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

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As forest demographics are altered by the global decline of old trees and reforestation efforts, younger trees are expected to have an increasingly important influence on carbon sequestration and forest ecosystem functioning. However, the relative resilience of these younger trees to climate change stressors is poorly understood. 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. Angiosperms show greater age differences than gymnosperms, and age-dependent sensitivity is more pronounced in humid climates compared with more arid regions. However, younger canopy-dominant trees also recover more quickly from drought. The future combination of increased drought events and an increased proportion of younger canopy-dominant trees suggests 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.

Forests regulate global climate[1] and provide stable understory microclimates that promote biodiversity[2,3]. However, more frequent and intense droughts can cause irreversible damage to plant hydraulics and induce forest dieback through concomitant abiotic and biotic stress[4–6], which can reduce carbon sequestration and generate a positive feedback loop on the pace of climate change[7–9]. While previous work suggests that most species have similar vulnerability to drought[10], substantial variability in drought responses has been shown for angiosperms and gymnosperms[11,12]. Drought can also alter the distribution of forest types, species composition and ecosystem services[4,13–15]. For example, widespread forest dieback can reduce the microclimatic buffering effect of canopy-dominant trees[3], rapidly increasing subcanopy temperatures and their temporal rate of change, with important consequences for forest biodiversity under climate change[2]. While shifting forest species composition alters drought sensitivity of the forests[16], warmer and drier conditions can hinder the ability of trees to return to pre-drought growth rates (drought resilience)[17]. Therefore, improved understanding of forest sensitivity and resilience to drought helps decrease the uncertainty in terrestrial carbon-cycle feedbacks.

Anthropogenic disturbances such as deforestation and selective logging, combined with climate-induced threats, have caused the decline of old canopy-dominant trees[18,19] that sequester large amounts

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of carbon while simultaneously buffering and stabilizing microclimates in the understory[2,3,20,21]. Globally, subsequent reforestation, whether through natural succession or tree planting[22], has led and will further lead to forests that are dominated by a younger age structure[19]. The area covered by younger trees reaching the upper layer of the forest canopy in the temperate biome (4 million km^2, <140 years old) already far exceeds the area covered by older trees (2.2 million km^2) (ref. [19]). Therefore, younger trees reaching the upper canopy layer, hereby referred as younger canopy-dominant trees, are an increasingly important component of forest ecosystems and functions. Hence, it is critically important to understand the extent to which these less-mature trees share the same resistance to climate extremes as older trees within the upper canopy layer. In response to drought, larger trees generally have greater decreases in growth than smaller trees[23]. However, while taller or bigger trees are generally assumed to be older trees, tree size, either measured by height or diameter at breast height, does not necessarily indicate and reflect tree age. This is especially true in harsh environments (for example, cold and dry climates) or for populations located close to the species' range limits, where individual trees of similar size from the same species could differ by several centuries in age[24]. If there are clear links (allometric equations) to relate tree height and tree diameter at breast height[25], the link between tree size (for example, tree height) and tree age is much less evident, especially so when comparing trees from the upper canopy layer (Extended Data Fig. 1). 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 ongoing 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 of microclimates 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 (Extended Data Fig. 2). 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 anthropogenic climate change.

In this Article, we investigate drought responses across several tree-age cohorts of canopy-dominant angiosperm and gymnosperm species by assessing (1) drought sensitivity (the percentage of growth reduction between drought and non-drought conditions), (2) drought resistance (growth rate during drought compared with pre-drought levels) and (3) drought resilience (the capacity to resume growth to pre-drought levels) (Methods). Drought conditions were defined by the three-month averaged Standardized Precipitation Evapotranspiration Index (SPEI), which accounts for site variations in both moisture supply and demand (Methods and Extended Data Figs. 3 and 4). 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 (Extended Data Fig. 5). We then classified 21,964 canopy-dominant individual trees into three 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% (the interquartile) were attributed to the intermediate canopy-dominant cohort (Extended Data Figs. 6 and 7), 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).

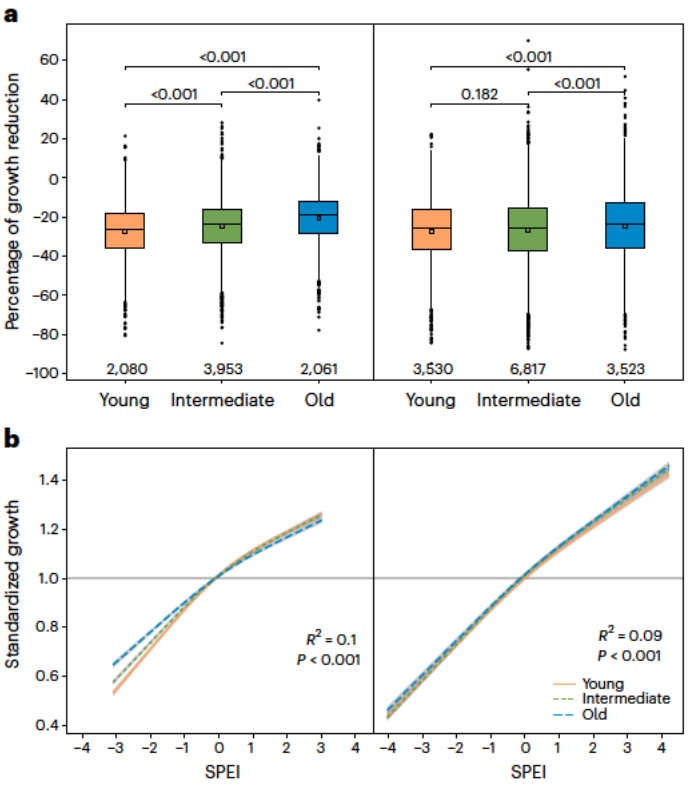

Fig. 1 | Drought-induced growth reduction of younger canopy-dominant trees is more pronounced than that for older canopy-dominant trees. a, Box plots of drought-induced tree-growth reduction as a percentage of difference between mean standardized growth during drought (SPEI ≤ −1.5) and mean standardized growth during non-drought (SPEI > −1.5) condition 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 each panel 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 each panel represent the number of tree individuals for the youngest, intermediate and oldest age cohort of canopy-dominant trees, respectively. **b**, Standardized growth of angiosperms (left) and gymnosperms (right) 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 box plot represent the median and the mean values, respectively. Age cohorts were assigned using species-specific age cut-offs (Extended Data Fig. 6 and Supplementary Table 12).

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 reduced by only 25% and 21%, respectively (Fig. 1a; $P_{young-Inter} < 0.001$, $P_{young-old} < 0.001$). Drought

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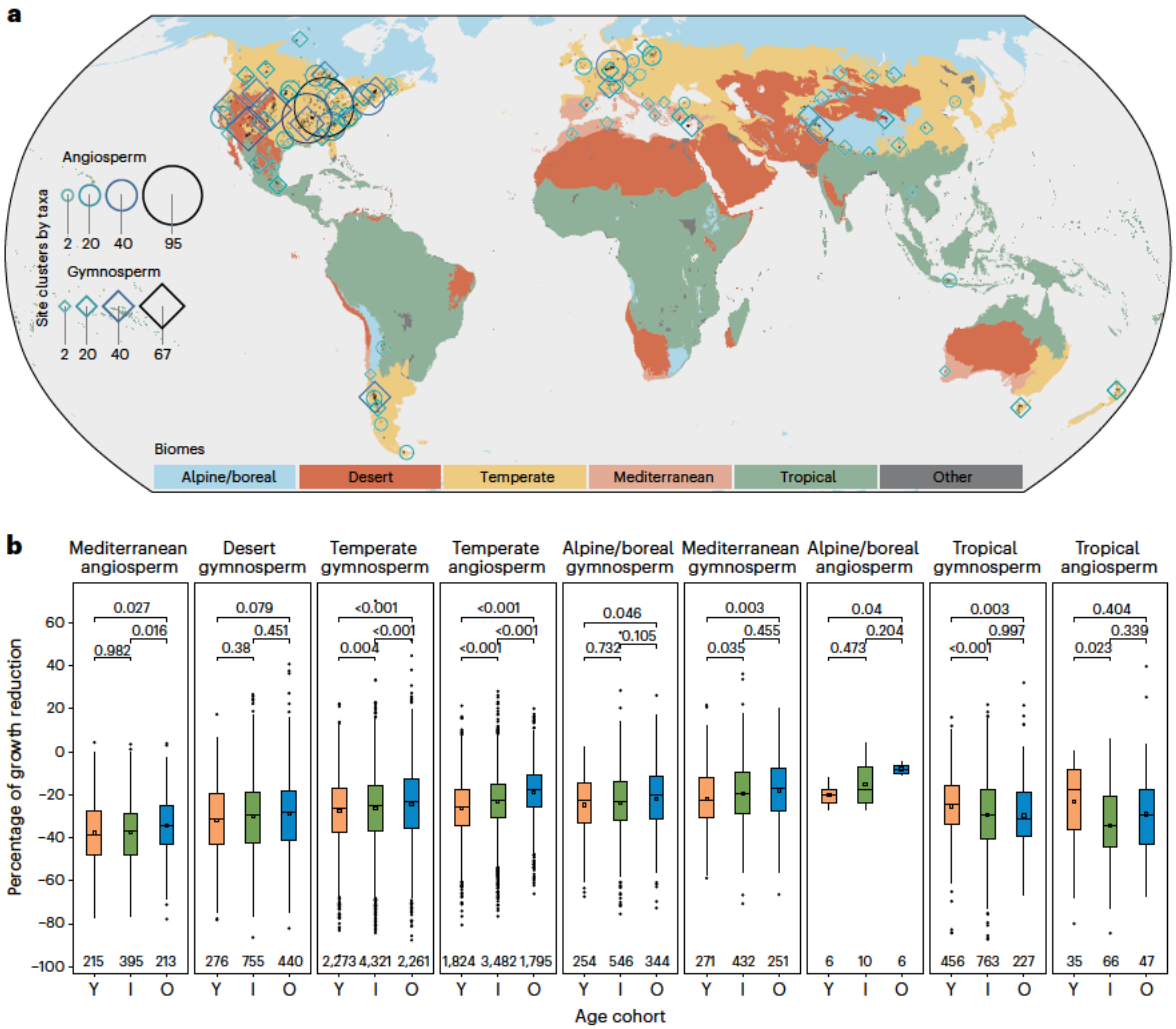

Fig. 2 | Drought-induced growth reduction varies across biomes. **a**, Geographical coverage and biomes of the tree-ring chronologies. Circle and square represent angiosperm ($n = 502$) and gymnosperm ($n = 928$) clusters, respectively. **b**, Percentage of growth reduction during drought events across 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 versus gymnosperms) are arranged on the basis of 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 **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 **b** represent number of tree individuals for the youngest, intermediate and oldest canopy-dominant cohorts, respectively. Boxes show the IQR while upper and lower whiskers are defined as Q3 + 1.5 × IQR and Q1 − 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 box plot represent the median and the mean values, respectively. Age cohorts were assigned using species-specific age cut-offs. Note that sample size for angiosperm in the alpine/boreal forests is low, and sampling in the tropical regions is under-represented, which may limit inference in these regions.

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; $P_{\text{young–Inter}} = 0.182$) but 2.5% 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 (using age as a continuous fixed effect; Methods) and found that younger canopy-dominant trees had a larger growth reduction during drought (Supplementary Table 1; $P < 0.001$). We also found that tree age had an interactive effect with tree taxa such that the percentage of growth reduction increased with age, and thus became less negative for old trees by 3.6% every 100 years for angiosperms, but only by 0.3% every 100 years for gymnosperms (Supplementary 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 for canopy-dominant trees. We then employed linear mixed-effects models to control for the potential confounding effect from tree height. Even after accounting for the effect of tree height, tree age was still the most prominent variable to explain drought-driven growth reduction within the canopy-dominant individual trees (Supplementary Tables 2–4). The percentage of growth reduction increased by 4.3% per one unit of standardized age, and thus became less negative for old trees, while the effect of standardized tree height was not significant (Supplementary Table 4; $P_{\text{age}} < 0.01$, $P_{\text{height}} = 0.71$).

For angiosperms, the difference in growth reduction among canopy-dominant cohorts was the greatest when moisture

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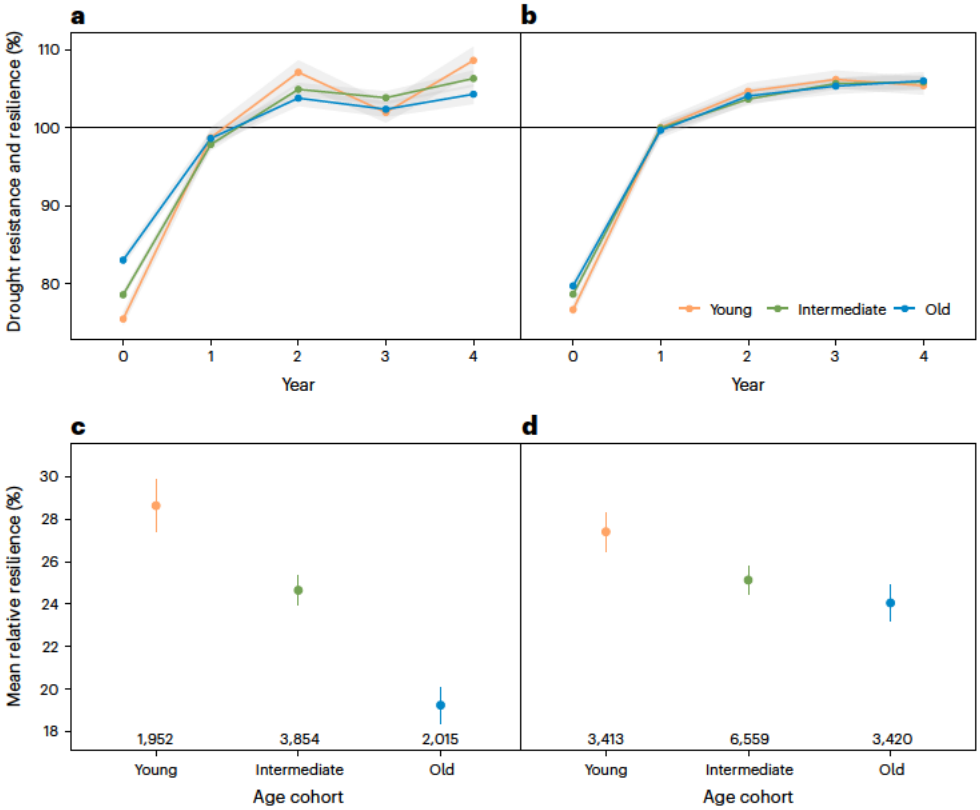

Fig. 3 | Age-dependent drought resistance and relative resilience converge between tree taxonomic groups. a,b, Temporal trends in drought resistance (year 0) and resilience (years 1–4) for young (orange), intermediate (green) and old (blue) cohorts of canopy-dominant trees for both angiosperms (**a**) and gymnosperms (**b**) compared to pre-drought growth rate 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 one, two, three and four 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 with 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 years 1 to 4 after drought and accounts 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 on the basis of species-specific age distribution (Extended Data Fig. 6 and Supplementary Table 12).

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 (SPEI < −3) (Fig. 1b; $P < 0.001$). Under extremely wet conditions (SPEI > 3), the youngest cohort of canopy-dominant trees for angiosperms had only 1.8% higher radial growth than the oldest canopy-dominant cohort. Gymnosperms experienced a wider range of SPEI, 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 experienced only 2% and 3% greater growth reduction than the oldest canopy-dominant cohort when SPEI went below −1.5 and −3, respectively (Fig. 1b; $P < 0.05$). The nonlinear relationship between moisture availability and relative change in 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 years[29].

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. 2). The average growth reductions of the youngest canopy-dominant cohort for angiosperms in Mediterranean (38%), temperate (26%) and alpine/boreal (20%) regions are 4%, 8% and 12% higher, respectively, than those of the oldest canopy-dominant cohort during drought (Fig. 2b; $P < 0.05$). The youngest canopy-dominant cohort for gymnosperms 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 with 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 6% and 4% more sensitive to drought, respectively, than the youngest canopy-dominant cohort (Fig. 2b).

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, with the oldest canopy-dominant cohort of angiosperms being more drought resistant than that of gymnosperms (Fig. 3a, b; $P < 0.001$). Importantly, 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 (relative resilience). Relative to pre-drought growth rate, the youngest cohort of canopy-dominant angiosperms recovered by

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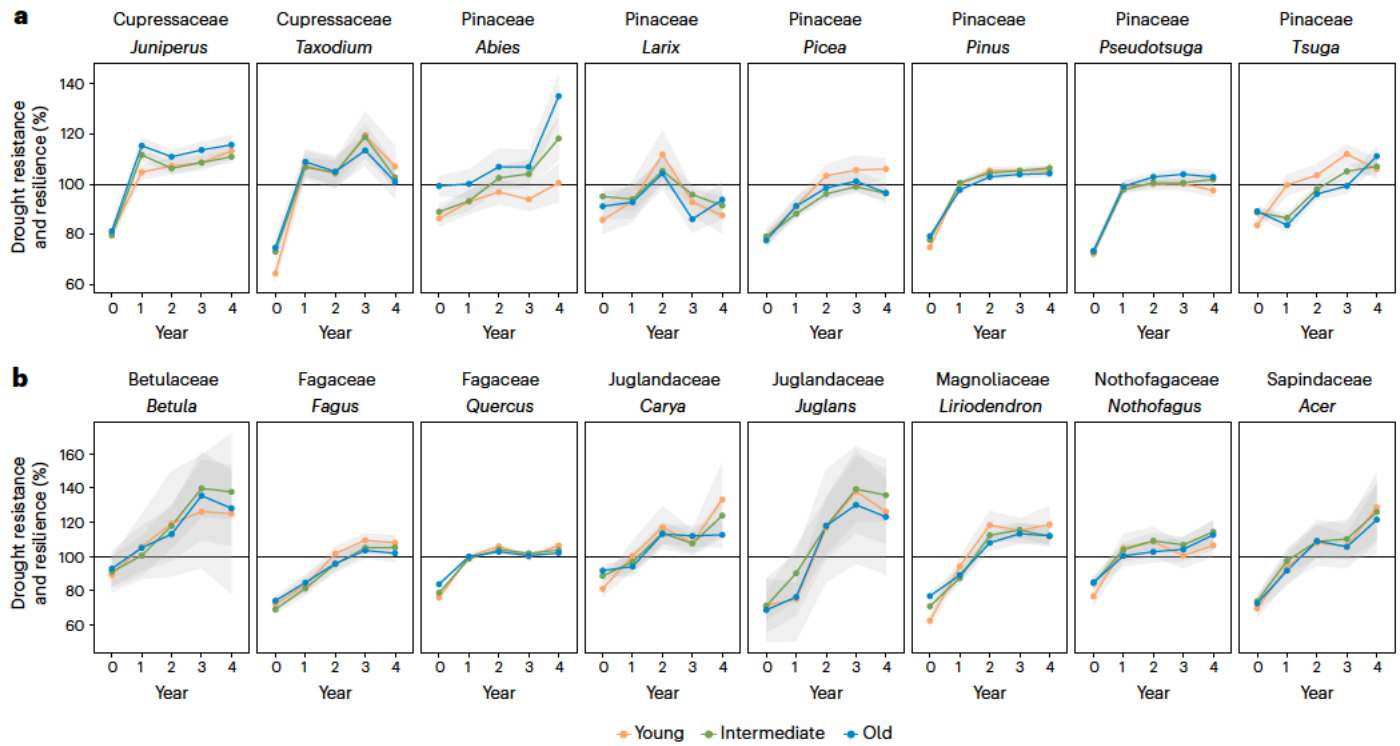

Fig. 4 | Variations of drought resistance and resilience in major tree genera. **a**,**b**, Temporal trends in drought resistance (year 0) and resilience (years 1–4) compared to pre-drought growth rate under non-drought conditions (SPEI > −1.5), with shaded 95% confidence interval, for young (orange), intermediate (green) and old (blue) cohorts of canopy-dominant trees for eight different genera (*Juniperus*, *Taxodium*, *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*) belonging to 91% of gymnosperm samples (**a**) and eight different genera (*Betula*, *Fagus*, *Quercus*, *Carya*, *Juglans*, *Liriodendron*, *Nothofagus*, *Acer*) belonging to 97% of angiosperm samples (**b**). Year 0 indicates averaged resistance coefficient during the drought year while years 1, 2, 3 and 4 indicate the resilience coefficient one, two, three and four years, respectively, after drought happens. The horizontal line at 100% indicates growth condition relative to the pre-drought level. The coefficients that are below the line indicate growth reduction while the coefficients that are above the line indicate growth enhancement compared with pre-drought condition. Age cohorts are assigned on the basis of species-specific age distribution (Extended Data Fig. 6 and Supplementary Table 12).

29%, on average, whereas the oldest cohort recovered only 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 angiosperm cohorts of canopy-dominant trees returned to pre-drought growth levels after the first year (all had a resilience index below 100% for year 1). The growth of angiosperms exceeded pre-drought levels (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 99.7% 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).

By contrast, previous research on 'drought legacies' (extended post-drought growth reductions and prolonged recoveries) showed that gymnosperms had more prevalent legacy effects[30]. While both angiosperms and gymnosperms had a resilience index above 100% for several years after drought (Fig. 3a,b), 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 (also three year for *Larix*) 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*, *Juglans*, *Liriodendron* and *Acer* (Fig. 4b), suggesting that longer-term legacy effects may be present in some angiosperm genera[16].

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 studies[23], 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 probably 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 droughts[33]. 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 ones[34]. For example, the mean rooting depth for *Quercus* (5.23 m) is deeper than for *Pinus* (2.45 m) (ref. [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, deeper rooting and thus 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 with a shallower rooting system 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 stomata more quickly during droughts to prevent dehydration and hydraulic damage. By contrast, angiosperms are more anisohydric, keeping stomata open for longer periods during droughts and allowing more stable gas exchange, transpiration and photosynthesis[10,36]. Among the angiosperms, the more isohydric genera (for example, *Liriodendron* and *Acer*) were less resistant to drought than was one of the most 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 period and have a higher carbon assimilation during droughts[37], allowing them to have less growth reduction and, thereby, be more drought tolerant than both mature gymnosperms and less mature angiosperms.

The youngest canopy-dominant angiosperms showed greater capacity to restore growth once favourable water status was returned even though angiosperms, using a more anisohydric strategy, tend to be more susceptible to xylem embolism[10]. Such plastic responses may be due to higher availability of parenchyma to allocate nonstructural carbohydrates for repairing drought-damaged tissues in angiosperms[12]. Likewise, photoprotective chemicals such as xanthophylls, α-tocopherol and ascorbate were reported in young individuals of an oak species (*Quercus pubescens*) to preserve photosynthetic apparatus[38], which may be an important mechanism to help restore photosynthesis once droughts end.

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 notorious 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, 26–28%; Fig. 2b) and temporarily converted the ecosystem into a net carbon source by releasing 0.5 PgC yr^{-1} into the atmosphere, which is equivalent to four years of net carbon storage in European ecosystems[7]. Thus, the substantially lower growth reduction of older canopy-dominant trees during drought, even an average of only 7–8% less compared with younger canopy-dominant trees, when taken at the global scale could have huge impacts on the regional carbon storage and the global carbon budget, particularly in temperate forests that currently are among the largest carbon sinks worldwide[39]. During extreme droughts, 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, droughts could also cause more-pronounced impacts on younger canopy-dominant angiosperms than on older ones, with important consequences for carbon sequestration and climate feedback loops in these ecosystems[28].

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 that the water balance of a given site is lower than usual, but the water balance may still be favourable for tree growth in humid regions, even when SPEI values are low[40]. 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 vapour-pressure deficit in xeric environments such as deserts may cause increased stomatal sensitivity of older canopy-dominant gymnosperms and limit evapotranspiration with less efficiency for 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 variability[32], 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 regions[41], 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 droughts 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 drought[12] and therefore predominate in future's 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 extremes[42]. 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 not only for their exceptional carbon residence and storage capacity[26,39] but also for their higher resistance to droughts so that the forests could have a diverse structure and composition to withstand and mitigate future emerging climate extremes[11].

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-022-01528-w.

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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 reconstruction[41] 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 Figs. 1, 6 and 7 and Supplementary Tables 12 and 13). We added the DEN database to our analyses 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 effect of tree height, which was obtained by feeding allometric equations with tree diameter data (see the following), on drought responses. We analysed 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 (the outermost ring) were not considered to ensure sufficient overlap with the observational records of the SPEI (from 1901 to 2015; see the following) and instances of drought and wet conditions (Extended Data Fig. 7).

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 R[46,47]. 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 (for example, the known decay of ring width when trees are aging as well as the suppression and release for shade-tolerant species)[16,46,48–50].

Given that temperature is typically the most limiting and sometimes the only factor affecting tree radial growth at high latitudes[40,50,51], 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 1,430 sites from both the ITRDB and DEN database that had a positive relationship (Extended Data Fig. 3) between standardized growth of site chronology and hydroclimate variability (SPEI03; see the following). From those 1,430 sites, we then considered only 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 in the preceding (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.[52] 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 and mixed forests; (5) temperate conifer forests; (6) boreal forests/taiga; (7) tropical grasslands, savannahs and shrublands; (8) temperate grasslands, savannahs and shrublands; (9) flooded grasslands and savannahs; (10) montane grasslands and shrublands; (11) tundra; (12) Mediterranean forests, woodlands and scrubs; (13) deserts and xeric shrublands; and (14) rock and 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 five major biomes (Fig. 2a): (i) alpine/boreal forests (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 and savannahs (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[41,53]. We also scrutinized the cross-dating quality of all individual tree-ring time series by removing poorly cross-dated individuals (for example, 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[54–59]. Researchers attempt to sample tree cores as close to the pith as possible within each of these study sites to maximize the time span of the drought reconstruction[60]. Although this sampling approach may produce bias towards more mature canopy-dominant trees[41], there are still substantial variations in individual tree ages for multiple tree species (Extended Data Figs. 1, 6 and 7 and Supplementary Tables 12 and 13).

To estimate tree age, we summed the number of total rings for each tree individual. A minor underestimation of the true tree age is still expected because samples were probably taken at or near breast height, some samples may miss the pith and some trees may have hollow centres due to heart-rotting fungus[61,62]. To minimize the underestimation of tree age, we used the tree core with the most total rings for individuals that have more than one core, allowing us to have 'maximum age' for every tree individual. As such, this underestimation of tree age is probably 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[63,64]. 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[16,27,65–67], 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. 2). 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 (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 on the basis of 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 (interquartile) were classified as the intermediate age cohort and those above the third quartile were classified as the older age cohort (Extended Data Fig. 6). The maximum, mean, median, and minimum ages of each age cohort of angiosperm and gymnosperm are listed in Supplementary Table 13. 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 (Supplementary Table 13). 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 (for example, 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 (SRWs) for each age cohort of both angiosperms and gymnosperms. The probability distributions and standard deviations between age cohorts were very similar within tree taxa (angiosperms and gymnosperms; Extended Data Fig. 5), 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 SPEI, a measure of the standardized difference between water supply (precipitation) and water demand (potential evapotranspiration)[68]. 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-than-usual and wetter-than-usual conditions, respectively[12,16,27,40,66]. We accessed the global SPEI dataset on 1 February 2021 using version 2.6, which provides SPEI data at 0.5° spatial resolution globally from 1901 to 2015 on a monthly basis[68].

Given that annual radial growth typically takes at least three months to complete at most of our sites (temperate forests)[16,27], we evaluated all possible three-month integrations of SPEI (SPEI03 where, for example, 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 1,430 sites (Extended Data Fig. 3). 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 (SPEI03 ≤ −1.5), non-drought (SPEI03 > −1.5) and normal (−1.5 < SPEI03 < 1.5) conditions at each site for subsequent analyses[27].

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. 4), indicating that each age cohort experienced similar interannual moisture variability across different locations.

Responses to drought

We calculated the percentage of growth reduction (PGR) for every individual tree during drought using the differences of the means of SRW between drought years and non-drought years ($\overline{\mathrm{SRW}}_{\mathrm{drought}} - \overline{\mathrm{SRW}}_{\mathrm{non-drought}}$)[16]:

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

We also repeated the same procedure with the normal conditions (−1.5 < SPEI03 < 1.5) as the baseline (see sensitivity analysis in Supplementary Fig. 1). Before 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 probably 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 nonlinear 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 (using both individual tree identification (ID) and site ID as random intercept terms in the model (see model formula that follows)). Specifically, we used the bam function in the mgcv package in R[47,69] 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:

$$\mathrm{SRW} = f\left(s\left(\mathrm{SPEI03}_{\mathrm{AgeCohort}}\right) + s\left(\mathrm{Site}_{\mathrm{random}}\right) + s\left(\mathrm{Individual}_{\mathrm{random}}\right)\right)$$

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 method, which allows flexible responses that vary by age cohort while also avoiding overfitting and undersmoothing[69,70]. The regression model was performed on Indiana University's large-memory computer cluster 'Carbonate'. The summary outputs of the regression models for both angiosperms and gymnosperms, separately, are listed in Supplementary Table 14.

To compare how different age cohorts responded during and after a drought event, we also calculated both drought resistance and resilience[71]. We first averaged SRW values five years before a drought event ($\mathrm{SRW}_{\mathrm{pre1-5}}$) to establish a baseline on how an individual behaves before a drought[71]. Drought resistance is the ratio between SRW during drought ($\mathrm{SRW}_{\mathrm{d}}$) and mean pre-drought SRW ($\mathrm{SRW}_{\mathrm{pre1-5}}$), therefore representing an individual tree's capacity to endure and function under drought stress:

$$\mathrm{Resistance} = \frac{\mathrm{SRW}_{\mathrm{d}}}{\mathrm{SRW}_{\mathrm{pre1-5}}}$$

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

$$\mathrm{Resilience} = \frac{\mathrm{SRW}_{\mathrm{post1-4}}}{\mathrm{SRW}_{\mathrm{pre1-5}}}$$

We calculated resilience for each of the four years following drought[71] since drought legacies can extend up to four years[30]. 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[71,72]:

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

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[71,73]. 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 considered only 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 years[30], 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 (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 (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 preceding criteria, 21,213 (7,821 angiosperms and 13,392 gymnosperms) and 19,513 (7,254 angiosperms and 12,259 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 whether the mean percentage growth reduction, resistance and relative resilience differed among young, intermediate and old age cohorts within each of the two tree taxonomic groups (angiosperms versus 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 (Supplementary Table 15).

Linear mixed-effects model

We fitted a linear mixed-effects model to examine the impacts of individual tree age as a continuous variable on the PGR with interaction between tree age and tree taxa using the lme4 package in R[47,74] (Supplementary Table 1). The linear mixed-effects model controls for the pseudo-replication in the data due to multiple observations from the same given species within the same given site (using both species ID and site ID as random intercept terms in the model (see model formula that follows)).

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

where A is overall intercept, β is the slope for the fixed effects and 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 DEN with both raw tree-ring width and tree diameter at breast height (DBH) measurement[43], which allows us to retrieve a subset of data consisting of 540 individual trees from 8 species (5 angiosperms and 3 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 equation[25]. We then calculated the individual tree height from the corresponding DBH measurement within the subset data on the basis of the species-specific height/diameter relationship.

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

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 package in R[47,75] and then tested for nine different candidate linear mixed-effects models to examine the best variable for explaining the PGR (Supplementary Table 2). 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 (the best model). The first two best models with delta AIC values less than two were reported in Supplementary Tables 3 and 4. The AIC ranking for the candidate models was done by the aictab function in the AICcmodavg package in R[47,76]. The candidate models and corresponding abbreviations are as follows:

$$\mathrm{PGR} = A + \beta(\mathrm{Age}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{A0}]$$

$$\mathrm{PGR} = A + \beta(\mathrm{Age}) + \beta(\mathrm{Taxa}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{A1}]$$

$$\mathrm{PGR} = A + \beta(\mathrm{Age} \times \mathrm{Taxa}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{A2}]$$

$$\mathrm{PGR} = A + \beta(\mathrm{Height}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{H0}]$$

$$\mathrm{PGR} = A + \beta(\mathrm{Height}) + \beta(\mathrm{Taxa}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{H1}]$$

$$\mathrm{PGR} = A + \beta(\mathrm{Height} \times \mathrm{Taxa}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{H2}]$$

$$\mathrm{PGR} = A + \beta(\mathrm{Age}) + \beta(\mathrm{Height}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{AH}]$$

$$\mathrm{PGR} = A + \beta(\mathrm{Taxa}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{T0}]$$

$$\mathrm{PGR} = A + \beta(\mathrm{Age}) + \beta(\mathrm{Height}) + \beta(\mathrm{Taxa}) + \varepsilon(\mathrm{Site}) + \varepsilon(\mathrm{Species}) \quad [\mathrm{All}]$$

The best model and the next-best model with less than two delta AIC units were A2 (AIC: 4,028.54) and All (AIC: 4,030.19), which together carried 80% of the cumulative model weight (Supplementary Table 2). The models including tree height but excluding tree age as a parameter (H0, H1 and H2) contained only 1% of the cumulative model weight (Supplementary Table 2). For model A2, the percentage of growth reduction increased by 5.3% per one unit of standardized age (Supplementary Table 3; $P < 0.01$) 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 percentage of growth reduction increased by 4.3% per one unit of standardized age (Supplementary Table 4; $P < 0.01$) while the percentage of growth reduction decreased by 0.7% per one unit of standardized height (Supplementary Table 4; $P = 0.71$).

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)[43].

Code availability

The codes used to calculate the results reported in this study have been deposited on Figshare[77]: https://figshare.com/projects/Younger_trees_in_the_upper_canopy_are_more_sensitive_but_also_more_resilient_to_drought/150312

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Author contributions

T.F.A., J. Li and J. Lenoir conceived the research, and T.F.A., J.T.M., S.M.R., J. Li, S.M.O.S., K.A.N., M.P.D., R.P.P., T.L., Z.C. and J. Lenoir

designed the study. J.T.M., J.Li, M.P.D., T.L. and Z.C. contributed data. T.F.A. performed analyses with contribution from J.T.M., S.M.R., J. Li, S.M.O.S., K.A.N., M.P.D., R.P.P., T.L., Z.C. and J. Lenoir. All authors discussed, interpreted results, drew conclusions and participated in writing the paper.

Competing interests
The authors declare no competing interests.

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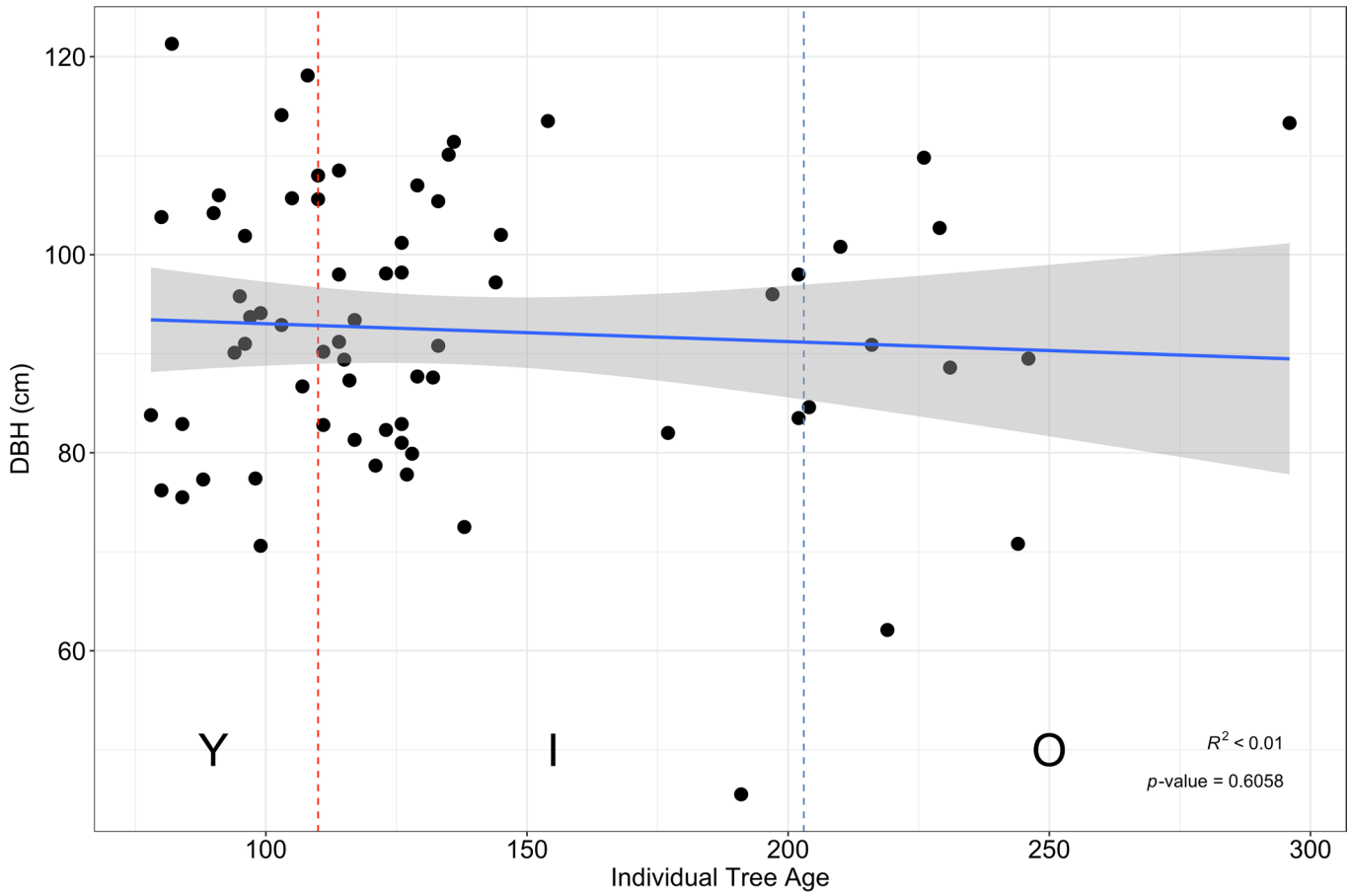

Extended Data Fig. 1 | The relationship between tree age and tree size of individual canopy-dominant trees. The relationship between individual tree age and diameter at breast height (DBH) for 68 canopy-dominant trees *Liriodendron tulipifera*, representing ~20% of total *L. tulipifera* samples. The 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*. Shaded ribbon indicates the 95% confidence interval for prediction from a linear model. The exact cutoff ages for *L. tulipifera* are listed in Supplementary Table 12.

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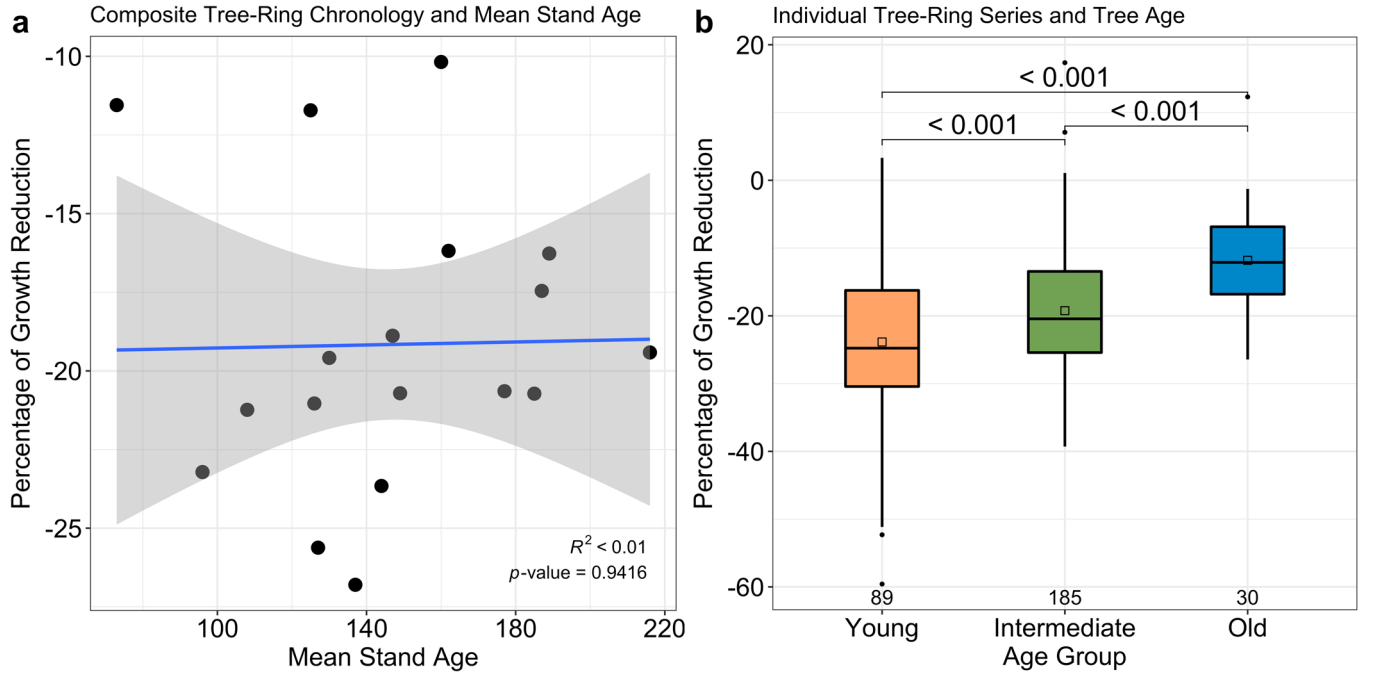

Extended Data Fig. 2 | Individual tree age is a better metric than mean stand age for examining age-dependent drought responses. Comparison of *Quercus alba* drought responses at 18 sites between composite chronology with mean stand age **(a)** and individual series with individual tree age approach **(b)** using the same dataset as in Au et al.[16]. 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. Shaded ribbon in panel a indicates the 95% confidence interval for prediction from a linear model. The age cohort classification in panel **b** follows the cutoff age for *Quercus alba* listed in the Supplementary Table 12. The numbers at the top of panel **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 b represent number of tree individuals for the youngest, intermediate and oldest age cohort of *Quercus alba*, respectively. 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.

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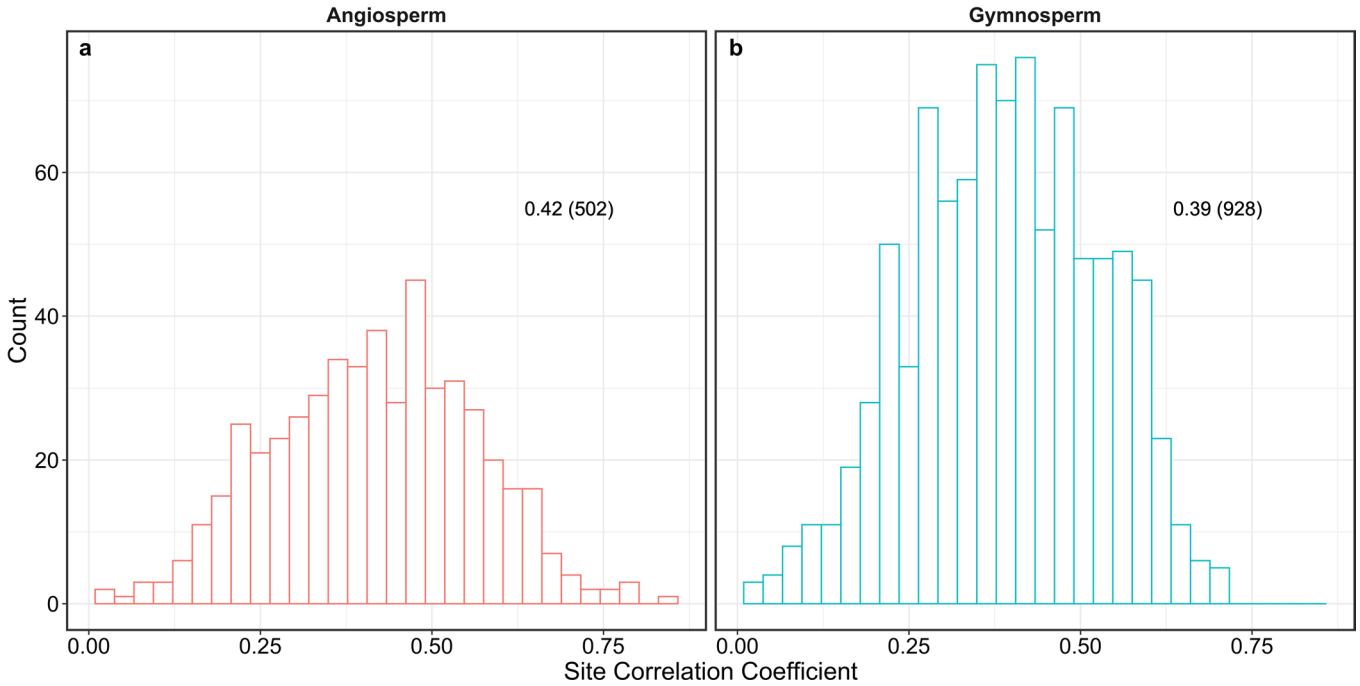

Extended Data Fig. 3 | Distribution of correlation coefficients between site-optimized 3-month SPEI and site chronologies. Numbers in the upper right and the parentheses indicate mean correlation and total number of sites, respectively for angiosperms **(a)** and gymnosperms **(b)**.

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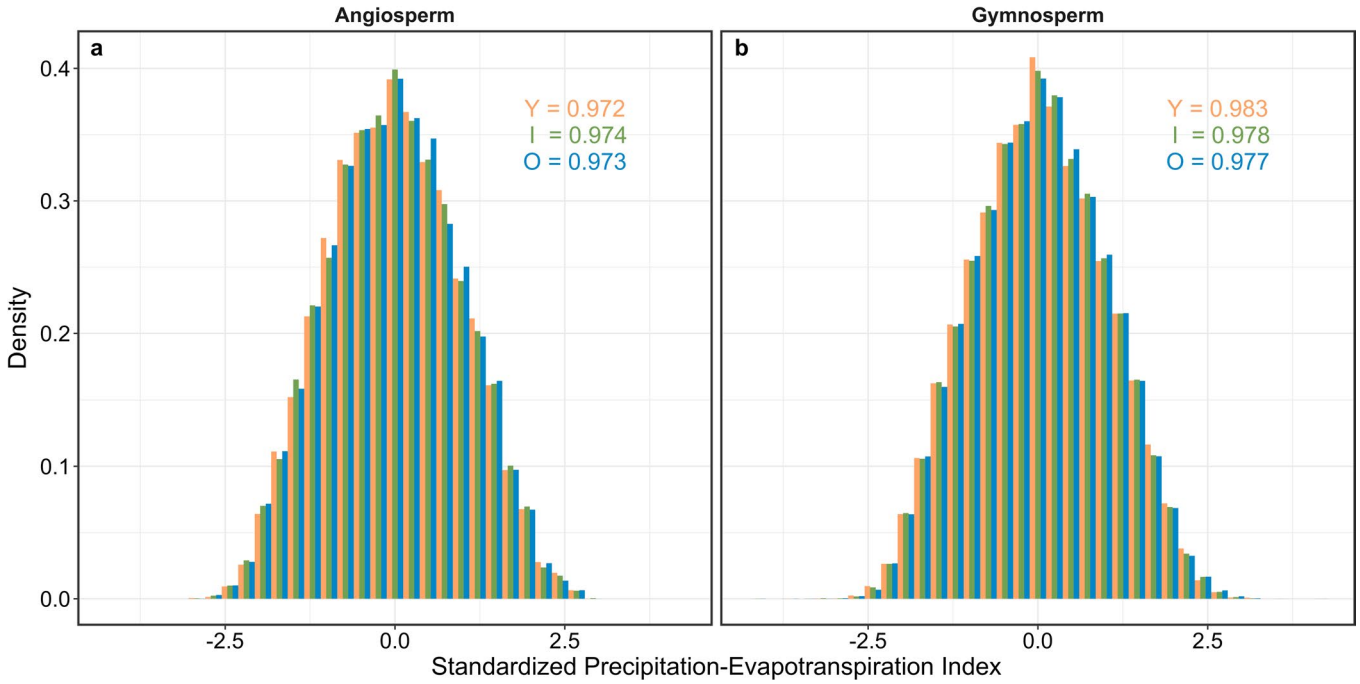

Extended Data Fig. 4 | Empirical probability densities of the Standardized Precipitation-Evapotranspiration Index across age cohorts. Numbers in the panels indicate standard deviations for the young (Y, orange), intermediate (I, green), and old (O, blue) age cohort, separately for angiosperms **(a)** and gymnosperms **(b)**, indicating that each age cohort experienced similar interannual moisture variability across different locations.

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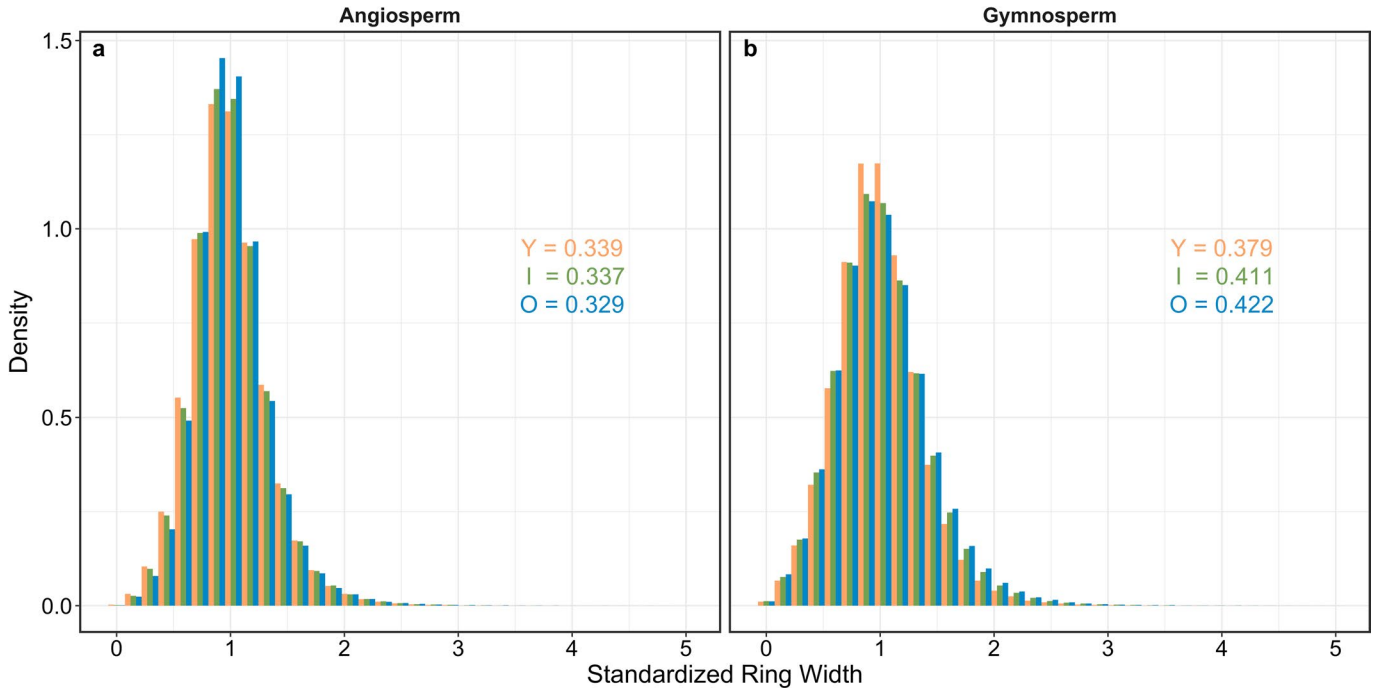

Extended Data Fig. 5 | Empirical probability densities of standardized ring width across age cohorts. Numbers in the panels indicate standard deviations of the young (Y, orange), intermediate (I, green), and old (O, blue) age cohort, separately for angiosperms **(a)** and gymnosperms **(b)**, indicating that the standardization did not lead to variability-induced sensitivity differences between age cohorts.

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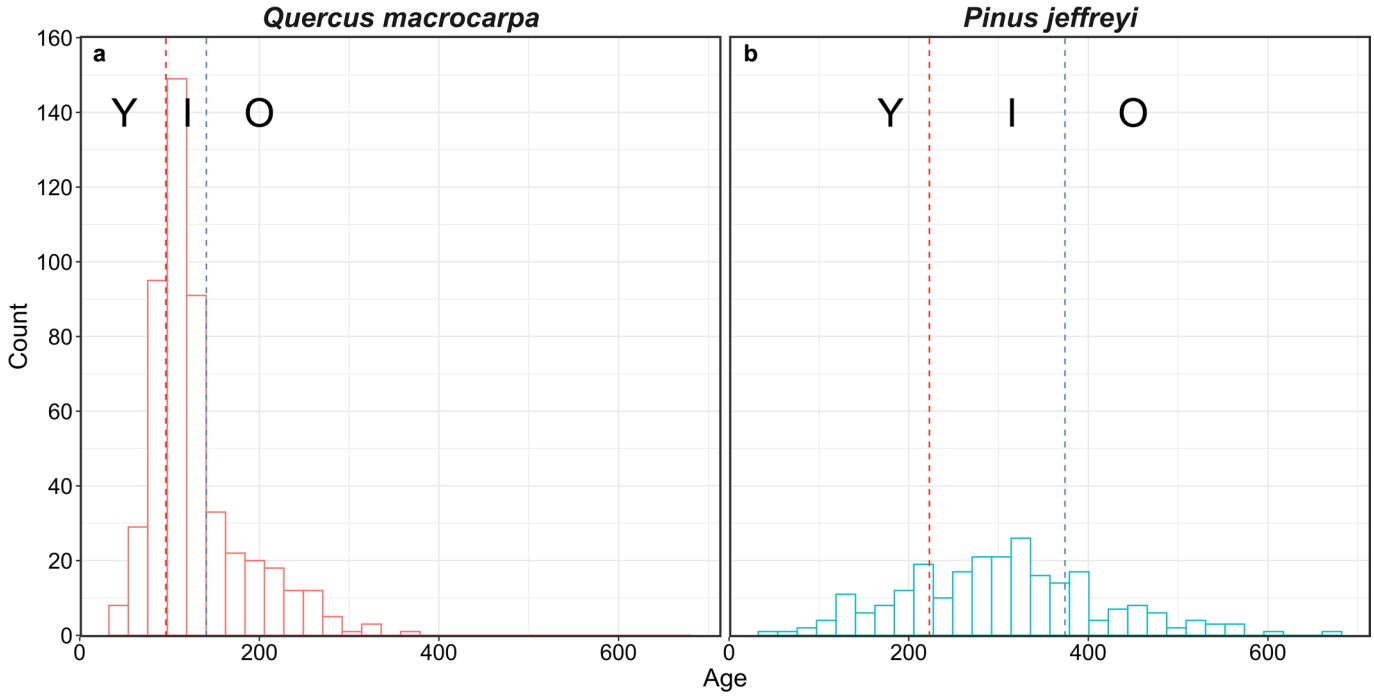

Extended Data Fig. 6 | Age grouping based on species-specific age distribution and longevity. Examples of age grouping into young (Y), intermediate (I), and old (O) tree cohorts based on species-specific distribution for an angiosperm species (*Quercus macrocarpa*) **(a)** and a gymnosperm species (*Pinus jeffreyi*) **(b)** in North America. 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. The exact cutoff ages are listed in Supplementary Table 12 and the maximum, mean, median, and minimum ages of each age cohort of angiosperm and gymnosperm are listed in Supplementary Table 13.

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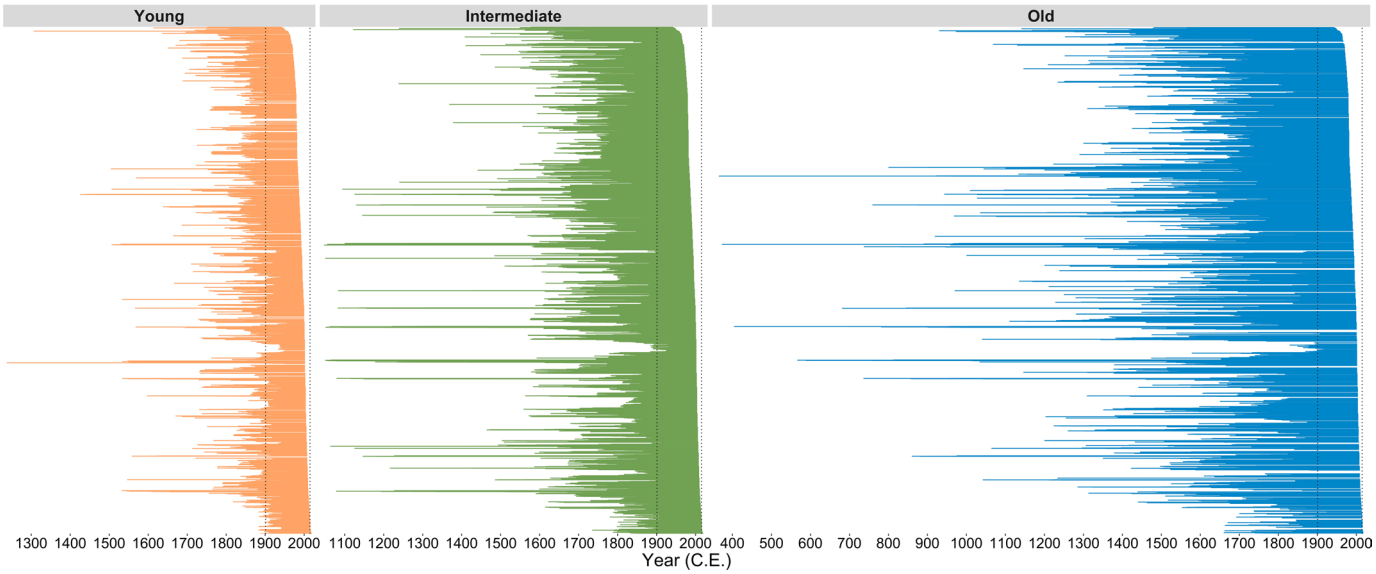

Extended Data Fig. 7 | Time span of all individual tree series of young, intermediate, and old age cohorts after age grouping from species-specific age distribution. The period between the two vertical dashed lines of each panel indicates the available period of global SPEI dataset (1901–2015) for drought responses analyses. The maximum, mean, median, and minimum ages of each age cohort of angiosperm and gymnosperm are listed in Supplementary Table 13. Note the x-axis scales are different in each panel.