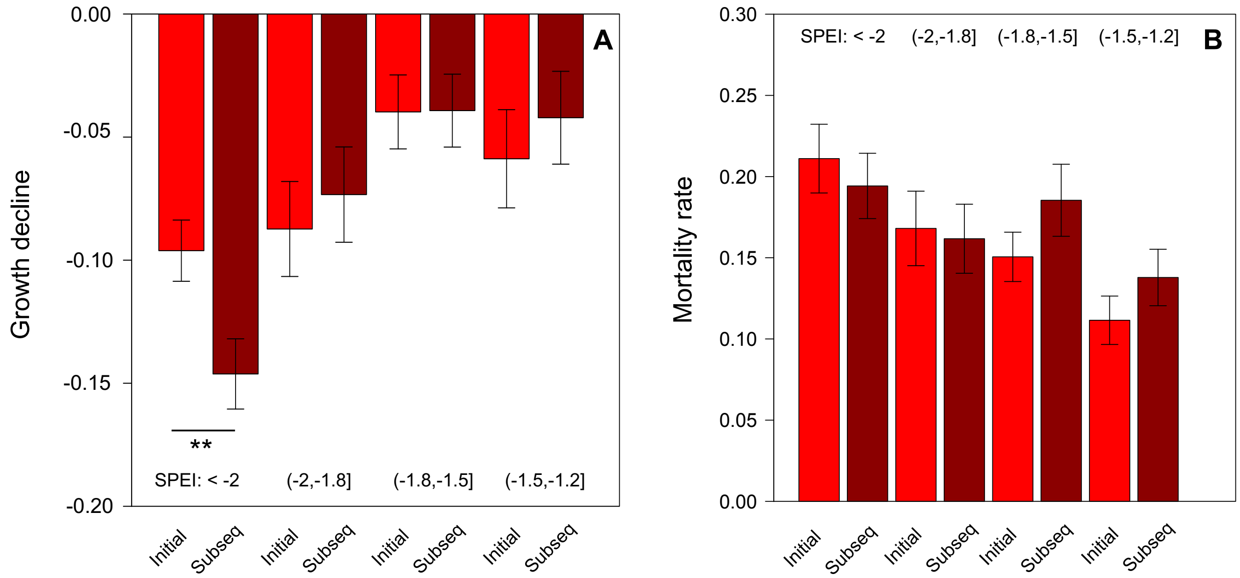

Figure 1: Impacts of a subsequent drought are more deleterious than an initial drought for trees. Growth declines (Δring width index; A) from 1,208 sites in the International Tree-Ring Data Bank to an initial drought (Initial, light red) and subsequent drought (Subseq, dark red), categorized by drought severity of both droughts via the Standardized Precipitation Evapotranspiration Index (SPEI) (left-to-right $N_{chronologies}$= 516, 214, 347, 291). Tree mortality rates (m^2 ha^{-1} yr^{-1}; B) across the U.S. Forest Inventory and Analysis plots to initial and subsequent droughts (left-to-right N_{plots}=6414, 1638, 2781, 958; $N_{grid\text{-}cells}$=140, 62, 112, 59). Error bars indicate ± 1 standard error. Stars indicate statistically significant differences (*p<0.05, **p<0.01)

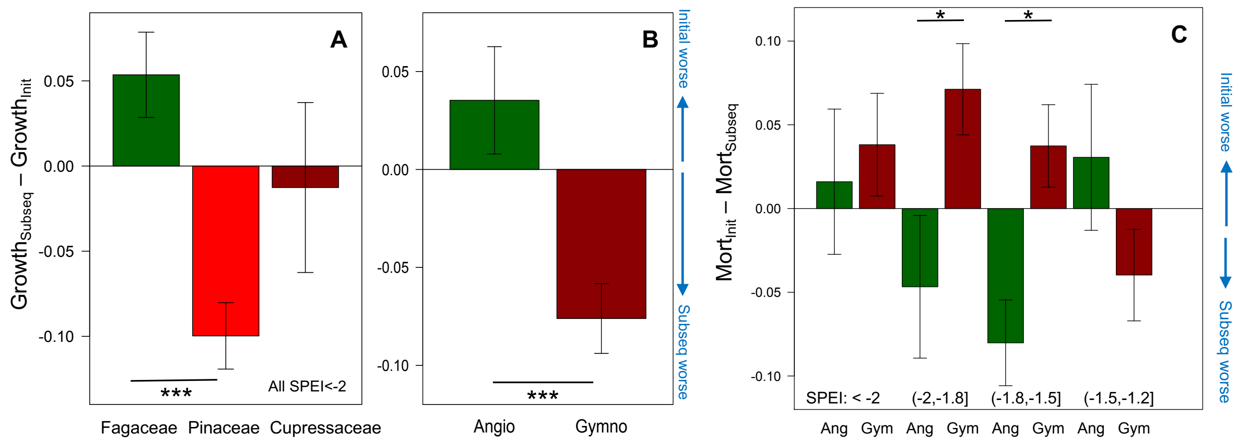

Figure 2: Impacts of multiple droughts on tree growth are mediated by clade. Growth declines differences from the International Tree-Ring Data Bank by family (A) and clade (B) where negative numbers indicate a more deleterious effect of the subsequent drought (left-to-right $N_{chronologies}$= 100, 332, 36, 106, 410). Tree mortality differences (C) across the U.S. Forest Inventory and Analysis plots between angiosperm-dominated (green) and gymnosperm-dominated (red) forests with negative numbers indicating a more deleterious effect of the subsequent drought, categorized by drought severity of both droughts via the Standardized Precipitation Evapotranspiration Index (SPEI) (left-to-right N_{plots}= 2740, 3674, 1011, 627, 1980, 801, 868, 90). Error bars indicate ± 1 standard error. Stars indicate statistically significant differences (***p<0.001; *p<0.05). Note that the order of subtraction is different between (A-B) and (C) to maintain the convention that negative values indicate a more deleterious impact of the subsequent drought across all panels.

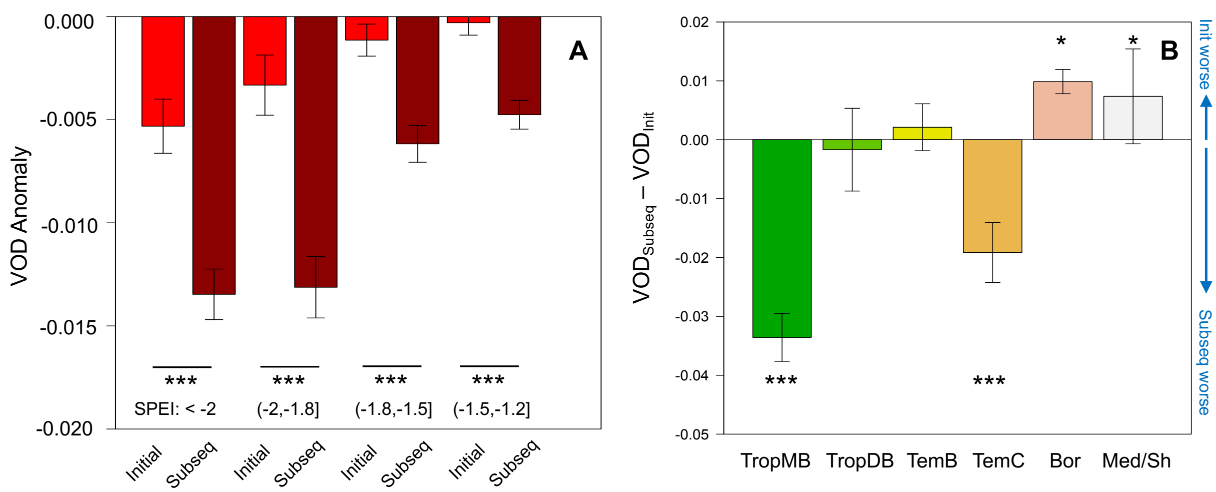

Figure 3: Ecosystem impacts of a subsequent drought are more deleterious than an initial drought. Vegetation optical depth (VOD) anomaly (A) in response to an initial drought (Initial, light red) and subsequent drought (Subseq, dark red), categorized by drought severity of both droughts via the Standardized Precipitation Evapotranspiration Index (SPEI) thresholds (left-to-right $N_{grid\text{-}cells}$= 745, 425, 1491, 2398). Differences in VOD anomalies (B) during a drought of SPEI < -2 across different forest biomes between initial and subsequent droughts, with negative numbers indicating a more deleterious effect of the subsequent drought. Biomes: tropical moist broadleaf (TropMB), tropical dry broadleaf (TropDB), temperate broadleaf (TemB), temperate conifer (TemC), boreal (Bor), and Mediterranean-type/shrubland (Med/Sh) (left-to-right $N_{grid\text{-}cells}$= 248, 50, 89, 46, 291, 21). Error bars indicate ± 1 standard error. Stars indicate statistically significant differences (***p<0.001)

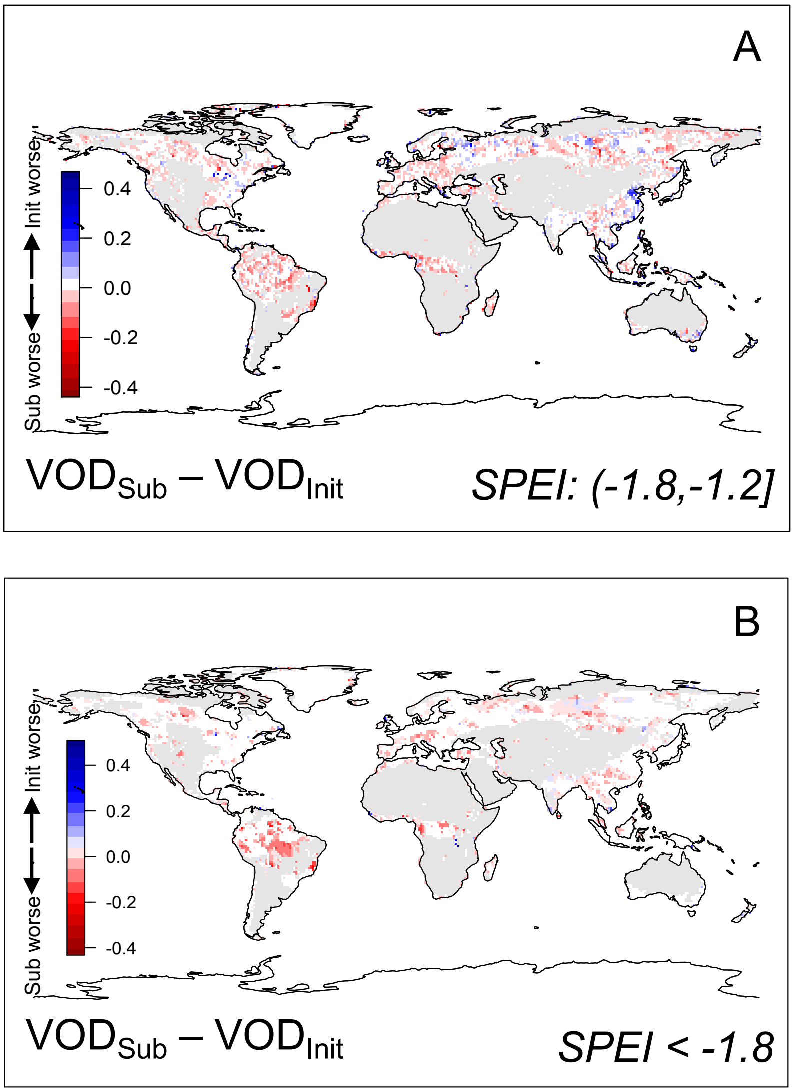

Figure 4: Ecosystem impacts of a subsequent drought compared to an initial drought diverge across global forests. Vegetation optical depth (VOD) anomalies in response to a subsequent drought (Sub) minus an initial drought (Init), with red colors indicating a more deleterious effect of the second drought, categorized by drought severity of both droughts via the Standardized Precipitation Evapotranspiration Index (SPEI) thresholds of a moderate drought (A; SPEI: (-1.8,-1.2]) or severe drought (B; SPEI < -1.8). Gray areas indicate regions not dominated by forests; white areas in Panel B indicate that two droughts exceeding that SPEI severity did not occur in the record.

Methods

Drought datasets

We used the Standardized Precipitation Evapotranspiration Index (SPEI) as our primary drought metric in this study for several reasons. First, as an agricultural drought index, SPEI integrates both water supply through precipitation and water demand through potential evapotranspiration (PET), which makes it a simple and physiologically-relevant drought index based on a water budget that is more relevant to ecosystem water stress than meteorological drought indices based only on precipitation and temperature[45–47]. SPEI has been widely used to assess ecosystem response to drought at multiple spatial and temporal scales[14,48,49]. Second, unlike other agricultural drought metrics such as the Palmer Drought Severity Index (PDSI), SPEI is standardized within each grid cell to a mean of zero and standard deviation of one with a gaussian distribution[46]. Thus, drought severity can be quantitatively compared across regions and ecosystems, normalized by each grid cell's climatology. Finally, current publicly available datasets of SPEI contain global coverage of drought data over the full historical record (1900-2019)[45], enabling us to maximize the sample size of ecological data collected over 1900-2018.

We downloaded the full SPEI Global Drought Monitor dataset on 1 March, 2019, which provides global SPEI data at 1-degree resolution from 1900-2019[45,46]. This dataset uses the precipitation data from the Global Precipitation Climatology Centre (GPCC) and calculates PET using a Thornthwaite algorithm, with temperature based on the National Oceanic and Atmospheric Administration National Center for Environmental Prediction's Global Historical Climatology Network (NOAA NCEP GHCN) dataset[47]. Because the Thornthwaite PET calculation is a simplification, we also performed analyses with SPEI calculated via the more robust Penman-Monteith PET algorithm in the Global SPEI Database[45]. We observed very similar patterns and because the SPEI Global Drought Monitor Database covers 1900-2019 (as opposed to 1900-2015 for the SPEI Global Database), we used it for our primary analysis. SPEI can be calculated with respect to different “integration windows” over which drought severity is calculated and normalized to the climatological period[49]. We chose a 12-month integration window because an annual time-step is consistent with both the tree-ring and forest inventory plot datasets. We calculated 12-month SPEI values for both calendar year and water year (Oct-Sept) in the Northern Hemisphere and observed very similar results in the tree-ring analysis and thus present calendar year results in all figures.

For all analyses, we examined four levels of drought severity that span a range from moderate to severe drought. We chose SPEI drought severity bins of [-1.2,-1.5), [-1.5,-1.8), [-1.8,-2) and <-2.0 for these drought severity levels. Because SPEI values are based on z-scores, an SPEI value of -2.0 indicates a 2 standard deviation drought. This range of values allowed us to assess whether ecosystem response to moderate drought differed from that of severe droughts.

Tree-ring analysis

To quantify tree growth responses to multiple droughts, we used tree-ring chronologies from the extensive International Tree-Ring Data Bank (ITRDB). The ITRDB is a publicly available dataset that contains tree-ring chronologies for >2,000 sites around the world. Following a recent global analysis that examined drought recovery periods in ITRDB tree-ring chronologies[13], we analyzed 1,208 chronologies that had standard formatting and included at least 25 years in the observational record (1900-2018) (Extended Data Fig. 8). These chronologies span >40 species and a wide array of temperate and boreal forest types, although they are concentrated in the Northern Hemisphere, primarily in North America and Europe. For each chronology, we analyzed the detrended ring width index where detrending had been performed by the individual data contributor of that chronology, following previous studies[13,50].

Based on the latitude and longitude coordinates of each chronology, we calculated the ring width reduction during the first two droughts that exceeded the given drought threshold in each chronology. We imposed a criterion that the two droughts had to be temporally separated by more than two years with SPEI values above the drought threshold in order to avoid counting multi-year single droughts as two different droughts. This minimum gap between droughts is based on previous research on these tree-ring chronologies that indicated that drought legacy effects typically lasted 1-2 years[13] and thus our analysis avoids these effects. For a given drought event if multiple years in a row exceeded the drought threshold, we used the ring width of the final year of the drought. For example, for a drought threshold of SPEI < -2, if a given chronology experienced an SPEI time-series of 0, -2.2, -2.1, 0, -2.1 and no other droughts, it would not be used due to insufficient time between two droughts. If the SPEI time-series were 0, -2.2, -2.1, 0, 0, -2.1, then Year 3 would be calculated as "Drought 1" and Year 6 as "Drought 2". These criteria allowed us to assess the impact of multiple droughts while avoiding a potential confounding effect of analyzing two years in essentially the same individual drought. We did a sensitivity analysis both on the drought severity recovery threshold (e.g. recovery threshold of SPEI>-1.2, SPEI>0, etc.) and 1-4 years of recovery period and neither had a major effect on our results. We did not include an upper limit to the time between two droughts because several of the hypothesized ecological and physiological mechanisms that might mediate changes in tree sensitivity to drought, such as changes in canopy architecture, allocation, or species composition, certainly operate on multi-decadal timescales[23]. Individual chronologies could occur in multiple drought severity bins if they experienced four droughts or more. We note that we did not explicitly include drought duration in these analyses, but we do not think it would likely influence our results given that we observed similar patterns across a wide suite of sensitivity analyses.

We detected no systematic differences in drought severity between initial and subsequent droughts in the ITRDB dataset (Extended Data Fig. 2). It is also highly unlikely that trends in ring width due to ontogeny/stand development, given that tree-ring chronologies are detrended to explicitly remove such patterns, or trends in drought metrics might confound our results. Nevertheless, we conducted a sensitivity analysis to ensure that detrending and/or removal of an autoregressive model ("prewhitening") did not influence our results. In this analysis, we compared the "standardized" chronology (.crn file) in ITRDB used in Fig. 1 with application of a single, consistent detrending spline method or a single, consistent detrending and prewhitening method (method "spline" and "ar", respectively, in the *detrend.series* function standard settings in dplR) and our results were robust (Extended Data Fig. 3). In addition, because only a subset of species in a given region or community yield easily readable tree ring series, this may amplify the phylogenetic drought response observed here. Finally, we note that the chronologies in the ITRDB dataset are not randomly-distributed and tend to over-estimate climate sensitivity due to site selection compared to randomly-distributed inventory plots[51], but this should not greatly influence our results. This is because spatial or population biases in ITRDB (higher climate sensitivities) would give, on average, a greater decline in growth during any given drought but should not, a priori, affect the temporal changes in growth responses between multiple droughts within the same chronology. This site selection bias would make scaling ITRDB tree-ring chronologies to whole-forest carbon pools challenging, however, and thus we use only VOD for whole-ecosystem assessments here.

Forest Inventory analysis

To quantify tree mortality responses to multiple droughts, we used the U.S. Forest Service Forest Inventory and Analysis (FIA) long-term permanent plot network. The FIA network contains >250,000 permanent plots on all lands with at least 10% tree cover in the contiguous United States[52–54]. Since the plot protocols were standardized nationwide in 2000, FIA plots are set up on a stratified random sampling design and tree status (living/dead) is measured on a plot return interval that varies by state, typically every five years (i.e. 20% of plots censused each year) in the eastern U.S. and every ten years (i.e. 10% of plots censused each year) in the western U.S.[52–54]. This means that as of 2018 many eastern states have 3-4 censuses and many western states have 1-2 censuses. States in the Intermountain West FIA region (Colorado, Arizona, New Mexico, Utah, Idaho, Montana) also estimated a mortality in the past five years during the initial census of plots, which allows these states' inventory plots with two censuses to be used in this study because the plots contain two mortality rates (i.e. mortality rate 0-5 years prior to census 1 and a mortality rate between census 1 and census 2). Thus, while FIA data in both the western US and eastern US can be used for this analysis, we note that limitations associated with relatively sparse temporal sampling of FIA remains an uncertainty and caveat.

We calculated total basal area mortality for forested plots with FIA plot condition classes that occupied >30% of a given plot area. Plots with fire damage, human damage, and treatments (e.g. timber harvesting) were excluded. For all states with 3+ censuses, we calculated mortality rates using the basal area mortality documented in the return census and measured plot return interval. For Intermountain West states with only 2 censuses, we calculated the initial mortality rate using the "estimated" 5-year mortality rate in the first census and then the documented mortality between the first and second census. This “estimated mortality” is determined by the FIA field crew during the first census as all trees that have died in the past five years based on crown decay conditions and has been validated[55,56], but we note that our results were robust to excluding plots with “estimated mortality” (Extended Data Fig. 9). We then implemented a similar algorithm to detect plots where two droughts of a given severity level had occurred. Specifically, we analyzed plots that had at least two mortality rate estimates and where each drought that exceeded the selected threshold had occurred in the five years prior to the census. When more than two droughts occurred at a plot, we analyzed the first and second droughts similar to the tree-ring analysis, provided the droughts were in different census intervals.

While there are many potential drivers of mortality rates in U.S. forests, our analysis aimed to screen out major alternate confounding drivers and drought has been identified in a wide body of literature of having a major impact on tree mortality in both eastern and western U.S. forests since 2000[57–60], which can be widely observed in FIA plot mortality rates[57,60,61]. We further analyzed mortality responses to multiple droughts by forest type, using the FIA “Field type code” variable, to categorize plots as angiosperm-dominated or gymnosperm-dominated forests. In addition, we detected no significant differences in drought severity between initial and subsequent at all drought severity levels in FIA data (Extended Data Fig. 2B), indicating that differences in drought severity were unlikely to drive our results.

Satellite vegetation optical depth analysis

Vegetation optical depth (VOD) is a measure of the degree to which graybody emission from the surface of the earth attenuates as it passes through both the woody and leafy components of the vegetation canopy. It is sensitive to canopy water content (CWC)[62], and thus varies with both biomass[63,64] and water stress[65,66]. The constant of proportionality between VOD and CWC is poorly understood. However, it appears to vary primarily with canopy type and electromagnetic frequency, suggesting it is relatively constant for a given land cover type[67]. At the annual and longer timescales considered here, variations in VOD can be interpreted as due to variations in biomass growth and mortality[68]. Here, we use VOD from the Land Parameter Data Record [69], which are retrieved from brightness temperatures measured by the Advanced Microwave Scanning Radiometer - Enhanced (AMSR-E)) and Advanced Microwave Scanning Radiometer 2 (AMSR-2). For full details on the retrieval methods see publications[70–72] We used data from January 2003–December 2018.

We aggregated annual VOD values to the same resolution (1 degree) as the SPEI drought dataset and subtracted the grid cell mean VOD to generate a time-series of VOD anomalies in each grid cell. Similar to the tree-ring analysis, we searched the SPEI time-series for each grid cell that contained two or more drought years that fell within the same SPEI drought severity bins. We further constrained this such that the grid cell had to have at least one non-drought year between the two drought years, so as to avoid counting the same multi-year drought as two individual drought events. We performed a sensitivity analysis of detrending individual VOD grid cells to ensure that directional trends, potentially due to other drivers such as land-use change, were not driving our results and our findings were robust (Extended Data Fig. 10). We used the biome map of Olson et al. (2001) to analyze VOD responses over forest and woodland biomes only (Fig. 3A) and to analyze impacts by individual biomes (Fig. 3B). While the VOD record is relatively short, it is similar in length to the FIA plot network and there are multiple regions in the world where two moderate or severe droughts occurred (Fig. 4), including two 1 in

100 year droughts in the Amazon rainforest[5,34,73]. Thus, it provides an integrated assessment of ecosystem-level drought impacts for many forest biomes across the globe[24,31,32].

We detected significant differences in drought severity between the initial and subsequent droughts in VOD grid cells that experienced two droughts for severe drought levels (see *Analyses and statistics*) (Extended Data Fig. 2), which must be accounted for to estimate ecosystem changes in sensitivity to drought between multiple droughts. We took two separate approaches to accounting for these drought severity differences. First, we performed an analysis where we only considered VOD grid cells where the SPEI values were nearly identical (i.e. within 0.1 of each other) for both droughts. Second, we built a model that accounted for drought severity in each grid cell. For each grid cell, we constructed an ordinary least squares regression between annual values of VOD anomaly and SPEI using a linear or quadratic relationship. We then calculated the relative drought impact of the first and second droughts in that grid cell as the residual of the drought years' VOD values from the regression, which subtracts out the effect of drought severity. Both approaches – and both functional forms in the second approach – revealed the similar findings that the impact of a second drought on ecosystem VOD was more severe than the first drought (Extended Data Fig. 6), indicating that the result is robust even when accounting for drought severity differences.

To ensure that our results were not influenced by substantial drought legacy effects in VOD, we calculated the VOD anomaly for each grid cell in the 1-7 years following droughts of severity SPEI (-2, -1.2] or SPEI < -2. We observed minor legacy effects lasting 1 year for SPEI (-2,-1.2] droughts and moderate legacy effects lasting 3 years for SPEI < -2 droughts. We conducted a sensitivity analysis where initial and subsequent droughts had to be separated by 3 years or more and observed that our findings were robust (Extended Data Fig. 7), indicating that our results are robust to drought legacy effects in VOD.

Analyses and statistics

For each of the three datasets (tree rings, forest inventory plots, VOD), we analyzed the impacts of the initial drought versus the subsequent drought using either paired t-tests (tree ring, VOD) or Wilcoxon signed rank tests (FIA) when data could not be transformed to meet assumptions of normality. Tree ring and VOD data were often transformed using an arctangent transformation. We note that we do not test for differences in tree or ecosystem sensitivity across drought severity categories (i.e. we only test for sensitivity differences between an initial and subsequent drought at the same drought severity level) and we used a Sidak correction for multiple hypothesis testing within each dataset's analyses where necessary[74]. We ensured that assumptions of normality and homogeneity of variances were met with Q-Q plots via the qqPlot diagnostic in the 'car' R package[75,76].

To ensure that tree or ecosystem sensitivity to multiple droughts was not driven by systematic drought severity differences, we tested for differences in drought severity using Wilcoxon signed rank tests. Statistically significant differences were detected only in the VOD dataset at SPEI <-2 drought severities ($p=0.005$) and were addressed as described above.

We tested for spatial autocorrelation in the differences between the initial and subsequent drought impacts using Moran's I[77] and found significant positive spatial autocorrelation in all three datasets ($p<0.01$). In the tree-ring and VOD datasets, autocorrelation was addressed by using spatial autoregressive models that model the correlation structure of the data, using the gls function in the 'nlme' R package[78]. Per standard practice[77], we included the latitude and longitude coordinates of each grid cell in the regression and tested the following spatial correlation structures – linear, quadratic ratio, exponential, spherical, and Gaussian – selecting the most likely and parsimonious model using the difference in Akaike Information Criterion of <-2 or more. The quadratic or exponential correlation structure was typically selected as most parsimonious. For FIA data, no transformations could achieve reasonable Q-Q plots for any family of generalized linear model and thus we first averaged individual plot values at a 1 degree grid to account for spatial autocorrelation and then subsequently modeled the correlation structure. All results were robust to accounting for spatial autocorrelation (Extended Data Fig. 5). All analyses were conducted in the R statistical software[79].

Data availability: All datasets are publicly available. The International Tree-Ring Data Bank is available from the National Oceanic and Atmospheric Administration (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring); the U.S. Forest Inventory and Analysis plot data are available from U.S. Department of Agriculture (https://www.fia.fs.fed.us/); and the vegetation optical depth data are available from the University of Montana (https://www.ntsg.umt.edu/project/default.php).

Code availability: All analysis was done in the open-source software R with the packages that are documented and cited in the Methods section of the paper. Code will be made available upon request.