



Younger trees in the upper canopy are more sensitive but also more resilient to drought

Tsun Fung Au, Justin Maxwell, Scott Robeson, Jinbao Li, Sacha Siani,
Kimberly Novick, Matthew Dannenberg, Richard Phillips, Teng Li, Zhenju
Chen, et al.

► To cite this version:

Tsun Fung Au, Justin Maxwell, Scott Robeson, Jinbao Li, Sacha Siani, et al.. Younger trees in the upper canopy are more sensitive but also more resilient to drought. *Nature Climate Change*, 2022, 12 (12), pp.1168-1174. 10.1038/s41558-022-01528-w . hal-03928624

HAL Id: hal-03928624

<https://u-picardie.hal.science/hal-03928624>

Submitted on 26 Oct 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Younger trees in the upper canopy layer are more sensitive but also more resilient to drought: age matters

Tsun Fung Au^{1,2*}, Justin T. Maxwell¹, Scott M. Robeson¹, Jinbao Li³, Sacha M. O. Siani¹, Kimberly Novick⁴, Matthew P. Dannenberg⁵, Richard Phillips⁶, Teng Li⁷, Zhenju Chen⁸, Jonathan Lenoir⁹

¹ Department of Geography, Indiana University, Bloomington, IN, United States.

² Institute for Global Change Biology, University of Michigan, MI, United States.

³ Department of Geography, The University of Hong Kong, Hong Kong SAR, China.

⁴ School of Public and Environmental Affairs, Indiana University, Bloomington, IN, United States.

⁵ Department of Geographical and Sustainability Sciences, University of Iowa, Iowa City, IA, United States

⁶ Department of Biology, Indiana University, Bloomington, IN, United States

⁷ School of Geography and Remote Sensing, Guangzhou University, Guangzhou 510006, China

⁸ College of Forestry, Shenyang Agricultural University, Shenyang 110866, China

⁹ UMR CNRS 7058 'Ecologie et Dynamique des Systèmes Anthropisés' (EDYSAN), Université de Picardie Jules Verne, Amiens, France

*Corresponding author: tomau123@indiana.edu

Abstract

As forest demographics are altered by the global decline of old trees and subsequent reforestation, younger trees are expected to have an increasingly important influence on carbon sequestration and forest ecosystem functioning under more frequent drought conditions. Here, we examine age-dependent drought sensitivity of over 20,000 individual trees across five continents and show that younger trees in the upper canopy layer have larger growth reductions during drought, with angiosperms showing greater age differences than gymnosperms. The age-dependent sensitivity is more pronounced in humid climates compared to more arid regions. However, younger canopy-dominant trees also recover more quickly from drought. The combination of increased drought events in the future together with an increased proportion of younger canopy-dominant trees suggests that droughts will have a larger adverse impact on carbon stocks in the short term, while the higher resilience of younger canopy-dominant trees could positively affect carbon stocks over time.

35 Main

36 Forests regulate global climate¹ and provide stable understory microclimates that promote
37 biodiversity^{2,3}. However, more frequent and intense drought can cause irreversible damage to
38 plant hydraulics and induce forest dieback through concomitant abiotic and biotic stress^{4,5,6},
39 which can reduce carbon sequestration and generate a positive feedback loop on the pace of
40 climate change^{7,8,9}. While previous work suggests that most species have similar vulnerability
41 to drought¹⁰, substantial variability in drought responses have been shown for angiosperms and
42 gymnosperms^{11,12}. Drought can also alter the distribution of forest types, species composition,
43 and ecosystem services^{4,13,14,15}. For instance, widespread forest dieback can reduce the
44 microclimatic buffering effect of canopy-dominant trees³, rapidly increasing subcanopy
45 temperatures and their temporal rate of change with important consequences for forest
46 biodiversity under climate change². While shifting forest species composition alters drought
47 sensitivity of the forests¹⁶, warmer and drier conditions can hinder the ability of trees to return
48 to pre-drought growth rates (i.e., drought resilience)¹⁷. Therefore, improved understanding of
49 forest sensitivity and resilience to drought helps decrease the uncertainty in terrestrial carbon-
50 cycle feedbacks.

51
52 Anthropogenic disturbances such as deforestation and selective logging, combined with
53 climate-induced threats, have caused the decline of old canopy-dominant trees^{18,19} that
54 sequester large amounts of carbon, while simultaneously buffering and stabilizing
55 microclimates in the understory^{2,3,20,21}. Globally, subsequent reforestation, whether through
56 natural succession or tree-planting²², has led and will further lead to forests that are dominated
57 by a younger age structure¹⁹. The area covered by younger trees in the temperate biome (4
58 million km², < 140 years old) already far exceeds the area covered by older trees (2.2 million
59 km²)¹⁹. Therefore, younger trees reaching the upper canopy layer, hereby referred as younger
60 canopy-dominant trees, are an increasingly important component of forest ecosystems and
61 functions, and it is critically important to understand the extent to which these less mature trees
62 share the same resistance to climate extremes than older trees within the upper canopy layer.
63 In response to drought, larger trees generally have greater decreases in growth than smaller
64 trees²³. However, while taller or bigger trees are assumed to be older trees, tree size, either
65 measured by height or diameter at breast height, does not necessarily indicate and reflect tree
66 age, especially in harsh environments (e.g., cold and dry climates) or for populations located
67 close to the species' range limits where individual trees of similar size from the same species
68 could differ by several centuries in age²⁴. If there are clear links (i.e., allometric equations) to

relate tree height and tree diameter at breast height²⁵, the link between tree size (e.g., tree height) and tree age is much less evident, especially so when comparing trees from the upper canopy layer. Besides, tree age is an important variable, and probably more relevant than tree height, for understanding and addressing global change challenges due to the ability of older trees to have longer carbon residence times and more carbon storage, in the end, than fast-growing younger trees from the upper canopy layer^{24,26}. The demographic shift towards a predominance of younger canopy-dominant trees and the ecological importance of older trees, necessitate a better understanding of age-dependent responses to drought stress within the upper canopy layer that provides a myriad microclimate in the understory. At the stand level, the relationship between stand age and drought responses has been examined for selected species and regions^{27,28}, but mean stand age across several vegetation layers may dilute potential age impacts, making it impossible to separate within-stand variations across multiple species and higher taxa. Further, how the age of canopy-dominant trees impacts drought resilience is largely unknown, but critical to resolve for a holistic perspective on how shifting age distributions will affect forest growth and survival under climate change.

Here, we investigate drought responses across tree-age cohorts of canopy-dominant angiosperm and gymnosperm species by assessing: (1) drought sensitivity (i.e., the percentage of growth reduction between drought and non-drought conditions); (2) drought resistance (i.e., growth rate during drought compared to pre-drought levels); and (3) drought resilience (i.e., the capacity to resume growth to pre-drought levels) (Methods). Drought conditions were defined by the 3-month averaged standardized precipitation evapotranspiration index (SPEI), which accounts for site variations in both moisture supply and demand. We gathered tree-ring width data from 119 drought-sensitive species (38 angiosperm species and 81 gymnosperm species) across North and South America, Eurasia, Africa, and Oceania. We then classified 21,964 canopy-dominant individual trees into 3 age cohorts based on species-specific age distributions. The youngest and the oldest 25% of a given species' population were attributed to young and old canopy-dominant cohorts, respectively, while the remaining 50% (i.e., the interquartile) were attributed to the intermediate canopy-dominant cohort (Extended Data Fig. 1), allowing us to examine how tree age influences the drought responses and how that influence varies across tree taxa and biomes. We also ran supplementary analyses (Methods) using tree age as a continuous variable to examine drought-driven growth reduction instead of using a factor variable with three levels (young, intermediate, and old canopy-dominant cohorts).

Results

Growth reduction in response to drought

The younger cohort of canopy-dominant individuals for both angiosperms and gymnosperms experienced significantly greater growth reductions in response to drought than the respective older canopy-dominant cohort of trees. Under drought conditions, the youngest canopy-dominant cohort of angiosperms showed a 28% reduction in growth, on average, whereas tree growth in the intermediate and older canopy-dominant cohorts was only reduced by 25% and 20%, respectively (Fig. 1a, $P_{\text{young-inter}}, P_{\text{young-old}} < 0.001$). Drought also reduced the growth of the youngest canopy-dominant cohort of gymnosperms by 27%, on average, and the response is nearly identical to that of the intermediate cohort (0.6% greater; Fig. 1a, $P_{\text{young-inter}} = 0.227$) but 2.4% greater than that of the oldest cohort (Fig. 1a, $P_{\text{young-old}} < 0.001$) of canopy-dominant trees.

To ensure that these results are robust regardless of age groupings, we used a linear mixed-effects model based on continuous variation of age (i.e., using age as a continuous fixed effect: see Methods) and found that younger canopy-dominant trees had a larger growth reduction to drought (Extended Data Table 1, $P < 0.001$). We also found that tree age had an interactive effect with tree taxa such that the growth was reduced by 3.6% for angiosperms but only by 0.2% for gymnosperms every 100 years (Extended Data Table 1, $P < 0.001$). Noteworthy, tree height and tree age are poorly correlated within the subset of individual trees for which we had data on both age and height ($r = 0.21$, $n = 540$). Thus, examining the effect of tree height alone on drought-driven growth reduction may tell a totally different story than the effect of tree age, especially so for canopy-dominant trees. We then employed linear mixed-effects models to control for the potential confounding effects from tree height. Tree age was still the most prominent variable to explain drought-driven growth reduction within the canopy-dominant individual trees with both age and height data (Tables S1, S2 and S3). The growth was reduced by 4.3% per one unit of standardized age while the growth reduction was increased by 0.7% per one unit of standardized height (Table S3, $P_{\text{age}} < 0.01$, $P_{\text{height}} = 0.72$).

For angiosperms, the difference in growth among canopy-dominant cohorts was the greatest when moisture availability was the most limiting. Specifically, the youngest cohort of canopy-dominant trees for angiosperms experienced 17% more growth reduction than the oldest canopy-dominant cohort during extreme drought ($\text{SPEI} < -3$) (Fig. 1b, $P < 0.001$). Under extremely wet conditions ($\text{SPEI} > 3$), the youngest cohort of canopy-dominant trees for

angiosperms had only 1.9% higher radial growth than the oldest canopy-dominant cohort. Gymnosperms experienced a wider range of SPEI (likely because they tend to inhabit more arid environments), but the differences in radial growth among age cohorts of canopy-dominant trees were minimal, even during extreme droughts. The youngest canopy-dominant cohort for gymnosperms only experienced 2% and 3% greater growth reduction than the oldest canopy-dominant cohort when SPEI went below -1.5 and -3 , respectively (Fig. 1b, $P < 0.1$). The nonlinear relationship between moisture availability and radial growth, particularly for young canopy-dominant angiosperms, suggests that decreases in growth during increasingly extreme dry years may not be sufficiently offset by increases in growth during increasingly extreme wet years²⁹.

Younger canopy-dominant trees were especially more vulnerable to drought-driven growth reductions in Mediterranean, temperate, and alpine/boreal regions ($P < 0.05$), but not in deserts and tropical regions (Fig. 2a). The average growth reduction of the youngest canopy-dominant cohort for angiosperms in Mediterranean (38%), temperate (26%), and alpine/boreal (20%) regions is 4%, 8%, and 12% higher than that of the oldest canopy-dominant cohort during drought (Fig. 2b, $P < 0.05$). The youngest canopy-dominant cohort for gymnosperm showed 22%, 28%, and 25% growth reductions in those same regions, which is 3-4% higher than growth reductions of the oldest canopy-dominant cohort (Fig. 2b, $P < 0.05$). In deserts, the differences in drought response between the youngest and oldest canopy-dominant cohorts for gymnosperms narrowed, with the youngest canopy-dominant cohort experiencing 32% growth reduction, on average, compared to 29% growth reduction for the oldest canopy-dominant cohort (Fig. 2b, $P < 0.1$). By contrast, in tropical regions, drought sensitivity was greater in the oldest canopy-dominant cohort for both angiosperms and gymnosperms, being on average 5.7% and 4.4% more sensitive to drought than the youngest canopy-dominant cohort, respectively (Fig. 2b, $P < 0.05$).

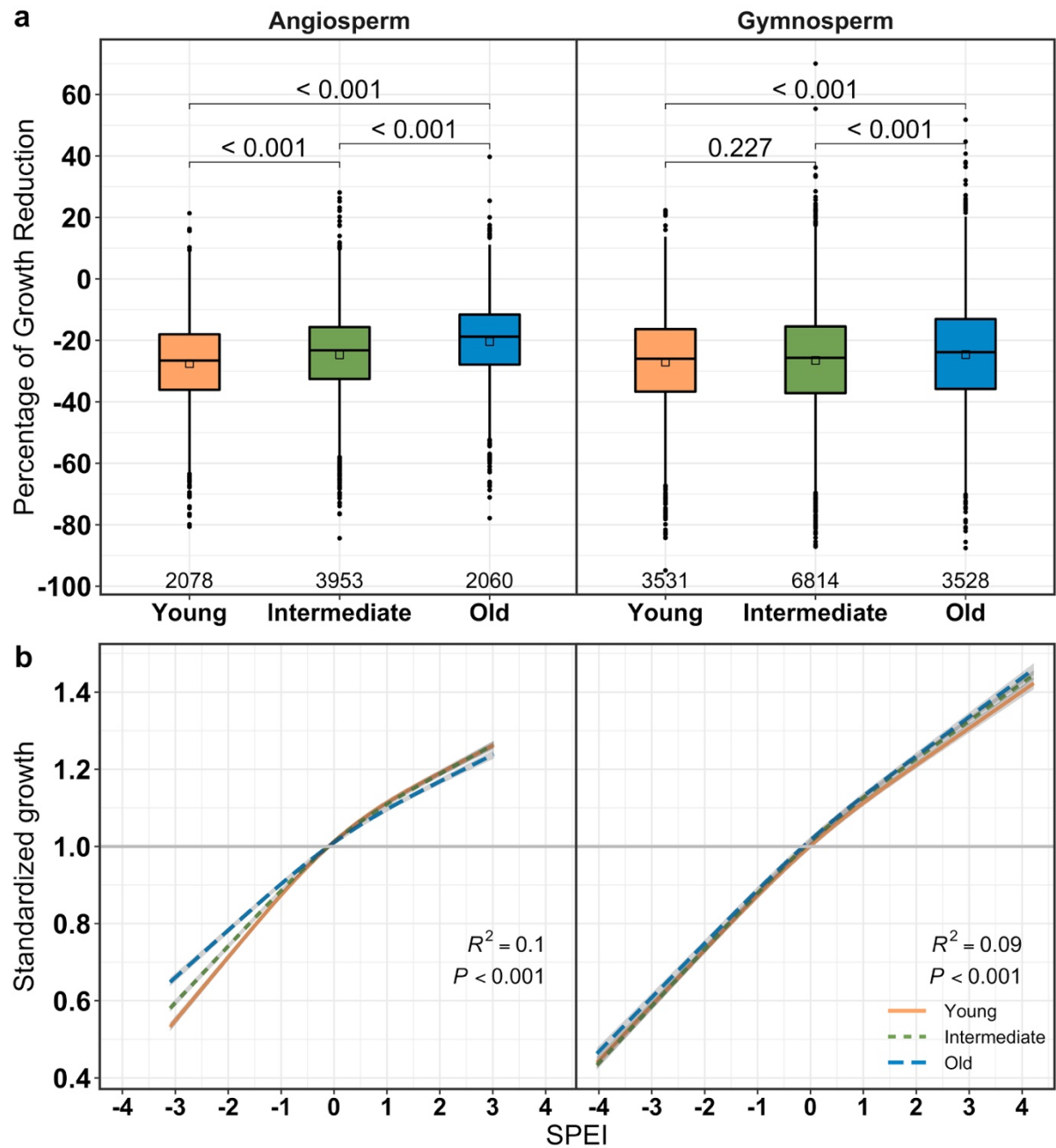


Fig. 1: Drought-induced growth reduction of younger canopy-dominant trees is more pronounced than for older canopy-dominant trees. **a**, Boxplots of drought-induced tree growth reduction as a percentage of difference between mean standardized growth during drought (standardized precipitation evapotranspiration index: $\text{SPEI} \leq -1.5$) and mean growth during non-drought condition ($\text{SPEI} > -1.5$) for young (orange), intermediate (green), and old (blue) cohorts of canopy-dominant trees for both angiosperms (left panel) and gymnosperms (right panel). The numbers at the top of panels represent the p -values of pairwise differences in percentage of growth reduction between age cohorts that were identified by Tukey honest

significant differences. The numbers at the bottom of panels represent number of tree individuals for the youngest, intermediate and oldest age cohort of canopy-dominant trees, respectively. **b**, Standardized growth of angiosperms and gymnosperms with species-specific age cohorts across moisture variability from dry (left) to wet (right) in terms of the SPEI from generalized additive mixed-effects models. Each curve represents the mean response of each age cohort with corresponding 95% confidence interval. The horizontal grey line (standardized growth = 1) indicates mean standardized growth for individual trees, where standardized growth above 1 indicates enhanced growth and below 1 indicates reduced growth. Numbers in the lower right of panels indicate R^2 and p -values for both models. Boxes show the interquartile range (IQR) while upper and lower whiskers are defined as the third quartile (Q3) plus 1.5*IQR and the first quartile (Q1) minus 1.5*IQR, respectively. Values that are less than $Q1-1.5*IQR$ or greater than $Q3+1.5*IQR$ are plotted as closed circles. The bold lines and open squares in the boxplot represent the median and the mean values, respectively. Age cohorts were assigned using species-specific age cutoffs (Extended Data Fig. 1 & Extended Data Table 2).

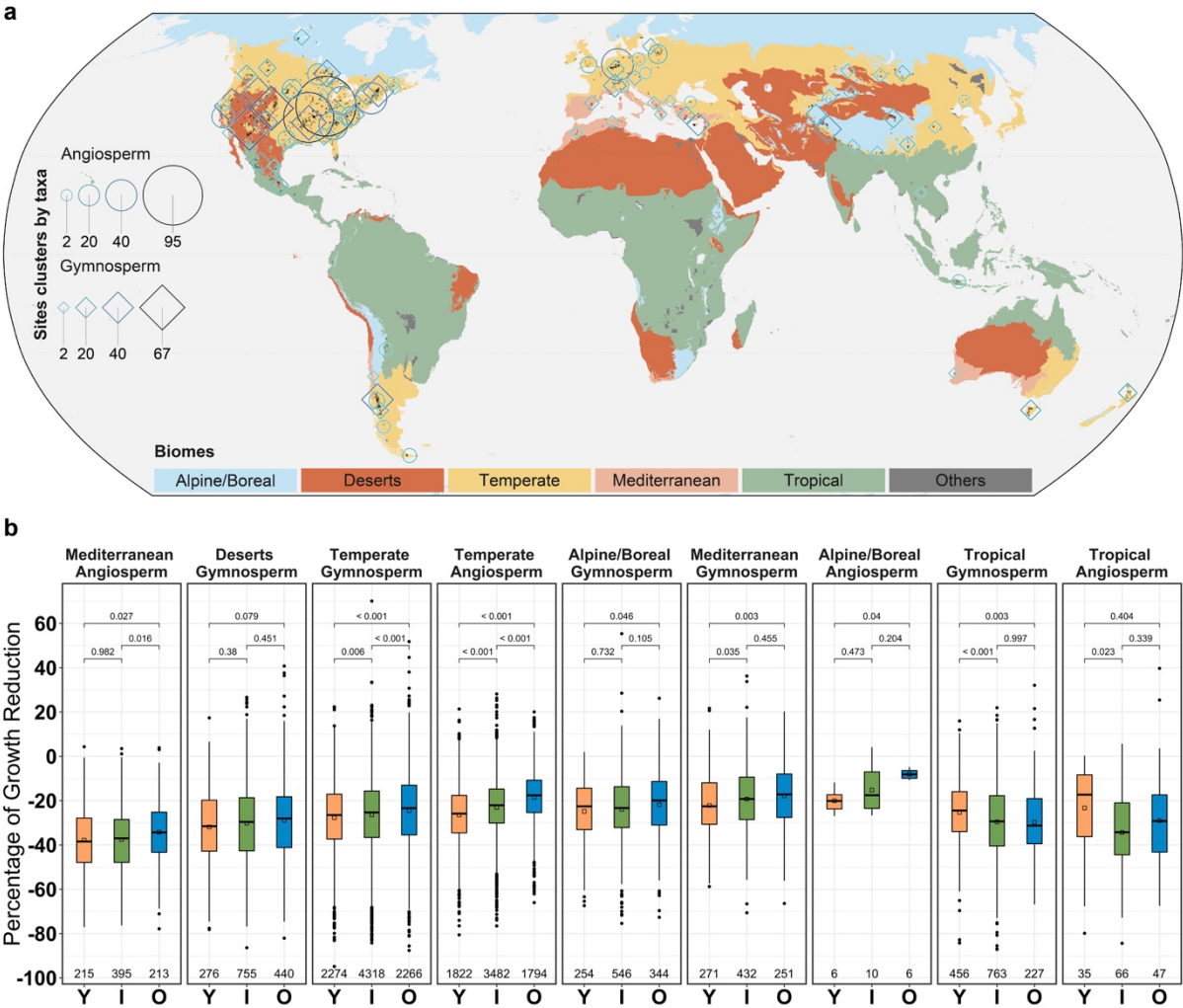


Fig. 2: Drought-induced growth reduction varies across biomes. **a**, Geographical coverage and biomes of the tree-ring chronologies. Circle and square represent angiosperm (n = 502) and gymnosperm (n = 928) clusters, respectively. **b**, Percentage of growth reduction during drought events across age cohorts of canopy-dominant trees (Y: young, I: intermediate, O: old) in five different biomes: alpine/boreal forests; deserts; Mediterranean regions; temperate regions; and tropical regions. Biomes and tree taxa (angiosperms vs. gymnosperms) are arranged based on the growth reduction percentage of the youngest cohort where the youngest cohort in the left panel has the highest growth reduction. The numbers at the top of panel in **b** represent the *p*-values of pairwise differences in percentage of growth reduction between age cohorts that were identified by Tukey honest significant differences. The numbers at the bottom of panel in **b** represent number of tree individuals for the youngest, intermediate, and oldest canopy-dominant cohorts, respectively. Age cohorts were assigned using species-specific age

cutoffs. Note that sample size for angiosperm in the Alpine/Boreal is low and sampling in the tropics is under-represented, which may limit inference in these regions.

Drought resistance and resilience

The youngest cohort of canopy-dominant trees for both angiosperms and gymnosperms was less drought-resistant than the respective oldest cohort of canopy-dominant trees, albeit the oldest canopy-dominant cohort of angiosperms was more drought-resistant than that of gymnosperms (Fig. 3a, 3b, $P < 0.001$). The growth of the youngest cohort of canopy-dominant trees was also more resilient in subsequent years after accounting for the growth reduction during drought (i.e., relative resilience). Relative to pre-drought growth rate, the youngest cohort of canopy-dominant angiosperms recovered by 29%, on average, whereas the oldest cohort only recovered 19% of their pre-drought growth rate, meaning that younger canopy-dominant trees of angiosperms are more resilient to drought (Fig. 3c, $P < 0.001$). The youngest cohort of canopy-dominant gymnosperms also had a higher mean relative resilience (27%) than that of the oldest cohort (24%) (Fig. 3d, $P < 0.001$).

Although age differences in resistance and mean relative resilience were found in angiosperms, none of the angiosperms' cohorts of canopy-dominant trees returned to pre-drought growth levels after the first year (i.e., all had year-1 resilience index below 100%). The growth of angiosperms exceeded pre-drought levels (i.e., 100%) in the second year after drought, with the youngest cohort of canopy-dominant angiosperms generally having better growth-restoring capacity than the other two older cohorts (Fig. 3a). For gymnosperms, different age cohorts of canopy-dominant trees showed very similar resilience patterns after a drought occurred (Fig. 3b). The growth of all age cohorts during the first-year post-drought was nearly the same (on average) as the pre-drought growth, with the resilience index ranging from 99.5% to 100%. In years 2-4 after drought, all age cohorts for both angiosperms and gymnosperms had resilience indices greater than 100% (indicating growth above pre-drought levels). The youngest cohort of canopy-dominant angiosperms tended to have a higher resilience than older cohorts in years 2 and 4 (Fig. 3a) while there were no significant differences among the gymnosperm cohorts of canopy-dominant trees (Fig. 3b).

In contrast, previous research on "drought legacies" (i.e., extended post-drought growth reductions and prolonged recoveries) showed that gymnosperms had more prevalent legacy effects³⁰. While both angiosperms and gymnosperms had a resilience index above 100% for

several years after drought (Fig. 3a, 3b), age-dependent resiliency varied in some genera for both angiosperms and gymnosperms (Fig. 4). For gymnosperms, *Larix*, *Picea*, and *Tsuga* showed reduced resilience for all age cohorts in the first year after drought, and the growth was restored to pre-drought levels by the second year (Fig. 4a). Older trees of *Larix* and *Tsuga* showed even more growth reduction one year after a drought event than during the drought event (Fig. 4a). Nevertheless, the growth of *Juniperus* and *Taxodium* was completely restored for all age cohorts of canopy-dominant trees in the first year after drought (Fig. 4a). For angiosperms, reduced resilience in the first year after drought was shown for all canopy-dominant age cohorts of *Fagus*, *Liriodendron*, and *Acer* (Fig. 4b), suggesting that longer-term legacy effects may be present in some angiosperm genera¹⁶.

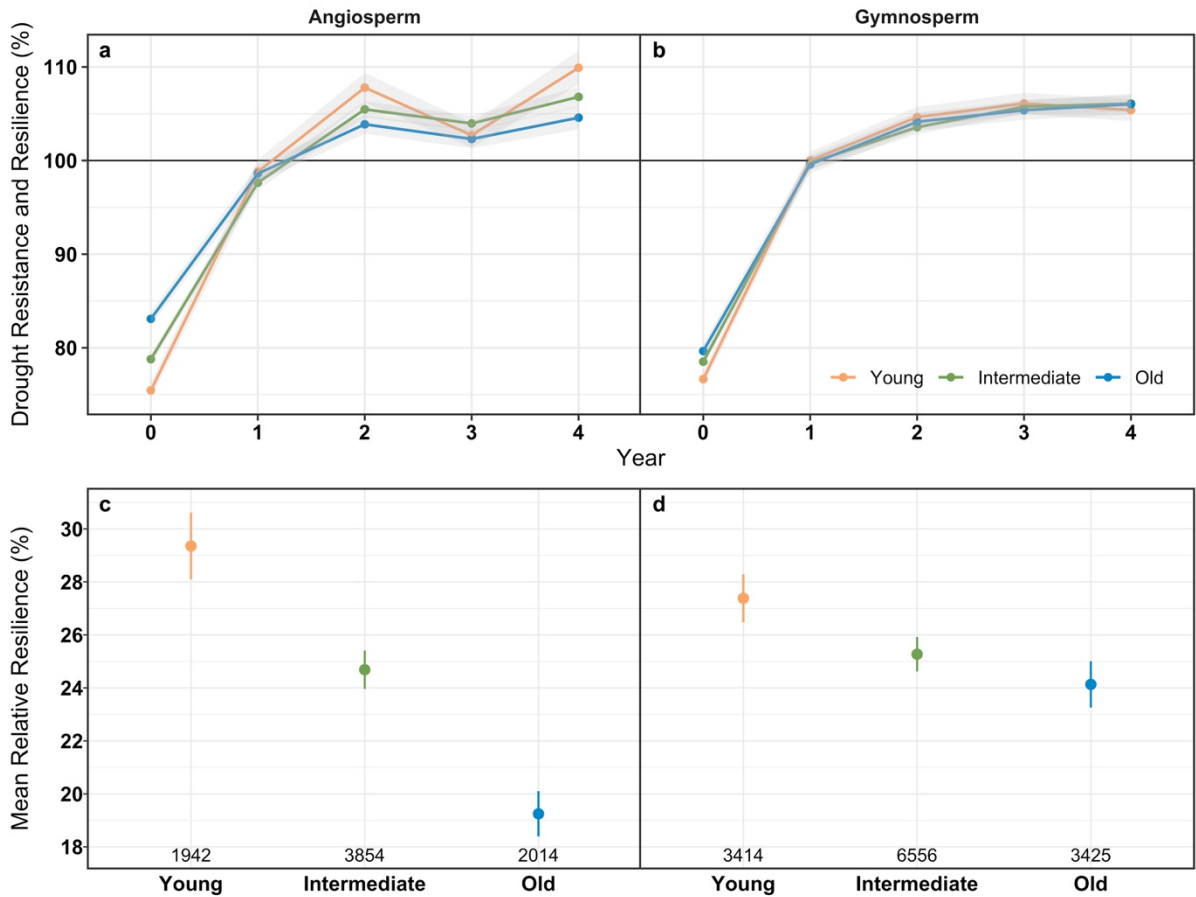


Fig. 3: Age-dependent drought resistance and relative resilience converge between tree taxonomic groups. a, b, Temporal trends in drought resistance (Year 0) and resilience (Year 1–4) for young (orange), intermediate (green), and old (blue) cohorts of canopy-dominant trees for both angiosperms (a) and gymnosperms (b) under non-drought conditions (SPEI > -1.5) with shaded 95% confidence interval. Year 0 indicates averaged resistance coefficients during

drought and years 1, 2, 3, and 4 indicate the resilience coefficients after 1, 2, 3, and 4 years following the drought events, relative to the pre-drought growth rate. The horizontal line at 100% indicates the mean pre-drought growth level. The coefficients that are below the line indicate growth reduction while the coefficients that are above the line indicate growth enhancement compared to pre-drought conditions. **c, d**, Mean drought relative resilience for young (orange), intermediate (green), and old (blue) cohorts of angiosperms (**c**) and gymnosperms (**d**) with 95% confidence interval. The relative resilience is averaged from year 1 to 4 after drought and accounted for the weighting of drought impacts on growth. A higher mean relative resilience value indicates post-drought growth enhancement and recovery from drought-induced reduction relative to the pre-drought growth rate. Age cohorts are assigned based on species-specific age distribution (Extended Data Fig. 1, Extended Data Table 2).

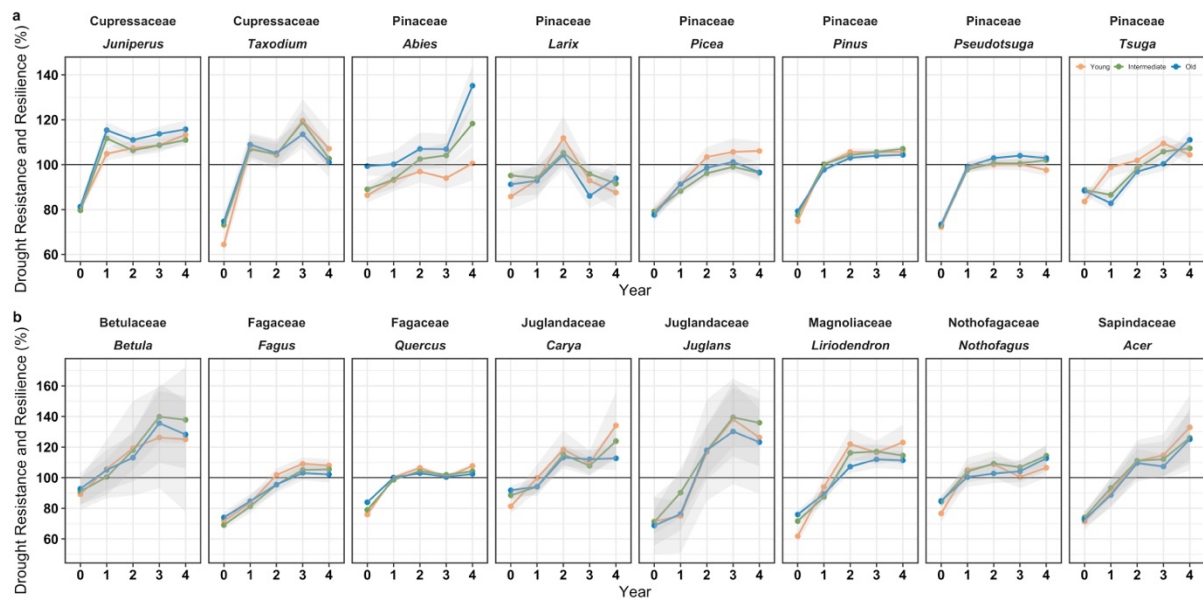


Fig. 4: Variations of drought resistance and resilience in major tree genera. **a**, Temporal trends in drought resistance (Year 0) and resilience (Year 1–4) relative to non-drought conditions, with shaded 95% confidence interval, for young (orange), intermediate (green), and old (blue) cohorts of canopy-dominant trees for 8 different genera (*Juniperus*, *Taxodium*, *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*) belonging to 91% of gymnosperm samples and **b**, 8 different genera (*Betula*, *Fagus*, *Quercus*, *Carya*, *Juglans*, *Liriodendron*, *Nothofagus*, *Acer*) belonging to 97% of angiosperm samples. Year 0 indicates averaged resistance coefficient during the drought year while year 1, 2, 3, and 4 indicate the resilience coefficient 1, 2, 3, and 4 years respectively after drought happens. The horizontal line at 100% indicates growth

278 condition relative to the pre-drought level. The coefficients that are below the line indicate
279 growth reduction while the coefficients that are above the line indicate growth enhancement
280 compared to pre-drought condition. Age cohorts are assigned based on species-specific age
281 distribution.

282

Discussion

Overall, younger canopy-dominant angiosperms have greater growth reduction during drought but recover faster than older ones. Gymnosperms have a less prominent age-dependency in drought sensitivity, but growth recovery is also faster for younger canopy-dominant gymnosperms after drought. While our results appear to contradict some former studies²³, a unique feature of this analysis is its focus on canopy-dominant trees, which reduces the confounding influence of effects from tree height and size in our analysis. Several causal mechanisms likely underlie the age and taxonomic differences in drought resistance and resilience. The differences in drought sensitivity across age cohorts of canopy-dominant trees could reflect the development of more extensive root systems as trees grow older, allowing better access to subsurface water^{31,32} and thus buffering the immediate impacts of most droughts³³. Younger canopy-dominant trees have shallower and less dense root systems that limit water uptake to sustain tree growth, making them more susceptible to the immediate impacts of droughts, even the less perceptible ones³⁴. The mean rooting depth for *Quercus* (5.23m) is deeper than *Pinus* (2.45m)³⁵ and the differences in rooting depth could lead to higher overall drought resistance for oaks (Fig. 4). Mature, older canopy-dominant trees with more extensive canopy cover and greater transpiration efficiency, through access to water in the deep soil layers, can also better regulate and stabilize the understory microclimate^{2,3,32}, potentially reducing the drought severity and buffering the water demand of the subcanopy trees and herbs. Transpiration of the younger canopy-dominant trees could be less efficient at maintaining a sufficient buffering capacity from drought^{2,3}, resulting in an increase of the drought severity experienced and higher water demand for the subcanopy. Gymnosperms tend to be more isohydric, closing their stomates more quickly during drought to prevent dehydration and hydraulic damage. In contrast, angiosperms are more anisohydric, keeping stomates open for longer periods during droughts and allowing more stable gas exchange, transpiration, and photosynthesis^{10,36}. Among the angiosperms, the more isohydric genera (e.g., *Liriodendron* and *Acer*) were less resistant to drought than the more anisohydric genus *Quercus*¹⁶ (Fig. 4b). Altogether, mature angiosperms could access deeper water reserves, have a better buffering capacity to maintain stable microclimate for a longer time period, and have a higher carbon assimilation during drought³⁷, allowing them to have less growth reduction and, thereby, be more drought tolerant.

The youngest canopy-dominant angiosperms showed greater capacity to restore growth once favorable water status was returned even though angiosperms, using a more anisohydric

strategy, tend to be more susceptible to xylem embolism¹⁰. Such plastic responses may be due to higher availability of parenchyma to allocate nonstructural carbohydrates for repairing drought-damaged tissues in angiosperms¹². Likewise, photoprotective chemicals such as xanthophylls, α -tocopherol, and ascorbate were reported in young individuals of an oak species (*Quercus pubescens*) to preserve photosynthetic apparatus³⁸, which may be an important mechanism to help restore photosynthesis once drought ends.

The age-dependent drought sensitivity is common and widespread across biomes and tree taxa, potentially with large implications for the global carbon cycle. For example, the infamous European drought event in 2003 reduced gross primary productivity by 30% (similar to the mean growth reduction of the youngest canopy-dominant cohort in temperate forests, 28%, Fig. 2b) and temporarily converted the ecosystem into a net carbon source by releasing 0.5 Petagram carbon yr⁻¹ into the atmosphere, which is equivalent to four years of net carbon storage in European ecosystems⁷. Thus, the substantially lower growth reduction of older canopy-dominant trees during drought, even on average of only 7-8% less compared to younger canopy-dominant trees, when taken at the *global* scale, could have huge impacts to the regional carbon storage and the global carbon budget, particularly in temperate forests that currently are among the largest carbon sinks worldwide³⁹. During extreme drought, such impacts of age-dependent sensitivity on carbon cycle are magnified with older angiosperms having 17% less growth reduction (Fig. 1b). In alpine/boreal regions experiencing the greatest magnitude of climate warming, drought could also cause more pronounced impacts on younger canopy-dominant angiosperms than older ones, with important consequences for carbon sequestration and climate feedback loops in these ecosystems²⁸.

Drought sensitivity also varies across biomes, with growth in humid biomes being less sensitive than in arid regions but with more age-dependent differences. Drought conditions defined by low SPEI values indicate the water balance of a given site is lower than usual, but the water balance may still be favorable for tree growth in humid regions, even when SPEI values are low⁴⁰. Trees growing in arid regions such as deserts could have been evolutionarily adapted to the xeric environments by having more rapid responses. For example, increased vapor pressure deficit in xeric environments like deserts may cause increased stomatal sensitivity of older canopy-dominant gymnosperms and limit evapotranspiration with less local regulation of microclimate^{34,36,40}, leading to similar growth reduction of all age cohorts among canopy-dominant trees. Taller and older trees in the tropics were also less sensitive to precipitation

variability³², but radial growth data from tropical regions are currently under-represented due to the long-held perception that indistinct seasonality prohibits tree-ring formation in tropical regions⁴¹, which inhibits robust interpretation of age-dependent drought sensitivity here.

Many other organisms exhibit age-dependent responses to external stress, and age-dependent drought responses, after accounting for height-dependent responses, may be much more widespread among angiosperms than previously known. Given that angiosperms are more abundant and diverse than gymnosperms in most biomes and forest stands are increasingly dominated by younger trees in the upper canopy layer, the short-term impacts of drought on the terrestrial carbon sink and the buffering capacity of the upper canopy may be more pronounced. Over the long term, younger canopy-dominant angiosperms are more resilient to droughts. In a warmer and dryer future with higher risks of prolonged droughts, angiosperms might be better prepared for drought¹² and therefore predominate the forests. As a result, plant traits, plant functional types, and ecosystem functioning of the forests could shift in the future, which would influence the predictions from dynamic global vegetation models. Recent advances in carbon cycle simulations allow inclusion of tree age but do not necessarily represent age-dependent sensitivity to climate extremes⁴². Considering tree age along with species composition and tree height could help improve the simulation of carbon cycle feedbacks. While reforestation with native tree species is beneficial, it takes considerable time for young trees to attain maturity, reach the upper canopy layer and gain the associated resistance to drought stress reported here. Thus, from a climate mitigation perspective, conservation priorities should still focus on preserving existing older canopy-dominant trees for their exceptional carbon residence and storage capacity^{26,39} so that the forests could have a diverse structure and composition to withstand and mitigate future emerging climate extremes¹¹.

Methods

Tree growth data

We accessed individual tree-ring width measurements of canopy-dominant trees from the International Tree-Ring Data Bank (ITRDB), the DendroEcological Network (DEN)⁴³, and previous publications^{16,44,45}. The ITRDB consists predominantly of canopy-dominant trees for climate reconstruction⁴¹ such that the size and height of trees sampled at a given site are usually similar. Yet, substantial variations in individual tree ages are still observed for the canopy-dominant trees from the ITRDB (Extended Data Fig. 1, Extended Data Fig. 2, Extended Data Fig. 3, Extended Data Table 2, Extended Data Table 3). We added the DEN database to our

analyses in order to have, for the same individual canopy-dominant tree, information on both tree age and tree diameter to test and control for the potential confounding effects of tree height, which was obtained by feeding allometric equations with tree diameter data (see below), on drought responses. We analyzed the impacts of tree age on drought-induced growth reduction, resistance, and resilience. Both site chronologies and tree ring time series that ended before the 1940s (i.e., the outermost ring) were not considered to ensure sufficient overlap with the observational records of the standardized precipitation evapotranspiration index (SPEI, i.e., from 1901 to 2015 see below) and instances of drought and wet conditions (Extended Data Fig. 2).

To allow meaningful age-dependent drought sensitivity, resistance, and resilience analysis, we first standardized individual tree-ring time series with a two-thirds smoothing spline and then computed site chronologies using the Tukey's biweight in the *dplR* package in R⁴⁶. Further, this standardization procedure removes any potential confounding effects with tree aging. Removing these low frequency signals associated with long-term biological growth trends and forest dynamics allows fair comparisons of drought sensitivity and responses between tree individuals with different ages (e.g., the known decay of ring width when trees are aging as well as the suppression and release for shade-tolerant species)^{16,46,47,48,49}.

Given that temperature is typically the most limiting and sometimes the only factor affecting tree radial growth at high latitudes^{40,49,50}, most of our study sites are situated between 60°N and 60°S where tree growth typically is more sensitive to soil moisture rather than to temperature. We then selected 1430 sites from both the ITRDB and DEN database that had a positive relationship (Extended Data Fig. 4) between standardized growth of site chronology and hydroclimate variability (SPEI03, see below). From those 1430 sites, we then only considered individual tree-ring time series with positive relationships (Pearson's correlation coefficient $r > 0.1$) to hydroclimate variability to avoid potential sampling error. Ultimately, we standardized the raw ring-width measurements of 21,964 individual trees with the same method as stated above (i.e., two-thirds smoothing spline). The tree-growth data consisted of 81 gymnosperm species and 38 angiosperm species (119 species in total) from 32 genera that inhabit diverse biomes from tropical to boreal forests.

Biome classification

We used the Olson et al.⁵¹ biome classification, which classified the land surface into 14 distinct biomes: (1) tropical moist broadleaf forests; (2) tropical dry broadleaf forests; (3) tropical coniferous forests; (4) temperate broadleaf & mixed forests; (5) temperate conifer forests; (6) boreal forests/taiga; (7) tropical grasslands, savannas & shrublands; (8) temperate grasslands, savannas & shrublands; (9) flooded grasslands & savannas; (10) montane grasslands & shrublands; (11) tundra; (12) Mediterranean forests, woodlands and scrubs; (13) deserts & xeric shrublands; and (14) rock & ice.

Using geographic coordinates of each tree-ring site from the ITRDB and DEN metadata, we extracted the biomes that each tree-ring site fell within and grouped them into 5 major biomes (Fig. 2A): (i) alpine/boreal (6, 10, 11 and 14); (ii) deserts (13); (iii) Mediterranean (12); (iv) temperate forests (4, 5 and 8); and (v) tropical forests (1, 2, 3 and 7). No trees were sampled in flooded grasslands & savannas (9).

Age estimation

All tree-ring data that were submitted to the ITRDB and DEN database have already been cross-dated and should therefore have accurate dates assigned for each ring width^{41,52}. We also scrutinized the cross-dating quality of all individual tree-ring time series by removing poorly cross-dated individuals (e.g., individuals with negative inter-series or segment correlation). Therefore, the resulting tree core data from the ITRDB and DEN database provide reliable dating of individual growth years, from which we estimated tree-age. Most of our study sites were used and published for drought reconstructions at continental scales^{53,54,55,56,57,58}. Researchers attempt to sample tree cores as close to the pith as possible within each of these study sites in order to maximize the time span of the drought reconstruction⁵⁹. Although this sampling approach may produce bias towards more mature canopy-dominant trees⁴¹, there are still substantial variations in individual tree ages for multiple tree species (Extended Data Fig. 1, Extended Data Fig. 2, Extended Data Fig. 3, Extended Data Table 2, Extended Data Table 3).

To estimate tree age, we summed the number of total rings for each tree individual. Although a minor underestimation of the true tree age is still expected because: samples were likely taken at or near breast height; some samples may miss the pith; and some trees may have a rotten heart^{60,61}. To minimize the underestimation of tree age due to the above reasons, we used the tree core with the most total rings for individuals which have more than one core, allowing us

to have “maximum age” for every tree individual. As such, this underestimation of tree age is likely the same for all individual trees and thus it should have no directional impact on the main findings. We also summed the ring widths and multiplied by two to estimate tree size (diameter) for all individuals. The correlations between tree age and diameter are weak, with values ranging between 0.37 (angiosperms) and 0.34 (gymnosperms), suggesting that our analysis using tree age is not just acting as a proxy for tree size but reflects a very different demographic parameter than tree size.

Age group classification

Arbitrary age groupings were commonly adopted in previous research to study age-dependent tree growth responses^{62,63}. However, such approaches may ignore species longevity and the age distribution within a population of canopy-dominant trees. Alternatively, previous research also used the mean stand age from canopy-dominant trees as another common approach^{16,27,64,65,66}, but if a forest stand has a diverse age distribution and structure, mean stand age may also dilute potential age impacts and variations within a stand or across landscape (Extended Data Fig. 5). In practice, calculating mean stand age may also consistently underestimate or overestimate the stand age when exceptionally young or old tree individuals were sampled. Therefore, both arbitrary age groupings and mean stand age are not very accurate approaches for comparing drought responses of multiple tree species across large spatial scales. Instead, *relative age* (i.e., individual tree age relative to longevity and age distribution of the focal species) using a rank-based grouping is more appropriate for comparing interspecific age-dependent responses.

To avoid species-specific longevity and sampling biases influencing our relative age classification, we classified all canopy-dominant tree individuals for a given species into three age cohorts based on the ranking of individual trees along the age distribution of the selected ITRDB and DEN dataset. Tree individuals whose ages fell below the first quartile of the age distribution of the focal species were classified into the younger age cohort, those between the first and the third quartile (i.e., interquartile) were classified as the intermediate age cohort and those above the third quartile were classified as the older age cohort (Extended Data Fig. 1). The maximum, mean, median, and minimum age of each age cohort of angiosperm and gymnosperm are listed in Extended Data Table 3. McDowell et al.¹⁹ defined young trees as being less than 140 years old. Our classification results in a similar definition for young trees, where the mean ages of the youngest cohort for both angiosperm and gymnosperm, that were

inferred from species-specific age distribution, are also less than 140 years old (Extended Data Table 3). Therefore, our age cohort method provides a precise classification with the flexibility to adjust for species-specific longevity and age-distribution, allowing more accurate interpretations of implications in the context of global demographic shifts in age structure.

To ensure that the spline-based standardization process did not induce more variability in any of the studied age cohorts (e.g., having more variability within the young age cohort due to the use of a more flexible spline model), we examined empirical probability distributions and estimated standard deviations of standardized ring widths (SRW) for each age cohort of both angiosperms and gymnosperms. The probability distributions and standard deviations between age cohorts were very similar within tree taxa (i.e., angiosperms and gymnosperms, Extended Data Fig. 6), indicating that the standardization did not lead to variability-induced sensitivity differences between age cohorts.

Drought data

To evaluate drought severity and its impacts on tree growth, we used the standardized precipitation evapotranspiration index (SPEI), a measure of the standardized difference between water supply (precipitation) and water demand (potential evapotranspiration)⁶⁷. As a result, SPEI is an ecologically relevant way to control for drought severity across locations and biomes with different baseline macroclimates and thus appropriate for determining the age-dependent drought responses at global scale, with negative and positive SPEI values indicating drier and wetter than usual conditions, respectively^{12,16,27,40,65}. We accessed the global SPEI dataset on the 1st February 2021 (<https://digital.csic.es/handle/10261/202305>), using version 2.6 which provides SPEI data at 0.5° spatial resolution globally from 1901 to 2015 on a monthly basis.

Given that annual radial growth typically takes at least three months to complete at most of our sites (i.e., temperate forests)^{16,27}, we evaluated all possible 3-month integrations of SPEI (i.e., SPEI03 where, for instance, month-tag “August” represents June-July-August). To allow for variations of drought timing across species and landscapes, we selected the SPEI03 period with the highest correlation to site SRW for each of the 1430 sites (Extended Data Fig. 4). The month-tags of the selected SPEI03 range from January to August for the Northern Hemisphere and October from the preceding year to April for the Southern Hemisphere. We then defined

drought ($\text{SPEI03} \leq -1.5$), non-drought ($\text{SPEI03} > -1.5$), and normal ($-1.5 < \text{SPEI03} < 1.5$) conditions at each site for subsequent analyses²⁷.

To ensure that larger variability of SPEI did not induce higher drought sensitivity in any of the three age cohorts of canopy-dominant trees, we examined empirical probability distributions and estimated standard deviations of SPEI for each age cohort of canopy-dominant trees for both angiosperms and gymnosperms. The probability distributions and standard deviations of SPEI between age cohorts are very similar within angiosperms and gymnosperms (Extended Data Fig. 7), indicating that each age cohort experienced similar interannual moisture variability across different locations.

Drought sensitivity, resistance, and resilience

We calculated the percentage of growth reduction (PGR) for every individual tree during drought using the differences of the means of standardized radial growth width (SRW) between drought years and non-drought years (i.e., $\overline{\text{SRW}}_{\text{drought}} - \overline{\text{SRW}}_{\text{non-drought}}$)¹⁶:

$$\text{PGR} = \frac{\overline{\text{SRW}}_{\text{drought}} - \overline{\text{SRW}}_{\text{non-drought}}}{\overline{\text{SRW}}_{\text{non-drought}}} \times 100$$

We also repeated the same procedure with the normal conditions ($-1.5 < \text{SPEI03} < 1.5$) as the baseline (see sensitivity analysis in Supplementary Information, shown in Fig. S1). Prior to calculating PGR, we set any SRW values larger than 5 or smaller than 0.01 to missing (NA, 0.004% and 0.37% of total observations, respectively) because these SRW values are likely due to measurement errors or non-drought-related missing rings.

To evaluate the continuous response of tree growth to moisture variability (as measured by SPEI03) across each age cohort, we used a generalized additive mixed-effects model to show and account for the non-linear nature of tree-growth response to moisture variability while controlling for the pseudo-replication in the data due to multiple tree-ring measurements from the same given tree within the same given site (i.e., using both individual tree ID and site ID as random intercept terms in the model: see model formula below). Specifically, we used the *bam* function in the *mgcv* package in R⁶⁸ to predict SRW as a function of age-specific drought

responses for both angiosperms and gymnosperms. We ran two separate models for angiosperms and gymnosperms with the same formula:

$$SRW = f(s(SPEI03_{AgeCohort}) + s(Site_{random}) + s(Individual_{random}))$$

where smooth terms (s) include SPEI03 during months specific to each age cohort at a given site and with random effects for each site and tree individual. The SPEI03 effects on SRW were estimated using three-knot thin plate regression splines with the fast restricted maximum likelihood (fREML) method, which allows flexible responses that vary by age cohort while also avoiding overfitting and undersmoothing^{68,69}. The regression model was performed on Indiana University's large-memory computer cluster "Carbonate". The summary output of the regression models for both angiosperms and gymnosperms, separately, is listed in Extended Data Table 4.

To compare how different age cohorts responded during and after a drought event, we also calculated both drought resistance and resilience⁷⁰. We first averaged SRW values five years prior to a drought event (SRW_{pre1-5}) to establish a baseline on how an individual behaves before a drought⁷⁰. Drought resistance is the ratio between SRW during drought (SRW_d) and mean pre-drought SRW (SRW_{pre1-5}), therefore representing an individual tree's capacity to endure and function under drought stress:

$$Resistance = \frac{SRW_d}{SRW_{pre1-5}}$$

We then defined drought resilience as the ratio between the SRW in each of the four years after drought ($SRW_{post1-4}$) and SRW_{pre1-5} , representing an individual tree's capacity to restore growth rates to the level observed before drought:

$$Resilience = \frac{SRW_{post1-4}}{SRW_{pre1-5}}$$

We calculated resilience for each of the four years following drought⁷⁰ since drought legacies can extend up to four years³⁰. We averaged the four consecutive years after a drought event to

get a mean resilience for each age cohort. We also calculated relative resilience to account for the differences in magnitude of drought resistance between age cohorts^{70,71}:

$$\text{Relative Resilience} = \text{Resilience} - \text{Resistance} = \frac{\text{SRW}_{\text{post1-4}} - \text{SRW}_d}{\text{SRW}_{\text{pre1-5}}}$$

We reported the drought resistance, resilience, and relative resilience as a percentage of growth reduction and recovery rate relative to pre-drought growth rate. Drought resistance or resilience greater than 100% means that trees have fully recovered to pre-drought growth rates, while values below 100% indicate that growth remains below pre-drought levels^{70,72}. Relative resilience greater than 0 means that trees have recovered from drought with more positive values indicating better recovery, while values below 0 represent that post-drought growth is lower than the growth during drought.

For all resistance, resilience, and relative resilience analyses, we considered individual trees that have both five consecutive years before a drought event and four consecutive years after a drought event. We also only considered single-year drought events instead of consecutive droughts in both resistance and resilience calculation to avoid including drought effects in either the pre-drought baseline or post-drought recovery estimates. Given that drought legacies can extend up to four years³⁰, we defined consecutive droughts as drought events that happened within three years before or after a given drought event. Drought resistance and resilience were considered under two scenarios (i.e., non-drought and normal conditions, see sensitivity analysis in Supplementary Information) to show how water availability before and after a drought event may impact resistance and resilience across age cohorts. Non-drought conditions excluded any drought but included exceptionally wet events (i.e., SPEI03 > 1.5) within three years before or after a given drought event. Normal conditions excluded both drought and exceptionally wet events within three years before or after a given drought event. After considering the above criteria, 21,205 (7810 angiosperms and 13,395 gymnosperms) and 19,482 (7266 angiosperms and 12,216 gymnosperms) tree individuals under non-drought and normal conditions scenarios, respectively were retained for the resistance and resilience analyses. For the tree individuals that experienced multiple single-drought events over their lifetimes, resistance and resilience indices were averaged for that individual.

We used one-way analysis of variance (ANOVA) and Tukey honest significant differences to examine if the mean percentage growth reduction, resistance, and relative resilience differed between young, intermediate, and old age cohorts within each of the two tree taxonomic groups (angiosperms vs. gymnosperms). We also evaluated the robustness of our findings by repeating the same analyses using log-transformed resistance and relative resilience indices (to make the distribution more symmetric by natural logarithm). We then compared the mean of log-transformed resistance and relative resilience between age cohorts within angiosperms and gymnosperms by ANOVA and Tukey honest significant differences. The results of log-transformed resistance and relative resilience were consistent with the untransformed data for non-drought conditions and normal conditions (Extended Data Table 5).

Linear Mixed Models

We fitted a linear mixed-effects model to examine the impacts of individual tree age as a continuous variable on the percentage of growth reduction (PGR, Fig. 1) with interaction between tree age and tree taxa using the *lme4* package in R⁷³. The linear mixed-effects model controls for the pseudo-replication in the data due to multiple observation from the same given species within the same given site (i.e., using both species ID and site ID as random intercept terms in the model: see model formula below).

$$PGR = A + \beta(Age \times Taxa) + \varepsilon(Site) + \varepsilon(Species)$$

where PGR is the percentage of growth reduction, A is overall intercept, β is the slope for the fixed effects, ε are the random effects for sites and species.

Examination of potential confounding effects from tree height

To account for potential confounding effect from tree height, we obtained an additional 29 sites from DendroEcological Network with both raw tree-ring width and tree diameter at breast height (DBH) measurement⁴³, which allows us to retrieve a subset data consisting of 540 individual trees from eight species (five angiosperms, three gymnosperms). We then used Tallo, a global tree allometric collection with both tree DBH and height data of nearly 500,000 individual trees from over 5,000 species, to infer the relationship between log-transformed tree height and DBH for those eight species with the following equation²⁵. We then calculated the individual tree height from corresponding DBH measurement within the subset data based on the species-specific height-diameter relationship.

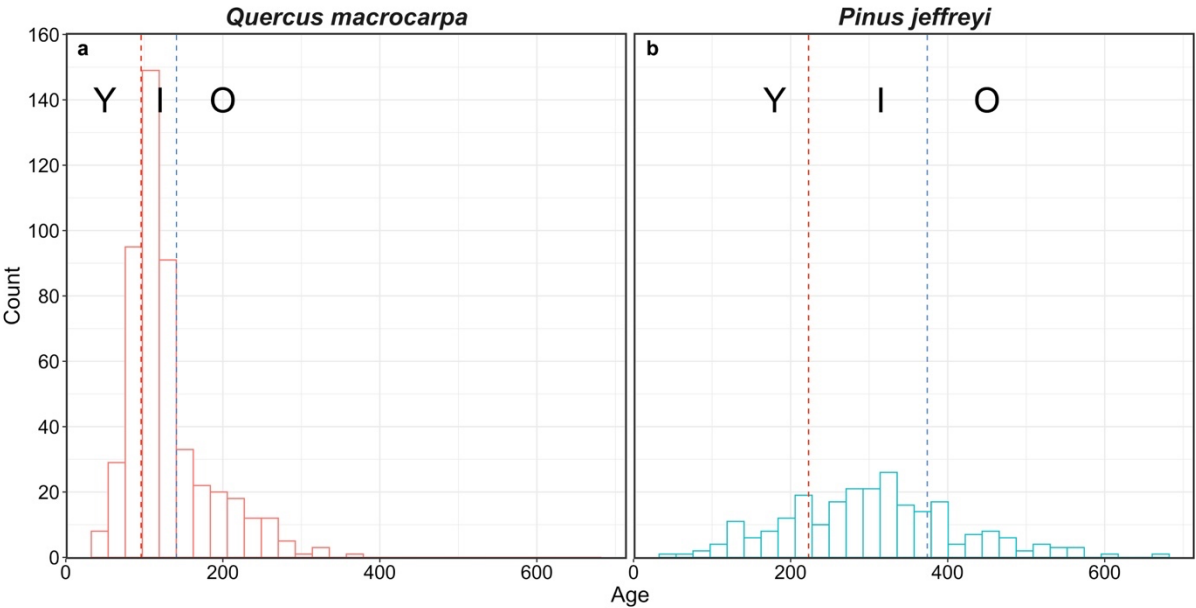
$$\log(\text{Height}) = \log(\text{DBH})$$

The tree age and tree height are poorly correlated ($r = 0.21$, $n = 540$), indicating these two variables are not redundant and can be included simultaneously as predictor variables in the same multiple regression model. We first standardized the tree age and tree height by using the *gscale* function provided in the *jtools* package⁷⁴ and then employed the following candidate linear mixed-effects models to examine the best variable for explaining the percentage of growth reduction (PGR). We used Akaike information criterion (AIC) to compare the fit of the following models and selected the best candidate model with the lowest AIC scores (i.e., the best model). The first two best models with delta AIC values less than two were reported in the Table S2 and S3. The AIC ranking for the candidate models was done by *aictab* function in *AICcmodavg* package⁷⁵. The candidate models and corresponding abbreviation are as below:

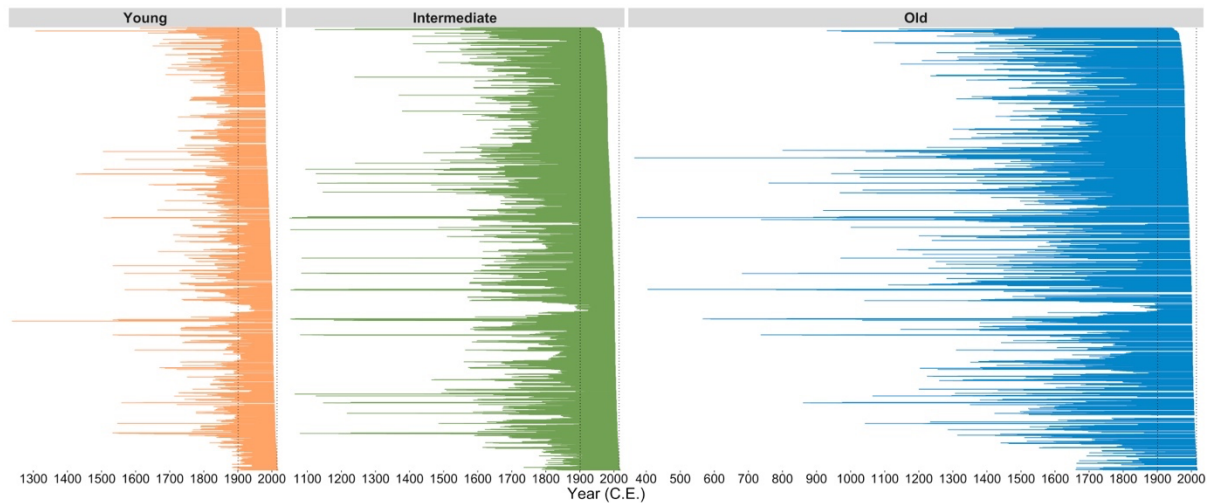
$\text{PGR} = A + \beta(\text{Age}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	A0 (Table S6)
$\text{PGR} = A + \beta(\text{Age}) + \beta(\text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	A1 (Table S4)
$\text{PGR} = A + \beta(\text{Age} \times \text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	A2 (Table S2)
$\text{PGR} = A + \beta(\text{Height}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	H0 (Table S10)
$\text{PGR} = A + \beta(\text{Height}) + \beta(\text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	H1 (Table S8)
$\text{PGR} = A + \beta(\text{Height} \times \text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	H2 (Table S7)
$\text{PGR} = A + \beta(\text{Age}) + \beta(\text{Height}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	AH (Table S5)
$\text{PGR} = A + \beta(\text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	T0 (Table S9)
$\text{PGR} = A + \beta(\text{Age}) + \beta(\text{Height}) + \beta(\text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$	All (Table S3)

The best model and the next-best model with less than two delta AIC units were A2 (AIC: 4030.94) and All (AIC: 4032.59), which together carried 80% of the cumulative model weight (Table S1). The models including tree height but excluding tree age as a parameter (i.e., H0, H1, and H2) only contained 1% of the cumulative model weight (Table S1). For the model A2, the growth was reduced by 5.3% per one unit of standardized age (Table S2, $P < 0.01$) while the interaction effect between age and tree taxa is weak probably due to under-representation of gymnosperms, leading to insufficient statistical power. For the model All, the growth was

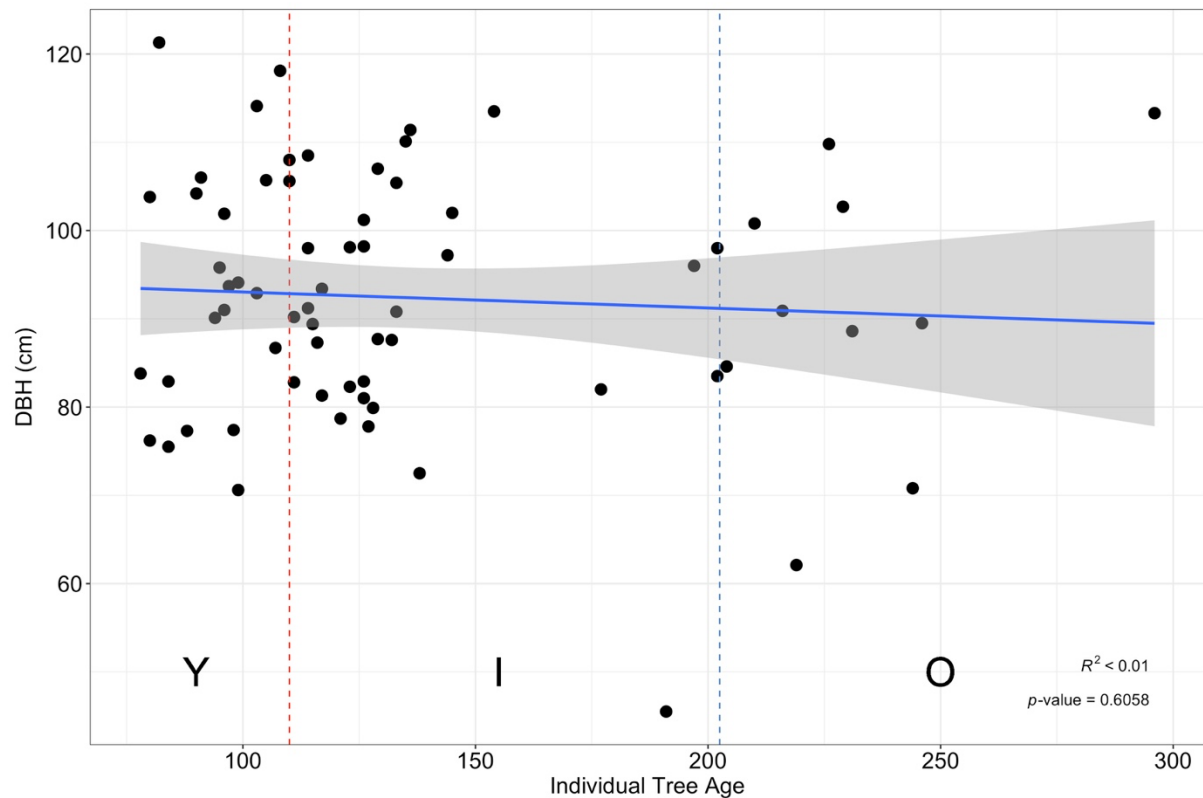
669 reduced by 4.3% per one unit of standardized age (Table S3, $P < 0.01$) while the growth
670 reduction was increased by 0.7% per one unit of standardized height (Table S3, $P = 0.72$).
671



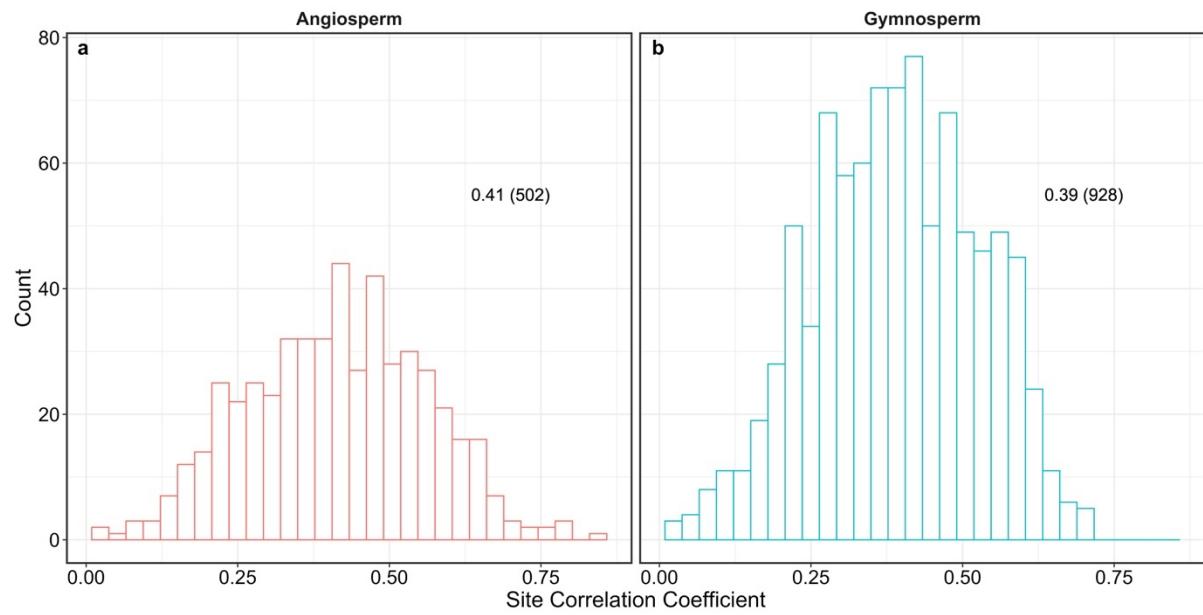
674 **Extended Data Fig. 1:** Examples of age grouping into young (Y), intermediate (I), and old (O)
675 tree cohorts based on species-specific distribution for (a) an angiosperm species (*Quercus*
676 *macrocarpa*) and (b) a gymnosperm species (*Pinus jeffreyi*) in North America. The dashed red
677 lines indicate the first quartile for the cutoff age of young and intermediate cohort, and the
678 dashed blue lines indicate the third quartile for the cutoff age of intermediate and old cohort.
679 The exact cutoff ages are listed in Extended Data Table 2 and the maximum, mean, median,
680 and minimum ages of each age cohort of angiosperm and gymnosperm are listed in Extended
681 Data Table 3.



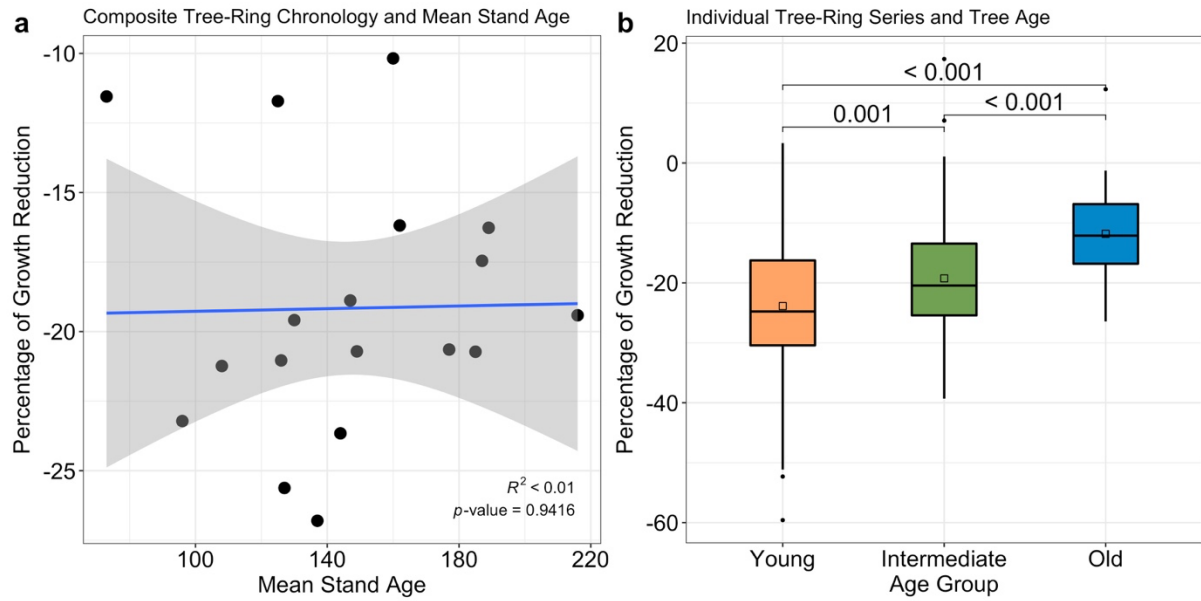
Extended Data Fig. 2: Time span of all individual tree series of young, intermediate, and old age cohorts after age grouping from species-specific age distribution. The period between the two vertical dashed lines of each panel indicates the available period of global SPEI dataset (1901–2015) for drought responses analyses. The maximum, mean, median, and minimum ages of each age cohort of angiosperm and gymnosperm are listed in Extended Data Table 3. Note the x-axis scales are different in each panel.



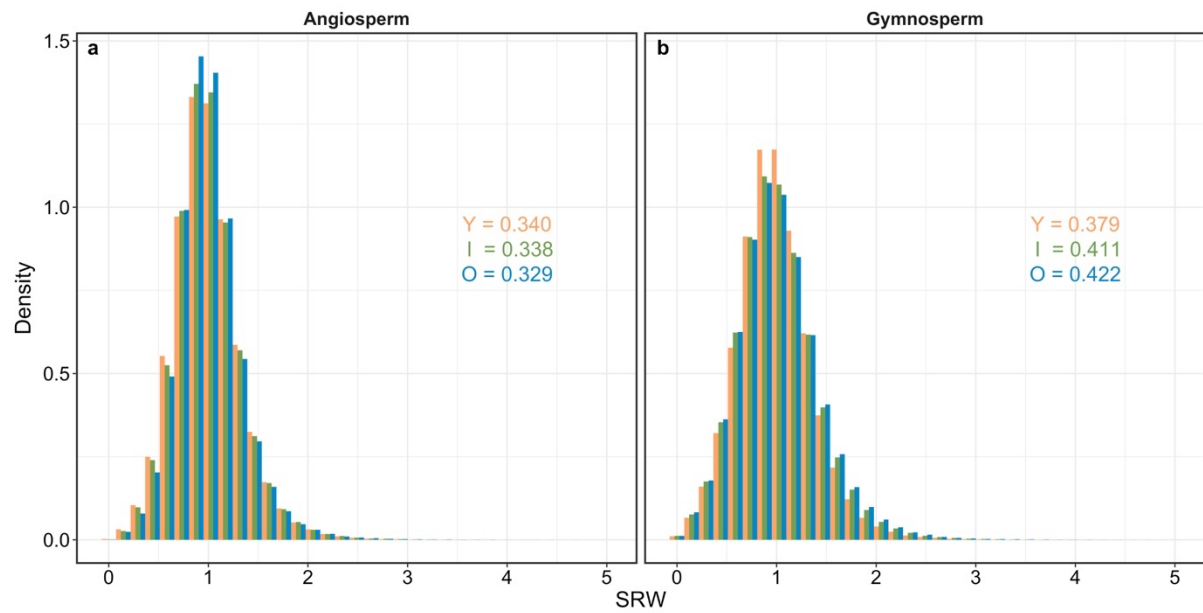
Extended Data Fig. 3: The relationship between individual tree age and diameter at breast height (DBH) for 68 canopy-dominant trees *Liriodendron tulipifera*, representing ~20% of total *L. tulipifera* samples. The dashed red lines indicate the first quartile for the cutoff age of young and intermediate cohort, and the dashed blue lines indicate the third quartile for the cutoff age of intermediate and old cohort for *L. tulipifera*. The exact cutoff ages for *L. tulipifera* are listed in Extended Data Table 2.



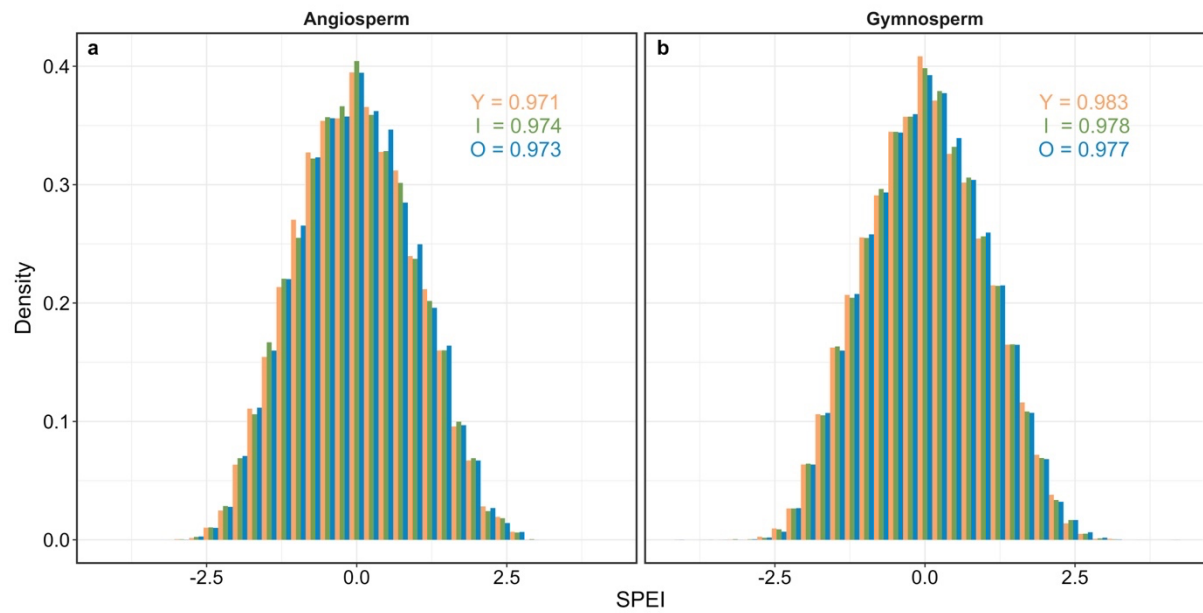
Extended Data Fig. 4: Distribution of correlation coefficients between site-optimized 3-month SPEI and site chronologies for (a) angiosperms and (b) gymnosperms. Numbers in the upper right and the parentheses indicate mean correlation and total number of sites, respectively.



Extended Data Fig. 5: Comparison of *Quercus alba* drought responses at 18 sites between (a) composite chronology with mean stand age and (b) individual series with individual tree age approach using the same dataset as in Au et al. 2020¹⁶. Hence, the same data can lead to very different results due to diluting effect of aggregating data at the coarser stand level. Here, we advocate for analysing the raw data on individual tree-ring time series rather than analysing the aggregated the information at the stand level for age-dependent drought responses.



Extended Data Fig. 6: Empirical probability densities of standardized radial growth (SRW) across young (orange), intermediate (green), and old (blue) cohorts for the (a) angiosperms and (b) gymnosperms, separately. Numbers in the panels indicate standard deviations of the young (Y), intermediate (I), and old (O) age cohort, separately for angiosperms and gymnosperms.



Extended Data Fig. 7: Empirical probability densities of the Standardized Precipitation-Evapotranspiration Index (SPEI) across young (orange), intermediate (green), and old (blue) cohorts for (a) angiosperms and (b) gymnosperms, separately. Numbers in the panels indicate standard deviations for the young (Y), intermediate (I), and old (O) age cohort, separately for angiosperms and gymnosperms.

Extended Data Table 1: Fixed effect estimates, standard error (SE), and degree of freedom (df) of the linear mixed model for predicting percentage of growth reduction in response to individual tree age.

Variables	Estimate \pm SE	df	t value	p value
Intercept	-27.85 \pm 1.18	120	-23.68	< 0.001
Age	0.037 \pm 0.003	21570	14.05	< 0.001
Taxa Gymnosperm	3.50 \pm 1.42	123.8	2.47	0.0151
Age: Taxa Gymnosperm	-0.033 \pm 0.003	21500	-11.90	< 0.001

Extended Data Table 2: Age cutoffs for 119 species of tree taxa angiosperm (A) and gymnosperm (G) based on species-specific age distributions that separate young, intermediate and old age cohorts. Q1 indicates the cutoff age of the first quartile while Q3 indicates the cutoff age of the third quartile. Min and Max indicate the minimum and maximum age of each canopy-dominant species within the dataset. Species codes PISP, JUSP, PCSP represent miscellaneous or unknown species from the *Pinus*, *Juniperus* and *Picea* genera, respectively.

Species Code	Latin Name	Genus	Family	Taxa	Min	Q1	Q3	Max
ABAL	<i>Abies alba</i>	<i>Abies</i>	Pinaceae	G	47	97.75	166.25	423
ABBO	<i>Abies borisii-regis</i>	<i>Abies</i>	Pinaceae	G	106	136	169	170
ABCE	<i>Abies cephalonica</i>	<i>Abies</i>	Pinaceae	G	61	85.75	133	303
ABCI	<i>Abies cilicica</i>	<i>Abies</i>	Pinaceae	G	93	105.5	202.5	280
ABFO	<i>Abies forestii</i>	<i>Abies</i>	Pinaceae	G	95	176	402.75	626
ABPI	<i>Abies pindrow</i>	<i>Abies</i>	Pinaceae	G	100	161.75	262.75	373
ABSB	<i>Abies spectabilis</i>	<i>Abies</i>	Pinaceae	G	39	99	249.5	396
ACRU	<i>Acer rubrum</i>	<i>Acer</i>	Sapindaceae	A	65	85	99	111
ACSH	<i>Acer saccharum</i>	<i>Acer</i>	Sapindaceae	A	47	89.75	127.5	207
ADUS	<i>Adesmia uspallatensis</i>	<i>Adesmia</i>	Fabaceae	A	69	89	129	149
AGAU	<i>Agathis australis</i>	<i>Agathis</i>	Araucariaceae	G	67	147.25	258.75	499
ARAR	<i>Araucaria araucana</i>	<i>Araucaria</i>	Araucariaceae	G	78	192	305.5	766
ATCU	<i>Athrotaxis cupressoides</i>	<i>Athrotaxis</i>	Cupressaceae	G	131	234.75	424.5	682
ATSE	<i>Athrotaxis selaginoides</i>	<i>Athrotaxis</i>	Cupressaceae	G	206	287.75	419	630
AUCH	<i>Austrocedrus chilensis</i>	<i>Austrocedrus</i>	Cupressaceae	G	52	156	287	830
BELE	<i>Betula lenta</i>	<i>Betula</i>	Betulaceae	A	73	115	146	182
BEUT	<i>Betula utilis</i>	<i>Betula</i>	Betulaceae	A	56	69.75	110.75	178
CAPR	<i>Callitris preissii</i>	<i>Callitris</i>	Cupressaceae	G	35	43	52.25	64
CDAT	<i>Cedrus atlantica</i>	<i>Cedrus</i>	Pinaceae	G	155	233	566.5	785
CDBR	<i>Cedrus brevifolia</i>	<i>Cedrus</i>	Pinaceae	G	39	105	219	368
CDDE	<i>Cedrus deodara</i>	<i>Cedrus</i>	Pinaceae	G	84	144.25	296	712
CDLI	<i>Cedrus libani</i>	<i>Cedrus</i>	Pinaceae	G	53	140	309	619
CHLA	<i>Chamaecyparis lawsoniana</i>	<i>Chamaecyparis</i>	Cupressaceae	G	91	170.75	267.5	379
CHOB	<i>Chamaecyparis obtusa</i>	<i>Chamaecyparis</i>	Cupressaceae	G	652	766	940	944
CUCH	<i>Cupressus chengiana</i>	<i>Cupressus</i>	Cupressaceae	G	80	123.5	262.25	328
CYGL	<i>Carya glabra</i>	<i>Carya</i>	Juglandaceae	A	68	97.25	179.5	263
CYOV	<i>Carya ovata</i>	<i>Carya</i>	Juglandaceae	A	72	104.25	169.75	354
FAGR	<i>Fagus grandifolia</i>	<i>Fagus</i>	Fagaceae	A	61	114.25	185	293
FASY	<i>Fagus sylvatica</i>	<i>Fagus</i>	Fagaceae	A	57	120	167	242
FOHO	<i>Fokienia hodginsii</i>	<i>Fokienia</i>	Cupressaceae	G	203	301.25	499.25	659
FRAM	<i>Fraxinus americans</i>	<i>Fraxinus</i>	Oleaceae	A	65	99	122	183
FRNI	<i>Fraxinus nigra</i>	<i>Fraxinus</i>	Oleaceae	A	38	68.5	101	198
JUAU	<i>Juglans australis</i>	<i>Juglans</i>	Juglandaceae	A	38	84.75	119	216
JUEX	<i>Juniperus excelsa</i>	<i>Juniperus</i>	Cupressaceae	G	98	225.5	460.25	915

JUFO	<i>Juniperus foetidissima</i>	<i>Juniperus</i>	Cupressaceae	G	239	315	514	601
JUNI	<i>Juglans nigra</i>	<i>Juglans</i>	Juglandaceae	A	125	175.5	206	233
JUOC	<i>Juniperus occidentalis</i>	<i>Juniperus</i>	Cupressaceae	G	82	222	354.5	1025
JUOS	<i>Juniperus osteosperma</i>	<i>Juniperus</i>	Cupressaceae	G	79	243.5	398.5	573
JUPH	<i>Juniperus phoenicea</i>	<i>Juniperus</i>	Cupressaceae	G	200	290.5	427.5	526
JUPR	<i>Juniperus przewalskii</i>	<i>Juniperus</i>	Cupressaceae	G	121	490.25	953.25	1621
JUSC	<i>Juniperus scopulorum</i>	<i>Juniperus</i>	Cupressaceae	G	84	231.25	397	777
JUSE	<i>Juniperus serayschanica</i>	<i>Juniperus</i>	Cupressaceae	G	33	100.75	168.5	223
JUSP		<i>Juniperus</i>	Cupressaceae	G	43	130	418	1257
JUTI	<i>Juniperus tibetica</i>	<i>Juniperus</i>	Cupressaceae	G	82	283	543.75	969
JUTU	<i>Juniperus turkestanica</i>	<i>Juniperus</i>	Cupressaceae	G	186	294.75	516.5	979
JUVI	<i>Juniperus virginiana</i>	<i>Juniperus</i>	Cupressaceae	G	35	112.75	203.5	506
LASI	<i>Larix sibirica</i>	<i>Larix</i>	Pinaceae	G	86	244	393	713
LITU	<i>Liriodendron tulipifera</i>	<i>Liriodendron</i>	Magnoliaceae	A	42	110	202.5	418
NOBE	<i>Nothofagus betuloides</i>	<i>Nothofagus</i>	Nothofagaceae	A	87	120.5	182.75	251
NOPU	<i>Nothofagus pumilio</i>	<i>Nothofagus</i>	Nothofagaceae	A	34	129.5	208.5	384
PCAB	<i>Picea abies</i>	<i>Picea</i>	Pinaceae	G	37	78	120	202
PCGL	<i>Picea glauca</i>	<i>Picea</i>	Pinaceae	G	64	114.75	198	379
PCLI	<i>Picea likiangensis</i>	<i>Picea</i>	Pinaceae	G	156	177	238.25	345
PCSH	<i>Picea schrenkiana</i>	<i>Picea</i>	Pinaceae	G	64	143.25	262	432
PCSM	<i>Picea smithiana</i>	<i>Picea</i>	Pinaceae	G	51	163.5	285	619
PCSP		<i>Picea</i>	Pinaceae	G	220	243.5	450	529
PCTI	<i>Picea tienschanica</i>	<i>Picea</i>	Pinaceae	G	110	188	249.5	279
PHAS	<i>Phyllocladus aspleniifolius</i>	<i>Phyllocladus</i>	Podocarpaceae	G	66	161	280	528
PHGL	<i>Phyllocladus glaucus</i>	<i>Phyllocladus</i>	Podocarpaceae	G	100	221.5	331	435
PHTR	<i>Phyllocladus trichomanoides</i>	<i>Phyllocladus</i>	Podocarpaceae	G	157	197	257.5	313
PIAM	<i>Pinus armandii</i>	<i>Pinus</i>	Pinaceae	G	158	352	437	535
PIBA	<i>Pinus balfouriana</i>	<i>Pinus</i>	Pinaceae	G	404	571	875	1230
PIBR	<i>Pinus brutia</i>	<i>Pinus</i>	Pinaceae	G	65	120	233.75	279
PICE	<i>Pinus cembra</i>	<i>Pinus</i>	Pinaceae	G	110	185	260.25	265
PICM	<i>Pinus cembroides</i>	<i>Pinus</i>	Pinaceae	G	57	90	135	389
PICO	<i>Pinus contorta</i>	<i>Pinus</i>	Pinaceae	G	120	169	288	489
PIEC	<i>Pinus echinata</i>	<i>Pinus</i>	Pinaceae	G	45	74	174	272
PIED	<i>Pinus edulis</i>	<i>Pinus</i>	Pinaceae	G	95	272.5	426.5	962
PIFL	<i>Pinus flexilis</i>	<i>Pinus</i>	Pinaceae	G	101	274.5	513	995
PIGE	<i>Pinus gerardiana</i>	<i>Pinus</i>	Pinaceae	G	115	186	370	747
PIHA	<i>Pinus halepensis</i>	<i>Pinus</i>	Pinaceae	G	39	58	131.5	153
PIHR	<i>Pinus hartwegii</i>	<i>Pinus</i>	Pinaceae	G	88	109.5	307.5	399
PIJE	<i>Pinus jeffreyi</i>	<i>Pinus</i>	Pinaceae	G	49	223	374	661
PIMK	<i>Pinus merkusii</i>	<i>Pinus</i>	Pinaceae	G	112	151.75	200.25	257
PIMO	<i>Pinus monophylla</i>	<i>Pinus</i>	Pinaceae	G	96	190	350	613

PIMZ	<i>Pinus montezumae</i>	<i>Pinus</i>	Pinaceae	G	69	84.75	180.5	203
PINI	<i>Pinus nigra</i>	<i>Pinus</i>	Pinaceae	G	35	133.5	301.5	674
PIPA	<i>Pinus palustris</i>	<i>Pinus</i>	Pinaceae	G	25	68.25	213	424
PIPN	<i>Pinus pinea</i>	<i>Pinus</i>	Pinaceae	G	22	56.25	94.5	126
PIPO	<i>Pinus ponderosa</i>	<i>Pinus</i>	Pinaceae	G	48	185.75	326	704
PIPU	<i>Pinus pungens</i>	<i>Pinus</i>	Pinaceae	G	111	119	126	171
PIRE	<i>Pinus resinosa</i>	<i>Pinus</i>	Pinaceae	G	50	135	227	430
PIRI	<i>Pinus rigida</i>	<i>Pinus</i>	Pinaceae	G	59	97	147	379
PIRO	<i>Pinus roxburghii</i>	<i>Pinus</i>	Pinaceae	G	67	108	185.5	326
PISF	<i>Pinus strobiformis</i>	<i>Pinus</i>	Pinaceae	G	93	145	251.5	514
PISI	<i>Pinus sibirica</i>	<i>Pinus</i>	Pinaceae	G	87	205.25	397.75	841
PISP		<i>Pinus</i>	Pinaceae	G	63	116	143	161
PIST	<i>Pinus strobus</i>	<i>Pinus</i>	Pinaceae	G	28	76	147	340
PISY	<i>Pinus sylvestris</i>	<i>Pinus</i>	Pinaceae	G	49	117	211	381
PITB	<i>Pinus tabulaeformis</i>	<i>Pinus</i>	Pinaceae	G	106	122.25	176	234
PIVI	<i>Pinus virginiana</i>	<i>Pinus</i>	Pinaceae	G	43	59	101.25	176
PIWA	<i>Pinus wallichiana</i>	<i>Pinus</i>	Pinaceae	G	72	138.5	255.25	379
PSMA	<i>Pseudotsuga macrocarpa</i>	<i>Pseudotsuga</i>	Pinaceae	G	28	149	288.5	658
PSME	<i>Pseudotsuga menziesii</i>	<i>Pseudotsuga</i>	Pinaceae	G	44	160	338	862
QUAL	<i>Quercus alba</i>	<i>Quercus</i>	Fagaceae	A	33	122	238	414
QUCE	<i>Quercus cerris</i>	<i>Quercus</i>	Fagaceae	A	59	102	136	142
QUCO	<i>Quercus coccinea</i>	<i>Quercus</i>	Fagaceae	A	37	57	81	118
QUDG	<i>Quercus douglasii</i>	<i>Quercus</i>	Fagaceae	A	28	98	199	448
QUFA	<i>Quercus falcata</i>	<i>Quercus</i>	Fagaceae	A	62	70.5	79.5	108
QUHA	<i>Quercus hartwissiana</i>	<i>Quercus</i>	Fagaceae	A	89	151	226.5	362
QULO	<i>Quercus lobata</i>	<i>Quercus</i>	Fagaceae	A	57	90.25	190.5	314
QULY	<i>Quercus lyrata</i>	<i>Quercus</i>	Fagaceae	A	73	154.75	228.5	329
QUMA	<i>Quercus macrocarpa</i>	<i>Quercus</i>	Fagaceae	A	33	96	141	362
QUMC	<i>Quercus macrolepis</i>	<i>Quercus</i>	Fagaceae	A	59	66.5	73.5	89
QUMG	<i>Quercus mongolica</i>	<i>Quercus</i>	Fagaceae	A	46	59	116.75	178
QUMO	<i>Quercus montana</i>	<i>Quercus</i>	Fagaceae	A	48	125	228.75	425
QUMU	<i>Quercus muehlenbergii</i>	<i>Quercus</i>	Fagaceae	A	47	136	191.5	425
QUPA	<i>Quercus palustris</i>	<i>Quercus</i>	Fagaceae	A	84	94.25	103.5	108
QUPE	<i>Quercus petraea</i>	<i>Quercus</i>	Fagaceae	A	44	118	165	441
QURO	<i>Quercus robur</i>	<i>Quercus</i>	Fagaceae	A	38	119	172.5	449
QURU	<i>Quercus rubra</i>	<i>Quercus</i>	Fagaceae	A	33	98.25	150.25	217
QUST	<i>Quercus stellata</i>	<i>Quercus</i>	Fagaceae	A	46	145	230	374
QUVE	<i>Quercus velutina</i>	<i>Quercus</i>	Fagaceae	A	36	70	121	259
SAAL	<i>Salix alba</i>	<i>Salix</i>	Salicaceae	A	65	65	79	91
TADI	<i>Taxodium distichum</i>	<i>Taxodium</i>	Cupressaceae	G	54	154.5	394.5	1621
TAMU	<i>Taxodium mucronatum</i>	<i>Taxodium</i>	Cupressaceae	G	48	115	300.5	751
TEGR	<i>Tectona grandis</i>	<i>Tectona</i>	Lamiaceae	A	61	109	217.5	391

THOC	<i>Thuja occidentalis</i>	<i>Thuja</i>	Cupressaceae	G	54	115.25	478	745
TOCI	<i>Toona ciliata</i>	<i>Toona</i>	Meliaceae	A	33	49.25	101	147
TSCA	<i>Tsuga canadensis</i>	<i>Tsuga</i>	Pinaceae	G	30	134	289	540
TSCR	<i>Tsuga caroliniana</i>	<i>Tsuga</i>	Pinaceae	G	232	244.5	280.5	307
TSME	<i>Tsuga mertensiana</i>	<i>Tsuga</i>	Pinaceae	G	93	187.75	251	443

743
744

Extended Data Table 3: The maximum, mean, median, and minimum age of young, intermediate, and old age cohort of angiosperm and gymnosperm.

Age Cohort	Angiosperms				Gymnosperms			
	Max	Mean	Median	Min	Max	Mean	Median	Min
Young	172	89	89	28	766	130	117	22
Intermediate	237	151	148	53	953	242	228	45
Old	449	237	242	74	1621	406	376	53

Extended Data Table 4: Generalized additive mixed-effect model summary for angiosperms and gymnosperms, including effective degrees of freedom (edf), referenced degrees of freedom (Ref. df), F statistics, and corresponding p-values.

Angiosperms					Gymnosperms			
Smooth terms	edf	Ref. df	F	p value	edf	Ref. df	F	p value
s(SPEI): Young	1.998	2	11132	< 0.001	1.994	2	13841	< 0.001
s(SPEI): Inter	1.999	2	21742	< 0.001	1.997	2	29788	< 0.001
s(SPEI): Old	1.995	2	8330	< 0.001	1.992	2	14859	< 0.001
s(site)	300	501	1.839	< 0.001	717.8	927	4.31	< 0.001
s(individual)	0.004	8088	0	1	0.089	13870	0	1

Extended Data Table 5: Difference of mean estimate of log-transformed resistance and relative resilience between age cohorts within angiosperms and gymnosperms for non-drought and normal conditions by Tukey Honest Significant Differences. The numbers with parentheses are the mean estimate under normal conditions. Numbers in bold indicate significant difference in mean estimate ($\alpha = 0.05$).

	Age Cohort	Angiosperm	Gymnosperm
Resistance	Young–Inter	0.051 (0.061)	0.025 (0.034)
	Inter–Old	0.056 (0.066)	0.013 (0.012)
	Young–Old	0.106 (0.127)	0.039 (0.046)
Resilience	Young–Inter	-0.023 (-0.025)	-0.016 (-0.014)
	Inter–Old	-0.036 (-0.030)	-0.007 (-0.005)
	Young–Old	-0.059 (-0.056)	-0.023 (-0.019)

Data availability

The data are accessible on the International Tree-Ring Data Bank (<https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring>) and the DendroEcological Network (<https://www.uvm.edu/femc/dendro#data>).

Code availability

The code used to calculate the results for this work is available from the corresponding author on reasonable request.

References

- Bonan GB. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 2008, **320**(5882): 1444-1449.
- Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, *et al.* Forest microclimate dynamics drive plant responses to warming. *Science* 2020, **368**(6492): 772-775.
- De Frenne P, Zellweger F, Rodriguez-Sanchez F, Scheffers BR, Hylander K, Luoto M, *et al.* Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution* 2019, **3**(5): 744-749.
- Anderegg WR, Kane JM, Anderegg LD. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature climate change* 2013, **3**(1): 30-36.
- Allen CD, Breshears DD, McDowell NG. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 2015, **6**(8): 1-55.

6. Novick KA, Ficklin DL, Stoy PC, Williams CA, Bohrer G, Oishi AC, *et al.* The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nature Climate Change* 2016, **6**(11): 1023-1027.
7. Ciais P, Reichstein M, Viovy N, Granier A, Ogée J, Allard V, *et al.* Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 2005, **437**(7058): 529-533.
8. Phillips OL, Aragão LE, Lewis SL, Fisher JB, Lloyd J, López-González G, *et al.* Drought sensitivity of the Amazon rainforest. *Science* 2009, **323**(5919): 1344-1347.
9. Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, *et al.* Forest disturbances under climate change. *Nature climate change* 2017, **7**(6): 395-402.
10. Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, *et al.* Global convergence in the vulnerability of forests to drought. *Nature* 2012, **491**(7426): 752-755.
11. Anderegg WR, Konings AG, Trugman AT, Yu K, Bowling DR, Gabbitas R, *et al.* Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature* 2018, **561**(7724): 538-541.
12. Anderegg WR, Trugman AT, Badgley G, Konings AG, Shaw J. Divergent forest sensitivity to repeated extreme droughts. *Nature Climate Change* 2020, **10**(12): 1091-1095.
13. Zhang T, Niinemets Ü, Sheffield J, Lichstein JW. Shifts in tree functional composition amplify the response of forest biomass to climate. *Nature* 2018, **556**(7699): 99-102.
14. Engelbrecht BM, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, *et al.* Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 2007, **447**(7140): 80-82.
15. Lenoir J, Gégout J-C, Marquet P, De Ruffray P, Brisse H. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 2008, **320**(5884): 1768-1771.
16. Au TF, Maxwell JT, Novick KA, Robeson SM, Warner SM, Lockwood BR, *et al.* Demographic shifts in eastern US forests increase the impact of late-season drought on forest growth. *Ecography* 2020, **43**(10): 1475-1486.
17. Schwalm CR, Anderegg WR, Michalak AM, Fisher JB, Biondi F, Koch G, *et al.* Global patterns of drought recovery. *Nature* 2017, **548**(7666): 202-205.
18. Lindenmayer DB, Laurance WF, Franklin JF. Global decline in large old trees. *Science* 2012, **338**(6112): 1305-1306.
19. McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B, Chini L, *et al.* Pervasive shifts in forest dynamics in a changing world. *Science* 2020, **368**(6494): eaaz9463.

- 840
841 20. Ellsworth D, Reich P. Canopy structure and vertical patterns of photosynthesis and
842 related leaf traits in a deciduous forest. *Oecologia* 1993, **96**(2): 169-178.
843
- 844 21. Stephenson NL, Das A, Condit R, Russo S, Baker P, Beckman NG, *et al.* Rate of tree
845 carbon accumulation increases continuously with tree size. *Nature* 2014, **507**(7490):
846 90-93.
847
- 848 22. Bastin J-F, Finegold Y, Garcia C, Mollicone D, Rezende M, Routh D, *et al.* The global
849 tree restoration potential. *Science* 2019, **365**(6448): 76-79.
850
- 851 23. Bennett AC, McDowell NG, Allen CD, Anderson-Teixeira KJ. Larger trees suffer most
852 during drought in forests worldwide. *Nature Plants* 2015, **1**(10): 1-5.
853
- 854 24. Piovesan G, Biondi F. On tree longevity. *New Phytologist* 2021, **231**(4): 1318-1337.
855
- 856 25. Jucker T, Fischer FJ, Chave J, Coomes DA, Caspersen J, Ali A, *et al.* Tallo: A global
857 tree allometry and crown architecture database. *Global change biology* 2022, **00**: 1–15.
858
- 859 26. Körner C. A matter of tree longevity. *Science* 2017, **355**(6321): 130-131.
860
- 861 27. D'orangeville L, Maxwell J, Kneeshaw D, Pederson N, Duchesne L, Logan T, *et al.*
862 Drought timing and local climate determine the sensitivity of eastern temperate forests
863 to drought. *Global change biology* 2018, **24**(6): 2339-2351.
864
- 865 28. Luo Y, Chen HY. Observations from old forests underestimate climate change effects
866 on tree mortality. *Nature communications* 2013, **4**(1): 1-6.
867
- 868 29. Dannenberg MP, Wise EK, Smith WK. Reduced tree growth in the semiarid United
869 States due to asymmetric responses to intensifying precipitation extremes. *Science*
870 *advances* 2019, **5**(10): eaaw0667.
871
- 872 30. Anderegg WR, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, *et al.* Pervasive
873 drought legacies in forest ecosystems and their implications for carbon cycle models.
874 *Science* 2015, **349**(6247): 528-532.
875
- 876 31. McCormick EL, Dralle DN, Hahm WJ, Tune AK, Schmidt LM, Chadwick KD, *et al.*
877 Widespread woody plant use of water stored in bedrock. *Nature* 2021, **597**(7875): 225-
878 229.
879
- 880 32. Giardina F, Konings AG, Kennedy D, Alemohammad SH, Oliveira RS, Uriarte M, *et*
881 *al.* Tall Amazonian forests are less sensitive to precipitation variability. *Nature*
882 *Geoscience* 2018, **11**(6): 405-409.
883
- 884 33. Phillips RP, Ibáñez I, D'Orangeville L, Hanson PJ, Ryan MG, McDowell NG. A
885 belowground perspective on the drought sensitivity of forests: towards improved
886 understanding and simulation. *Forest Ecology and Management* 2016, **380**: 309-320.
887
- 888 34. Meinzer FC, Lachenbruch B, Dawson TE. *Size-and age-related changes in tree*
889 *structure and function*, vol. 4. Springer Science & Business Media, 2011.

- 890
891 35. Fan Y, Miguez-Macho G, Jobbágy EG, Jackson RB, Otero-Casal C. Hydrologic
892 regulation of plant rooting depth. *Proceedings of the National Academy of Sciences*
893 2017, **114**(40): 10572-10577.
894
895 36. Klein T. The variability of stomatal sensitivity to leaf water potential across tree species
896 indicates a continuum between isohydric and anisohydric behaviours. *Functional*
897 *Ecology* 2014, **28**(6): 1313-1320.
898
899 37. Cavender-Bares J, Bazzaz F. Changes in drought response strategies with ontogeny in
900 *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* 2000,
901 **124**(1): 8-18.
902
903 38. Gallé A, Haldimann P, Feller U. Photosynthetic performance and water relations in
904 young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery.
905 *New Phytologist* 2007, **174**(4): 799-810.
906
907 39. Keith H, Mackey BG, Lindenmayer DB. Re-evaluation of forest biomass carbon stocks
908 and lessons from the world's most carbon-dense forests. *Proceedings of the National*
909 *Academy of Sciences* 2009, **106**(28): 11635-11640.
910
911 40. Vicente-Serrano SM, Gouveia C, Camarero JJ, Beguería S, Trigo R, López-Moreno JJ,
912 *et al.* Response of vegetation to drought time-scales across global land biomes.
913 *Proceedings of the National Academy of Sciences* 2013, **110**(1): 52-57.
914
915 41. Zhao S, Pederson N, D'Orangeville L, HilleRisLambers J, Boose E, Penone C, *et al.*
916 The International Tree-Ring Data Bank (ITRDB) revisited: Data availability and global
917 ecological representativity. *Journal of Biogeography* 2019, **46**(2): 355-368.
918
919 42. Fisher RA, Koven CD, Anderegg WR, Christoffersen BO, Dietze MC, Farrior CE, *et*
920 *al.* Vegetation demographics in Earth System Models: A review of progress and
921 priorities. *Global change biology* 2018, **24**(1): 35-54.
922
923 43. Rayback SA, Duncan JA, Schaberg PG, Kosiba AM, Hansen CF, Murakami PF. The
924 DendroEcological Network: A cyberinfrastructure for the storage, discovery and
925 sharing of tree-ring and associated ecological data. *Dendrochronologia* 2020, **60**:
926 125678.
927
928 44. Maxwell JT, Harley GL, Matheus TJ, Strange BM, Van Aken K, Au TF, *et al.* Sampling
929 density and date along with species selection influence spatial representation of tree-
930 ring reconstructions. *Climate of the Past* 2020, **16**(5): 1901-1916.
931
932 45. Maxwell JT, Harley GL, Mandra TE, Yi K, Kannenberg SA, Au TF, *et al.* Higher CO₂
933 concentrations and lower acidic deposition have not changed drought response in tree
934 growth but do influence iWUE in hardwood trees in the Midwestern USA. *Journal of*
935 *Geophysical Research: Biogeosciences* 2019.
936
937 46. Bunn AG. A dendrochronology program library in R (dplR). *Dendrochronologia* 2008,
938 **26**(2): 115-124.
939

47. Cook ER, Kairiukstis LA. *Methods of dendrochronology: applications in the environmental sciences*. Springer Science & Business Media, 2013.
48. Cook ER, Peters K. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. 1981.
49. Fritts H. Tree rings and climate. London, New York, San Francisco.: Academic Press; 1976.
50. Wilson R, Anchukaitis K, Briffa KR, Büntgen U, Cook E, D'arrigo R, *et al*. Last millennium northern hemisphere summer temperatures from tree rings: Part I: The long term context. *Quaternary Science Reviews* 2016, **134**: 1-18.
51. Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV, Underwood EC, *et al*. Terrestrial Ecoregions of the World: A New Map of Life on EarthA new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 2001, **51**(11): 933-938.
52. Holmes R. Program COFECHA user's manual. *Laboratory of Tree-Ring Research, The University of Arizona, Tucson* 1983.
53. Palmer JG, Cook ER, Turney CS, Allen K, Fenwick P, Cook BI, *et al*. Drought variability in the eastern Australia and New Zealand summer drought atlas (ANZDA, CE 1500–2012) modulated by the Interdecadal Pacific Oscillation. *Environmental Research Letters* 2015, **10**(12): 124002.
54. Cook ER, Anchukaitis KJ, Buckley BM, D'Arrigo RD, Jacoby GC, Wright WE. Asian monsoon failure and megadrought during the last millennium. *Science* 2010, **328**(5977): 486-489.
55. Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW. Long-term aridity changes in the western United States. *Science* 2004, **306**(5698): 1015-1018.
56. Cook ER, Seager R, Heim Jr RR, Vose RS, Herweijer C, Woodhouse C. Megadroughts in North America: Placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context. *Journal of Quaternary Science* 2010, **25**(1): 48-61.
57. Cook ER, Seager R, Kushnir Y, Briffa KR, Büntgen U, Frank D, *et al*. Old World megadroughts and pluvials during the Common Era. *Science advances* 2015, **1**(10): e1500561.
58. Morales MS, Cook ER, Barichivich J, Christie DA, Villalba R, LeQuesne C, *et al*. Six hundred years of South American tree rings reveal an increase in severe hydroclimatic events since mid-20th century. *Proceedings of the National Academy of Sciences* 2020, **117**(29): 16816-16823.
59. Stokes M, Smiley T. 1968: An introduction to tree-ring dating. Chicago: University of Chicago Press. 1968.

60. Lockwood BR, Maxwell JT, Robeson SM, Au TF. Assessing bias in diameter at breast height estimated from tree rings and its effects on basal area increment and biomass. *Dendrochronologia* 2021; 125844.
61. Locosselli GM, Brien RJ, de Souza Leite M, Gloor M, Krottenthaler S, de Oliveira AA, *et al.* Global tree-ring analysis reveals rapid decrease in tropical tree longevity with temperature. *Proceedings of the National Academy of Sciences* 2020, **117**(52): 33358-33364.
62. Rozas V, DeSoto L, Olano JM. Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytologist* 2009, **182**(3): 687-697.
63. Carrer M, Urbinati C. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 2004, **85**(3): 730-740.
64. Gazol A, Camarero J, Anderegg W, Vicente-Serrano S. Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Global Ecology and Biogeography* 2017, **26**(2): 166-176.
65. Li X, Piao S, Wang K, Wang X, Wang T, Ciais P, *et al.* Temporal trade-off between gymnosperm resistance and resilience increases forest sensitivity to extreme drought. *Nature Ecology & Evolution* 2020, **4**(8): 1075-1083.
66. Pardos M, Del Río M, Pretzsch H, Jactel H, Bielak K, Bravo F, *et al.* The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe. *Forest Ecology and Management* 2021, **481**: 118687.
67. Vicente-Serrano SM, Beguería S, López-Moreno JI. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of climate* 2010, **23**(7): 1696-1718.
68. Wood SN. *Generalized additive models: an introduction with R*. CRC press, 2017.
69. Rollinson CR, Alexander MR, Dye AW, Moore DJ, Pederson N, Trouet V. Climate sensitivity of understory trees differs from overstory trees in temperate mesic forests. *Ecology* 2021, **102**(3): e03264.
70. Lloret F, Keeling EG, Sala A. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 2011, **120**(12): 1909-1920.
71. Li X, Piao S, Wang K, Wang X, Wang T, Ciais P, *et al.* Reply to: Disentangling biology from mathematical necessity in twentieth-century gymnosperm resilience trends. *Nature Ecology & Evolution* 2021, **5**(6): 736-737.
72. Zheng T, Martínez-Vilalta J, García-Valdés R, Gazol A, Camarero JJ, Mencuccini M. Disentangling biology from mathematical necessity in twentieth-century gymnosperm resilience trends. *Nature ecology & evolution* 2021: 1-3.

73. Bates D, Mächler M, Bolker B, Walker S. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 2015, **67**(1): 1 - 48.
74. Long JA. jtools: Analysis and presentation of social scientific data. R package version 2.2.0. 2022.
75. Mazerolle MJ. AICcmodavg: Model selection and multimodel inference based on AIC. R package version 2.3-1. 2020.

Acknowledgments

We thank Neil Pederson, Ying Zhao, Yuting Jin, and Suet Lin Kong for providing feedback and data. We thank all contributors to the ITRDB and DEN to make this analysis feasible. The research is supported by Indiana University College of Arts and Sciences Dissertation Research Fellowship.

Author Contributions

T.F.A. and J.L. conceived and designed the study with all authors providing input. J.T.M., J.L., M.P.D., T.L., and Z.C. contributed data. T.F.A. performed analyses with contribution from S.M.R. and J.L. All authors discussed, interpreted results, drew conclusions and wrote the paper.

Competing interests

The authors declare no competing interests.

Corresponding author

Correspondence and requests for materials should be addressed to Tsun Fung Au.