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1 Younger trees in the upper canopy layer are more sensitive but also more 2 resilient to drought: age matters

3
4 Tsun Fung Au^{1,2*}, Justin T. Maxwell¹, Scott M. Robeson¹, Jinbao Li³, Sacha M. O. Siani¹, Kimberly
5 Novick⁴, Matthew P. Dannenberg⁵, Richard Phillips⁶, Teng Li⁷, Zhenju Chen⁸, Jonathan Lenoir⁹

6
7 ¹ Department of Geography, Indiana University, Bloomington, IN, United States.

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

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

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

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

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

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

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

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

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18 *Corresponding author: tomau123@indiana.edu

19 20 21 **Abstract**

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

34

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

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

84

85 Here, we investigate drought responses across tree-age cohorts of canopy-dominant
86 angiosperm and gymnosperm species by assessing: (1) drought sensitivity (i.e., the percentage
87 of growth reduction between drought and non-drought conditions); (2) drought resistance (i.e.,
88 growth rate during drought compared to pre-drought levels); and (3) drought resilience (i.e.,
89 the capacity to resume growth to pre-drought levels) (Methods). Drought conditions were
90 defined by the 3-month averaged standardized precipitation evapotranspiration index (SPEI),
91 which accounts for site variations in both moisture supply and demand. We gathered tree-ring
92 width data from 119 drought-sensitive species (38 angiosperm species and 81 gymnosperm
93 species) across North and South America, Eurasia, Africa, and Oceania. We then classified
94 21,964 canopy-dominant individual trees into 3 age cohorts based on species-specific age
95 distributions. The youngest and the oldest 25% of a given species' population were attributed
96 to young and old canopy-dominant cohorts, respectively, while the remaining 50% (i.e., the
97 interquartile) were attributed to the intermediate canopy-dominant cohort (Extended Data Fig.
98 1), allowing us to examine how tree age influences the drought responses and how that
99 influence varies across tree taxa and biomes. We also ran supplementary analyses (Methods)
100 using tree age as a continuous variable to examine drought-driven growth reduction instead of
101 using a factor variable with three levels (young, intermediate, and old canopy-dominant
102 cohorts).

103 **Results**

104 *Growth reduction in response to drought*

105 The younger cohort of canopy-dominant individuals for both angiosperms and gymnosperms
106 experienced significantly greater growth reductions in response to drought than the respective
107 older canopy-dominant cohort of trees. Under drought conditions, the youngest canopy-
108 dominant cohort of angiosperms showed a 28% reduction in growth, on average, whereas tree
109 growth in the intermediate and older canopy-dominant cohorts was only reduced by 25% and
110 20%, respectively (Fig. 1a, $P_{\text{young-inter}}, P_{\text{young-old}} < 0.001$). Drought also reduced the growth of
111 the youngest canopy-dominant cohort of gymnosperms by 27%, on average, and the response
112 is nearly identical to that of the intermediate cohort (0.6% greater; Fig. 1a, $P_{\text{young-inter}} = 0.227$)
113 but 2.4% greater than that of the oldest cohort (Fig. 1a, $P_{\text{young-old}} < 0.001$) of canopy-dominant
114 trees.

115

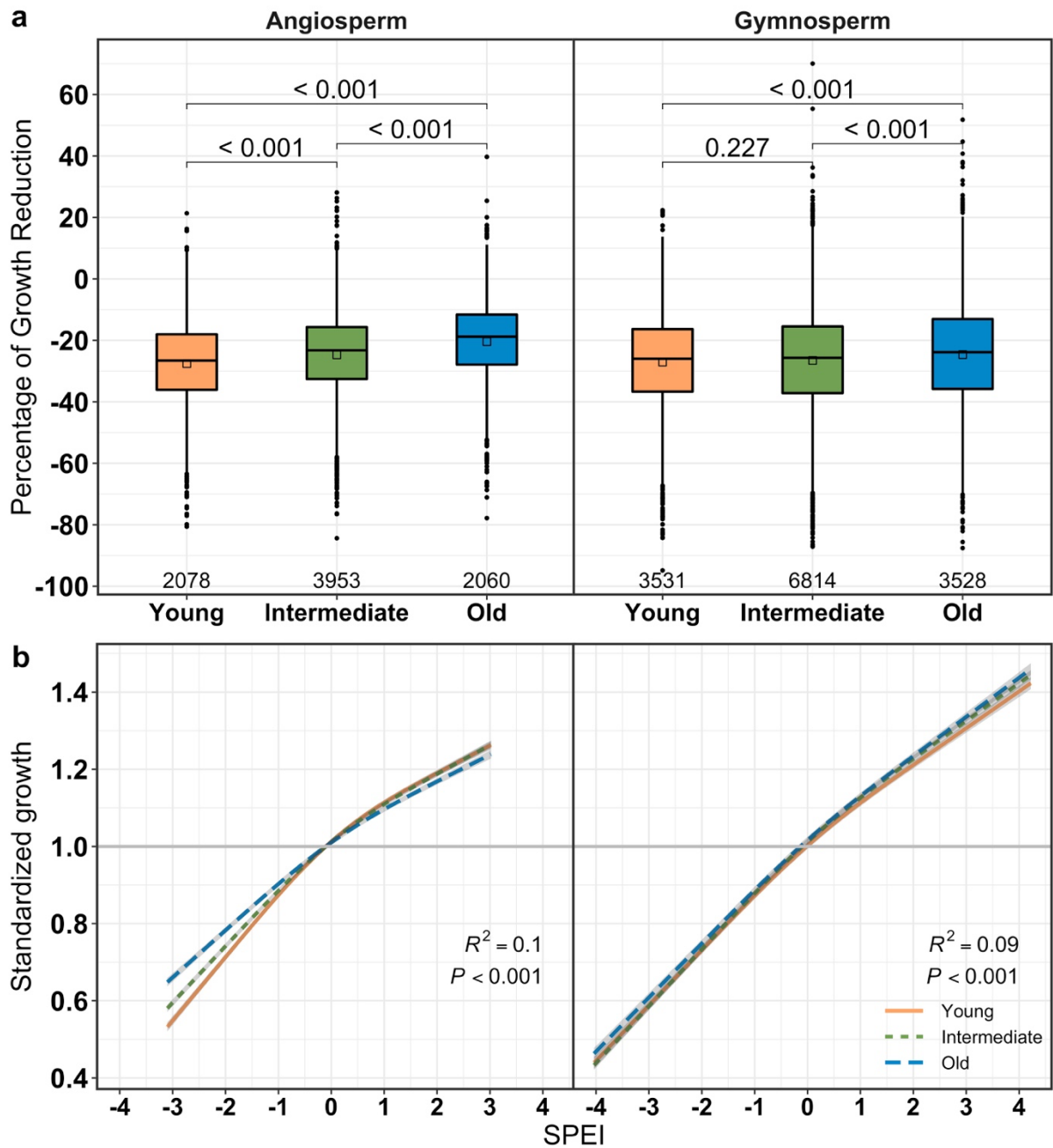
116 To ensure that these results are robust regardless of age groupings, we used a linear mixed-
117 effects model based on continuous variation of age (i.e., using age as a continuous fixed effect:
118 see Methods) and found that younger canopy-dominant trees had a larger growth reduction to
119 drought (Extended Data Table 1, $P < 0.001$). We also found that tree age had an interactive
120 effect with tree taxa such that the growth was reduced by 3.6% for angiosperms but only by
121 0.2% for gymnosperms every 100 years (Extended Data Table 1, $P < 0.001$). Noteworthy, tree
122 height and tree age are poorly correlated within the subset of individual trees for which we had
123 data on both age and height ($r = 0.21$, $n = 540$). Thus, examining the effect of tree height alone
124 on drought-driven growth reduction may tell a totally different story than the effect of tree age,
125 especially so for canopy-dominant trees. We then employed linear mixed-effects models to
126 control for the potential confounding effects from tree height. Tree age was still the most
127 prominent variable to explain drought-driven growth reduction within the canopy-dominant
128 individual trees with both age and height data (Tables S1, S2 and S3). The growth was reduced
129 by 4.3% per one unit of standardized age while the growth reduction was increased by 0.7%
130 per one unit of standardized height (Table S3, $P_{\text{age}} < 0.01$, $P_{\text{height}} = 0.72$).

131

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

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

147
148 Younger canopy-dominant trees were especially more vulnerable to drought-driven growth
149 reductions in Mediterranean, temperate, and alpine/boreal regions ($P < 0.05$), but not in deserts
150 and tropical regions (Fig. 2a). The average growth reduction of the youngest canopy-dominant
151 cohort for angiosperms in Mediterranean (38%), temperate (26%), and alpine/boreal (20%)
152 regions is 4%, 8%, and 12% higher than that of the oldest canopy-dominant cohort during
153 drought (Fig. 2b, $P < 0.05$). The youngest canopy-dominant cohort for gymnosperm showed
154 22%, 28%, and 25% growth reductions in those same regions, which is 3-4% higher than
155 growth reductions of the oldest canopy-dominant cohort (Fig. 2b, $P < 0.05$). In deserts, the
156 differences in drought response between the youngest and oldest canopy-dominant cohorts for
157 gymnosperms narrowed, with the youngest canopy-dominant cohort experiencing 32% growth
158 reduction, on average, compared to 29% growth reduction for the oldest canopy-dominant
159 cohort (Fig. 2b, $P < 0.1$). By contrast, in tropical regions, drought sensitivity was greater in the
160 oldest canopy-dominant cohort for both angiosperms and gymnosperms, being on average
161 5.7% and 4.4% more sensitive to drought than the youngest canopy-dominant cohort,
162 respectively (Fig. 2b, $P < 0.05$).



163

164

165 **Fig. 1: Drought-induced growth reduction of younger canopy-dominant trees is more**

166 **pronounced than for older canopy-dominant trees. a, Boxplots of drought-induced tree**

167 **growth reduction as a percentage of difference between mean standardized growth during**

168 **drought (standardized precipitation evapotranspiration index: $SPEI \leq -1.5$) and mean growth**

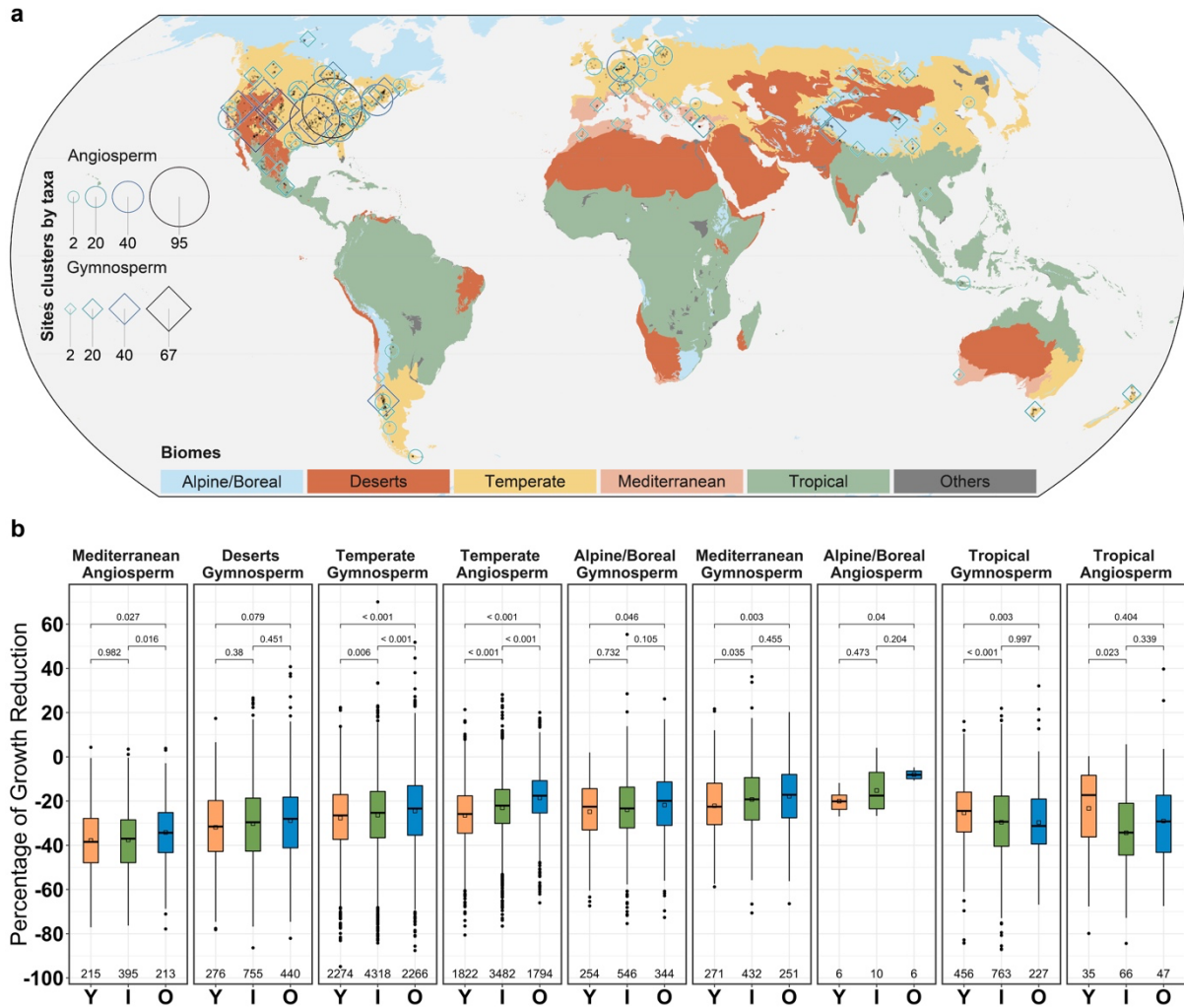
169 **during non-drought condition ($SPEI > -1.5$) for young (orange), intermediate (green), and old**

170 **(blue) cohorts of canopy-dominant trees for both angiosperms (left panel) and gymnosperms**

171 **(right panel). The numbers at the top of panels represent the p -values of pairwise differences**

172 **in percentage of growth reduction between age cohorts that were identified by Tukey honest**

173 significant differences. The numbers at the bottom of panels represent number of tree
174 individuals for the youngest, intermediate and oldest age cohort of canopy-dominant trees,
175 respectively. **b**, Standardized growth of angiosperms and gymnosperms with species-specific
176 age cohorts across moisture variability from dry (left) to wet (right) in terms of the SPEI from
177 generalized additive mixed-effects models. Each curve represents the mean response of each
178 age cohort with corresponding 95% confidence interval. The horizontal grey line (standardized
179 growth = 1) indicates mean standardized growth for individual trees, where standardized
180 growth above 1 indicates enhanced growth and below 1 indicates reduced growth. Numbers in
181 the lower right of panels indicate R^2 and p -values for both models. Boxes show the interquartile
182 range (IQR) while upper and lower whiskers are defined as the third quartile (Q3) plus 1.5*IQR
183 and the first quartile (Q1) minus 1.5*IQR, respectively. Values that are less than $Q1-1.5*IQR$
184 or greater than $Q3+1.5*IQR$ are plotted as closed circles. The bold lines and open squares in
185 the boxplot represent the median and the mean values, respectively. Age cohorts were assigned
186 using species-specific age cutoffs (Extended Data Fig. 1 & Extended Data Table 2).
187



189

190

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

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

205

206 *Drought resistance and resilience*

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

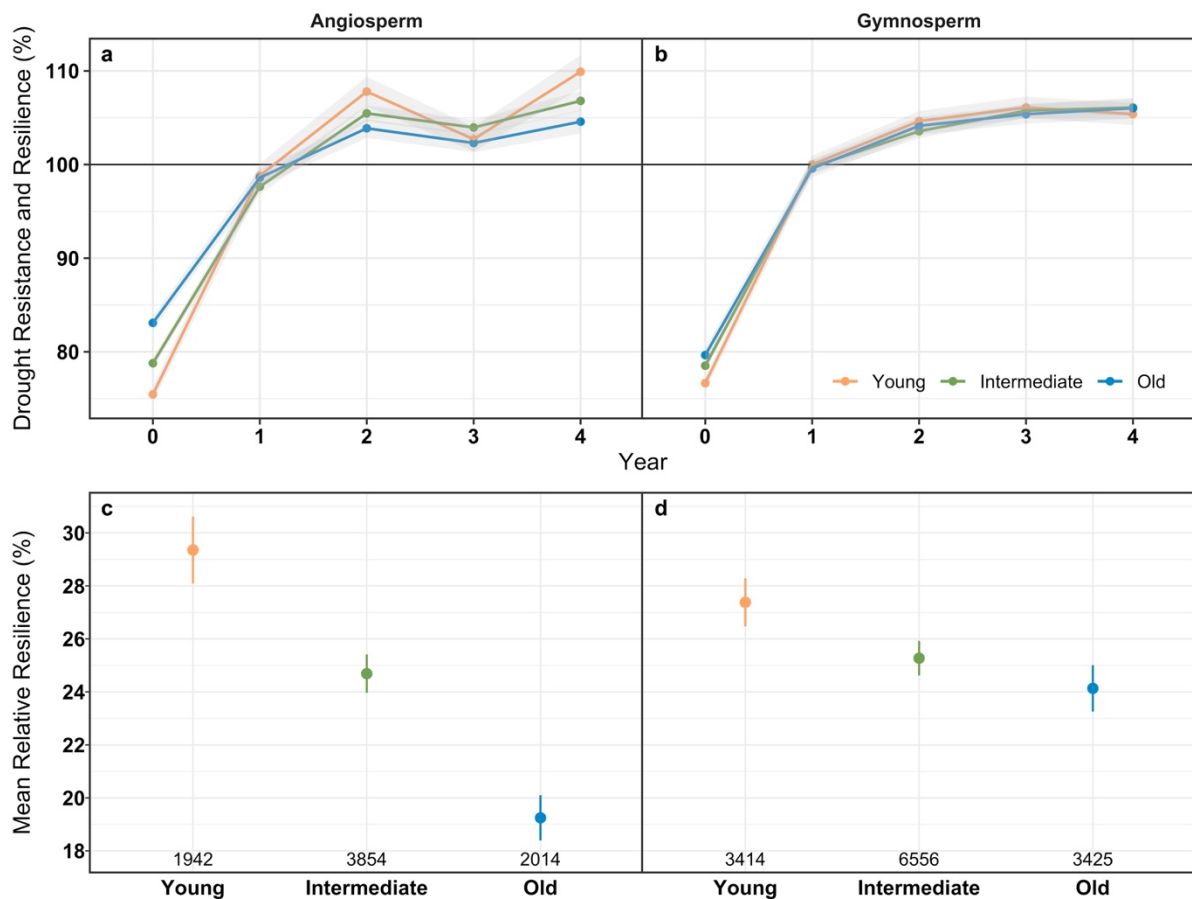
218

219 Although age differences in resistance and mean relative resilience were found in angiosperms,
220 none of the angiosperms' cohorts of canopy-dominant trees returned to pre-drought growth
221 levels after the first year (i.e., all had year-1 resilience index below 100%). The growth of
222 angiosperms exceeded pre-drought levels (i.e., 100%) in the second year after drought, with
223 the youngest cohort of canopy-dominant angiosperms generally having better growth-restoring
224 capacity than the other two older cohorts (Fig. 3a). For gymnosperms, different age cohorts of
225 canopy-dominant trees showed very similar resilience patterns after a drought occurred (Fig.
226 3b). The growth of all age cohorts during the first-year post-drought was nearly the same (on
227 average) as the pre-drought growth, with the resilience index ranging from 99.5% to 100%. In
228 years 2-4 after drought, all age cohorts for both angiosperms and gymnosperms had resilience
229 indices greater than 100% (indicating growth above pre-drought levels). The youngest cohort
230 of canopy-dominant angiosperms tended to have a higher resilience than older cohorts in years
231 2 and 4 (Fig. 3a) while there were no significant differences among the gymnosperm cohorts
232 of canopy-dominant trees (Fig. 3b).

233

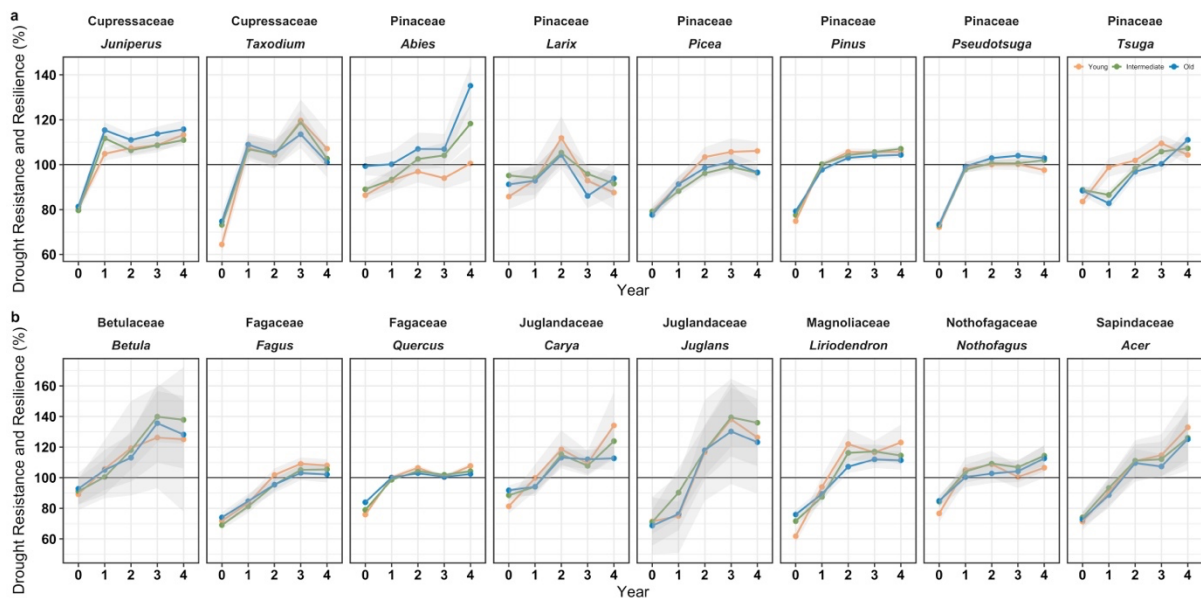
234 In contrast, previous research on "drought legacies" (i.e., extended post-drought growth
235 reductions and prolonged recoveries) showed that gymnosperms had more prevalent legacy
236 effects³⁰. While both angiosperms and gymnosperms had a resilience index above 100% for

237 several years after drought (Fig. 3a, 3b), age-dependent resiliency varied in some genera for
 238 both angiosperms and gymnosperms (Fig. 4). For gymnosperms, *Larix*, *Picea*, and *Tsuga*
 239 showed reduced resilience for all age cohorts in the first year after drought, and the growth was
 240 restored to pre-drought levels by the second year (Fig. 4a). Older trees of *Larix* and *Tsuga*
 241 showed even more growth reduction one year after a drought event than during the drought
 242 event (Fig. 4a). Nevertheless, the growth of *Juniperus* and *Taxodium* was completely restored
 243 for all age cohorts of canopy-dominant trees in the first year after drought (Fig. 4a). For
 244 angiosperms, reduced resilience in the first year after drought was shown for all canopy-
 245 dominant age cohorts of *Fagus*, *Liriodendron*, and *Acer* (Fig. 4b), suggesting that longer-term
 246 legacy effects may be present in some angiosperm genera¹⁶.
 247



248
 249
 250 **Fig. 3: Age-dependent drought resistance and relative resilience converge between tree**
 251 **taxonomic groups. a, b,** Temporal trends in drought resistance (Year 0) and resilience (Year
 252 1–4) for young (orange), intermediate (green), and old (blue) cohorts of canopy-dominant trees
 253 for both angiosperms (a) and gymnosperms (b) under non-drought conditions (SPEI > -1.5)
 254 with shaded 95% confidence interval. Year 0 indicates averaged resistance coefficients during

255 drought and years 1, 2, 3, and 4 indicate the resilience coefficients after 1, 2, 3, and 4 years
 256 following the drought events, relative to the pre-drought growth rate. The horizontal line at
 257 100% indicates the mean pre-drought growth level. The coefficients that are below the line
 258 indicate growth reduction while the coefficients that are above the line indicate growth
 259 enhancement compared to pre-drought conditions. **c, d**, Mean drought relative resilience for
 260 young (orange), intermediate (green), and old (blue) cohorts of angiosperms (**c**) and
 261 gymnosperms (**d**) with 95% confidence interval. The relative resilience is averaged from year
 262 1 to 4 after drought and accounted for the weighting of drought impacts on growth. A higher
 263 mean relative resilience value indicates post-drought growth enhancement and recovery from
 264 drought-induced reduction relative to the pre-drought growth rate. Age cohorts are assigned
 265 based on species-specific age distribution (Extended Data Fig. 1, Extended Data Table 2).



267
 268

269 **Fig. 4: Variations of drought resistance and resilience in major tree genera.** **a**, Temporal
 270 trends in drought resistance (Year 0) and resilience (Year 1–4) relative to non-drought
 271 conditions, with shaded 95% confidence interval, for young (orange), intermediate (green), and
 272 old (blue) cohorts of canopy-dominant trees for 8 different genera (*Juniperus*, *Taxodium*, *Abies*,
 273 *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*) belonging to 91% of gymnosperm samples and **b**, 8
 274 different genera (*Betula*, *Fagus*, *Quercus*, *Carya*, *Juglans*, *Liriodendron*, *Nothofagus*, *Acer*)
 275 belonging to 97% of angiosperm samples. Year 0 indicates averaged resistance coefficient
 276 during the drought year while year 1, 2, 3, and 4 indicate the resilience coefficient 1, 2, 3, and
 277 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

283 Discussion

284 Overall, younger canopy-dominant angiosperms have greater growth reduction during drought
285 but recover faster than older ones. Gymnosperms have a less prominent age-dependency in
286 drought sensitivity, but growth recovery is also faster for younger canopy-dominant
287 gymnosperms after drought. While our results appear to contradict some former studies²³, a
288 unique feature of this analysis is its focus on canopy-dominant trees, which reduces the
289 confounding influence of effects from tree height and size in our analysis. Several causal
290 mechanisms likely underlie the age and taxonomic differences in drought resistance and
291 resilience. The differences in drought sensitivity across age cohorts of canopy-dominant trees
292 could reflect the development of more extensive root systems as trees grow older, allowing
293 better access to subsurface water^{31,32} and thus buffering the immediate impacts of most
294 droughts³³. Younger canopy-dominant trees have shallower and less dense root systems that
295 limit water uptake to sustain tree growth, making them more susceptible to the immediate
296 impacts of droughts, even the less perceptible ones³⁴. The mean rooting depth for *Quercus*
297 (5.23m) is deeper than *Pinus* (2.45m)³⁵ and the differences in rooting depth could lead to higher
298 overall drought resistance for oaks (Fig. 4). Mature, older canopy-dominant trees with more
299 extensive canopy cover and greater transpiration efficiency, through access to water in the deep
300 soil layers, can also better regulate and stabilize the understory microclimate^{2,3,32}, potentially
301 reducing the drought severity and buffering the water demand of the subcanopy trees and herbs.
302 Transpiration of the younger canopy-dominant trees could be less efficient at maintaining a
303 sufficient buffering capacity from drought^{2,3}, resulting in an increase of the drought severity
304 experienced and higher water demand for the subcanopy. Gymnosperms tend to be more
305 isohydric, closing their stomates more quickly during drought to prevent dehydration and
306 hydraulic damage. In contrast, angiosperms are more anisohydric, keeping stomates open for
307 longer periods during droughts and allowing more stable gas exchange, transpiration, and
308 photosynthesis^{10,36}. Among the angiosperms, the more isohydric genera (e.g., *Liriodendron* and
309 *Acer*) were less resistant to drought than the more anisohydric genus *Quercus*¹⁶ (Fig. 4b).
310 Altogether, mature angiosperms could access deeper water reserves, have a better buffering
311 capacity to maintain stable microclimate for a longer time period, and have a higher carbon
312 assimilation during drought³⁷, allowing them to have less growth reduction and, thereby, be
313 more drought tolerant.

314

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

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

323

324 The age-dependent drought sensitivity is common and widespread across biomes and tree taxa,
325 potentially with large implications for the global carbon cycle. For example, the infamous
326 European drought event in 2003 reduced gross primary productivity by 30% (similar to the
327 mean growth reduction of the youngest canopy-dominant cohort in temperate forests, 28%, Fig.
328 2b) and temporarily converted the ecosystem into a net carbon source by releasing 0.5 Peta-
329 gram carbon yr⁻¹ into the atmosphere, which is equivalent to four years of net carbon storage
330 in European ecosystems⁷. Thus, the substantially lower growth reduction of older canopy-
331 dominant trees during drought, even on average of only 7-8% less compared to younger
332 canopy-dominant trees, when taken at the *global* scale, could have huge impacts to the regional
333 carbon storage and the global carbon budget, particularly in temperate forests that currently are
334 among the largest carbon sinks worldwide³⁹. During extreme drought, such impacts of age-
335 dependent sensitivity on carbon cycle are magnified with older angiosperms having 17% less
336 growth reduction (Fig. 1b). In alpine/boreal regions experiencing the greatest magnitude of
337 climate warming, drought could also cause more pronounced impacts on younger canopy-
338 dominant angiosperms than older ones, with important consequences for carbon sequestration
339 and climate feedback loops in these ecosystems²⁸.

340

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

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

354

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

375

376 **Methods**

377 *Tree growth data*

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

385 analyses in order to have, for the same individual canopy-dominant tree, information on both
386 tree age and tree diameter to test and control for the potential confounding effects of tree height,
387 which was obtained by feeding allometric equations with tree diameter data (see below), on
388 drought responses. We analyzed the impacts of tree age on drought-induced growth reduction,
389 resistance, and resilience. Both site chronologies and tree ring time series that ended before the
390 1940s (i.e., the outermost ring) were not considered to ensure sufficient overlap with the
391 observational records of the standardized precipitation evapotranspiration index (SPEI, i.e.,
392 from 1901 to 2015 see below) and instances of drought and wet conditions (Extended Data Fig.
393 2).

394

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

403

404 Given that temperature is typically the most limiting and sometimes the only factor affecting
405 tree radial growth at high latitudes^{40,49,50}, most of our study sites are situated between 60°N and
406 60°S where tree growth typically is more sensitive to soil moisture rather than to temperature.
407 We then selected 1430 sites from both the ITRDB and DEN database that had a positive
408 relationship (Extended Data Fig. 4) between standardized growth of site chronology and
409 hydroclimate variability (SPEI03, see below). From those 1430 sites, we then only considered
410 individual tree-ring time series with positive relationships (Pearson's correlation coefficient r
411 > 0.1) to hydroclimate variability to avoid potential sampling error. Ultimately, we
412 standardized the raw ring-width measurements of 21,964 individual trees with the same method
413 as stated above (i.e., two-thirds smoothing spline). The tree-growth data consisted of 81
414 gymnosperm species and 38 angiosperm species (119 species in total) from 32 genera that
415 inhabit diverse biomes from tropical to boreal forests.

416

417 *Biome classification*

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

425

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

431

432 *Age estimation*

433 All tree-ring data that were submitted to the ITRDB and DEN database have already been
434 cross-dated and should therefore have accurate dates assigned for each ring width^{41,52}. We also
435 scrutinized the cross-dating quality of all individual tree-ring time series by removing poorly
436 cross-dated individuals (e.g., individuals with negative inter-series or segment correlation).
437 Therefore, the resulting tree core data from the ITRDB and DEN database provide reliable
438 dating of individual growth years, from which we estimated tree-age. Most of our study sites
439 were used and published for drought reconstructions at continental scales^{53,54,55,56,57,58}.
440 Researchers attempt to sample tree cores as close to the pith as possible within each of these
441 study sites in order to maximize the time span of the drought reconstruction⁵⁹. Although this
442 sampling approach may produce bias towards more mature canopy-dominant trees⁴¹, there are
443 still substantial variations in individual tree ages for multiple tree species (Extended Data Fig.
444 1, Extended Data Fig. 2, Extended Data Fig. 3, Extended Data Table 2, Extended Data Table
445 3).

446

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

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

459

460 *Age group classification*

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

474

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

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

490

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

499

500 *Drought data*

501 To evaluate drought severity and its impacts on tree growth, we used the standardized
502 precipitation evapotranspiration index (SPEI), a measure of the standardized difference
503 between water supply (precipitation) and water demand (potential evapotranspiration)⁶⁷. As a
504 result, SPEI is an ecologically relevant way to control for drought severity across locations and
505 biomes with different baseline macroclimates and thus appropriate for determining the age-
506 dependent drought responses at global scale, with negative and positive SPEI values indicating
507 drier and wetter than usual conditions, respectively^{12,16,27,40,65}. We accessed the global SPEI
508 dataset on the 1st February 2021 (<https://digital.csic.es/handle/10261/202305>), using version
509 2.6 which provides SPEI data at 0.5° spatial resolution globally from 1901 to 2015 on a
510 monthly basis.

511

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

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

521

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

529

530 *Drought sensitivity, resistance, and resilience*

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

534

$$535 \quad \text{PGR} = \frac{\overline{\text{SRW}}_{\text{drought}} - \overline{\text{SRW}}_{\text{non-drought}}}{\overline{\text{SRW}}_{\text{non-drought}}} \times 100$$

536

537 We also repeated the same procedure with the normal conditions ($-1.5 < \text{SPEI03} < 1.5$) as the
538 baseline (see sensitivity analysis in Supplementary Information, shown in Fig. S1). Prior to
539 calculating PGR, we set any SRW values larger than 5 or smaller than 0.01 to missing (NA,
540 0.004% and 0.37% of total observations, respectively) because these SRW values are likely
541 due to measurement errors or non-drought-related missing rings.

542

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

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

552

$$553 \quad SRW = f(s(\text{SPEI03}_{\text{AgeCohort}}) + s(\text{Site}_{\text{random}}) + s(\text{Individual}_{\text{random}}))$$

554

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

563

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

570

$$571 \quad \text{Resistance} = \frac{SRW_d}{SRW_{\text{pre1-5}}}$$

572

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

576

$$577 \quad \text{Resilience} = \frac{SRW_{\text{post1-4}}}{SRW_{\text{pre1-5}}}$$

578

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

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

583

$$584 \quad \text{Relative Resilience} = \text{Resilience} - \text{Resistance} = \frac{\text{SRW}_{\text{post1-4}} - \text{SRW}_d}{\text{SRW}_{\text{pre1-5}}}$$

585

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

593

594 For all resistance, resilience, and relative resilience analyses, we considered individual trees
595 that have both five consecutive years before a drought event and four consecutive years after a
596 drought event. We also only considered single-year drought events instead of consecutive
597 droughts in both resistance and resilience calculation to avoid including drought effects in
598 either the pre-drought baseline or post-drought recovery estimates. Given that drought legacies
599 can extend up to four years³⁰, we defined consecutive droughts as drought events that happened
600 within three years before or after a given drought event. Drought resistance and resilience were
601 considered under two scenarios (i.e., non-drought and normal conditions, see sensitivity
602 analysis in Supplementary Information) to show how water availability before and after a
603 drought event may impact resistance and resilience across age cohorts. Non-drought conditions
604 excluded any drought but included exceptionally wet events (i.e., SPEI03 > 1.5) within three
605 years before or after a given drought event. Normal conditions excluded both drought and
606 exceptionally wet events within three years before or after a given drought event. After
607 considering the above criteria, 21,205 (7810 angiosperms and 13,395 gymnosperms) and
608 19,482 (7266 angiosperms and 12,216 gymnosperms) tree individuals under non-drought and
609 normal conditions scenarios, respectively were retained for the resistance and resilience
610 analyses. For the tree individuals that experienced multiple single-drought events over their
611 lifetimes, resistance and resilience indices were averaged for that individual.

612

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

623

624 *Linear Mixed Models*

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

631

$$632 \text{PGR} = A + \beta(\text{Age} \times \text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species})$$

633

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

636

637 *Examination of potential confounding effects from tree height*

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

647

648

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

649

650 The tree age and tree height are poorly correlated ($r = 0.21$, $n = 540$), indicating these two
651 variables are not redundant and can be included simultaneously as predictor variables in the
652 same multiple regression model. We first standardized the tree age and tree height by using the
653 *gscale* function provided in the *jtools* package⁷⁴ and then employed the following candidate
654 linear mixed-effects models to examine the best variable for explaining the percentage of
655 growth reduction (PGR). We used Akaike information criterion (AIC) to compare the fit of the
656 following models and selected the best candidate model with the lowest AIC scores (i.e., the
657 best model). The first two best models with delta AIC values less than two were reported in the
658 Table S2 and S3. The AIC ranking for the candidate models was done by *aictab* function in
659 *AICcmodavg* package⁷⁵. The candidate models and corresponding abbreviation are as below:
660

$$\text{PGR} = A + \beta(\text{Age}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{A0 (Table S6)}$$

$$\text{PGR} = A + \beta(\text{Age}) + \beta(\text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{A1 (Table S4)}$$

$$\text{PGR} = A + \beta(\text{Age} \times \text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{A2 (Table S2)}$$

$$\text{PGR} = A + \beta(\text{Height}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{H0 (Table S10)}$$

$$\text{PGR} = A + \beta(\text{Height}) + \beta(\text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{H1 (Table S8)}$$

$$\text{PGR} = A + \beta(\text{Height} \times \text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{H2 (Table S7)}$$

$$\text{PGR} = A + \beta(\text{Age}) + \beta(\text{Height}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{AH (Table S5)}$$

$$\text{PGR} = A + \beta(\text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{T0 (Table S9)}$$

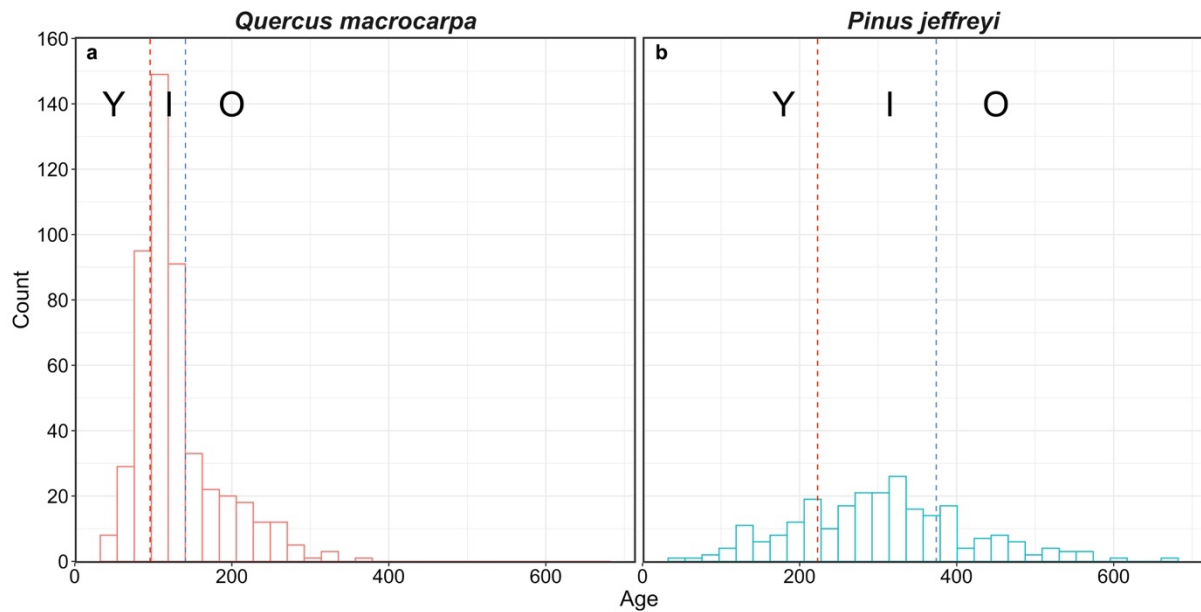
$$\text{PGR} = A + \beta(\text{Age}) + \beta(\text{Height}) + \beta(\text{Taxa}) + \varepsilon(\text{Site}) + \varepsilon(\text{Species}) \quad \text{All (Table S3)}$$

661

662 The best model and the next-best model with less than two delta AIC units were A2 (AIC:
663 4030.94) and All (AIC: 4032.59), which together carried 80% of the cumulative model weight
664 (Table S1). The models including tree height but excluding tree age as a parameter (i.e., H0,
665 H1, and H2) only contained 1% of the cumulative model weight (Table S1). For the model A2,
666 the growth was reduced by 5.3% per one unit of standardized age (Table S2, $P < 0.01$) while
667 the interaction effect between age and tree taxa is weak probably due to under-representation
668 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

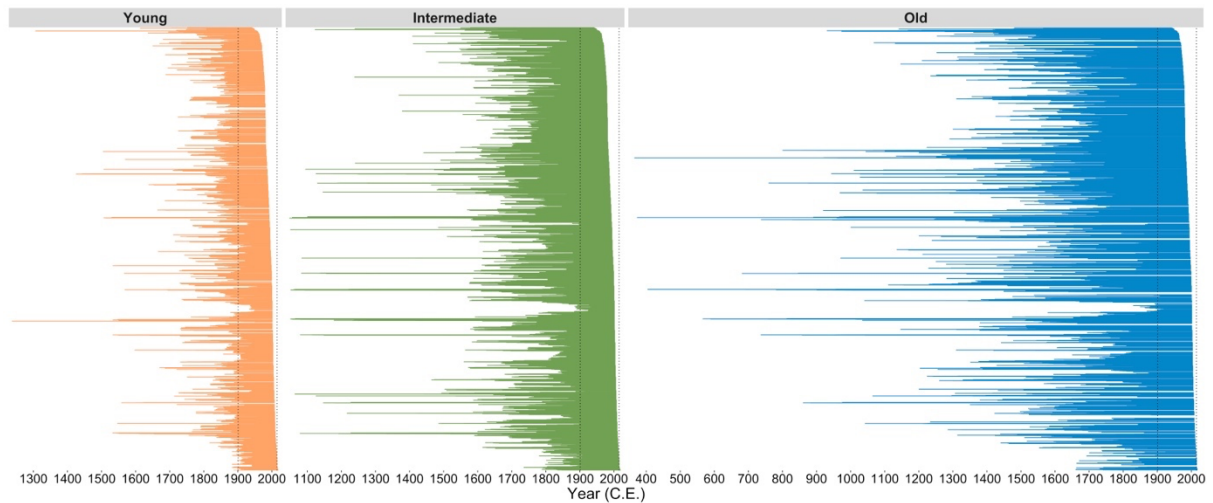
672 **Extended Data**



673

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.

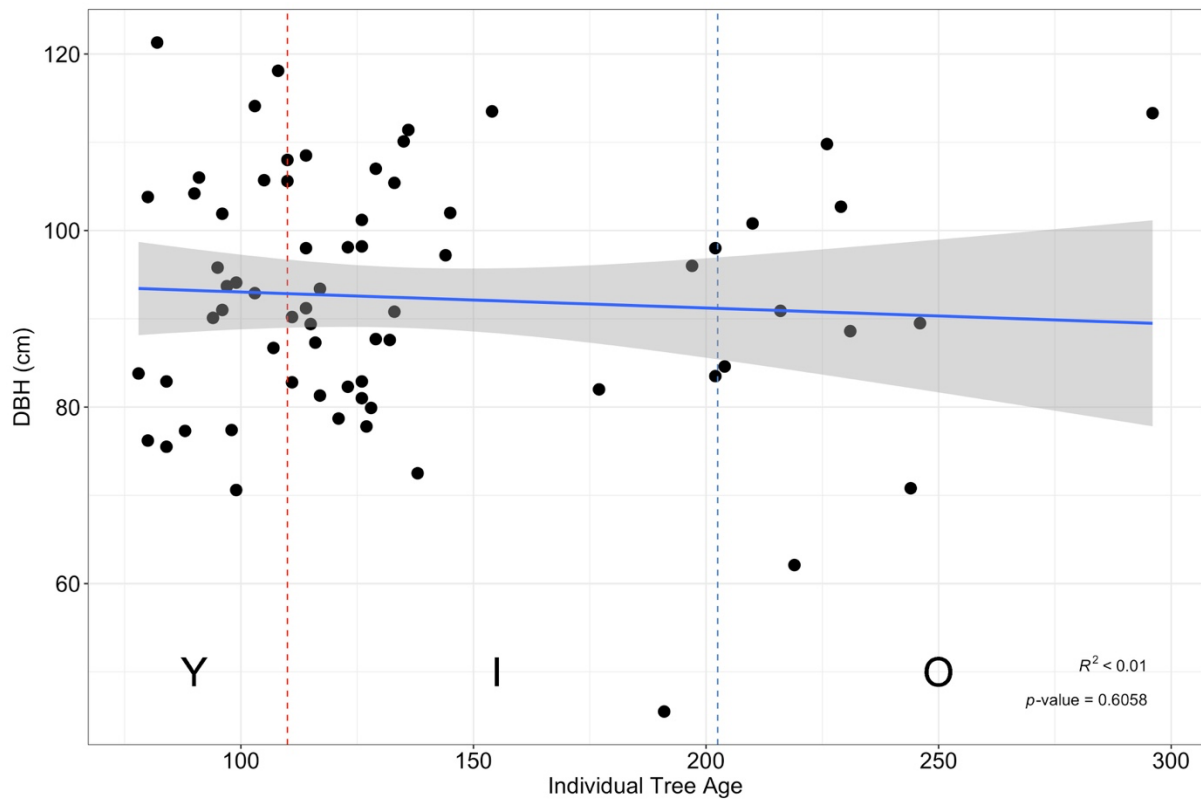
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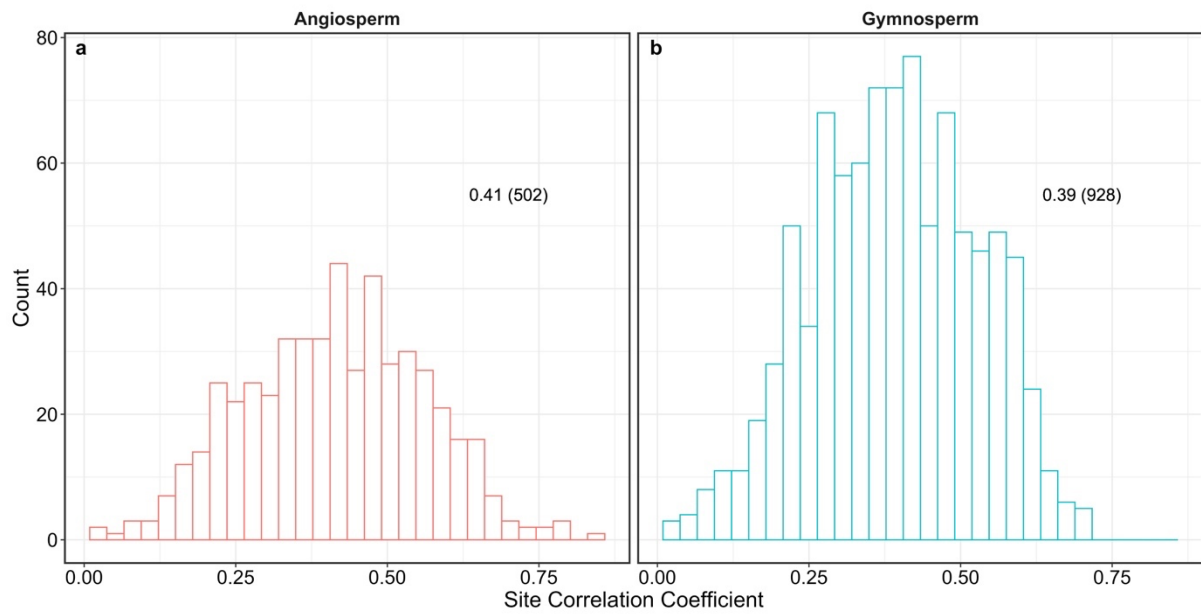
684 **Extended Data Fig. 2:** Time span of all individual tree series of young, intermediate, and old
 685 age cohorts after age grouping from species-specific age distribution. The period between the
 686 two vertical dashed lines of each panel indicates the available period of global SPEI dataset
 687 (1901–2015) for drought responses analyses. The maximum, mean, median, and minimum
 688 ages of each age cohort of angiosperm and gymnosperm are listed in Extended Data Table 3.
 689 Note the x-axis scales are different in each panel.

690



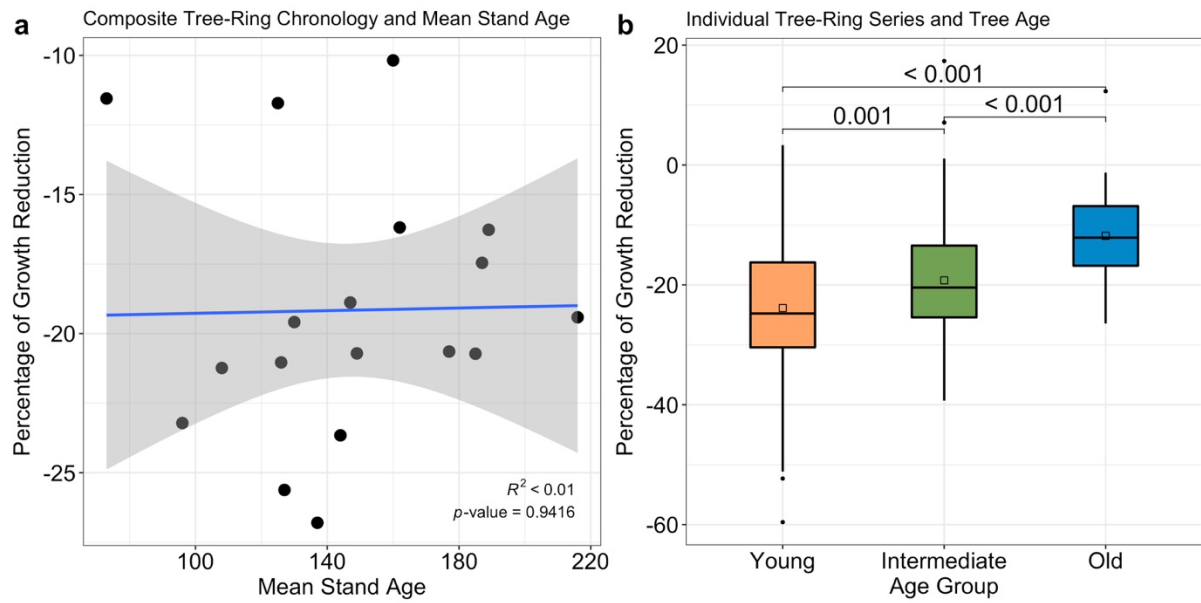
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Extended Data Fig. 3: The relationship between individual tree age and diameter at breast height (DBH) for 68 canopy-dominant trees *Liriodendron tulipifera*, representing ~20% of total *L. tulipifera* samples. The dashed red lines indicate the first 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.



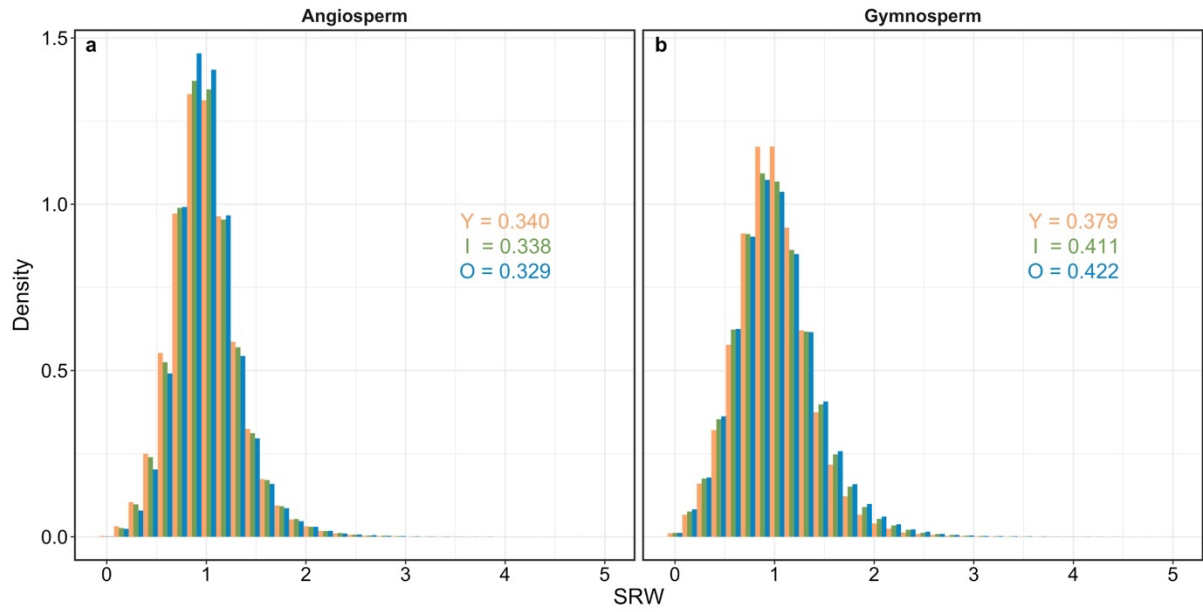
700

701 **Extended Data Fig. 4:** Distribution of correlation coefficients between site-optimized 3-month
 702 SPEI and site chronologies for (a) angiosperms and (b) gymnosperms. Numbers in the upper
 703 right and the parentheses indicate mean correlation and total number of sites, respectively.
 704



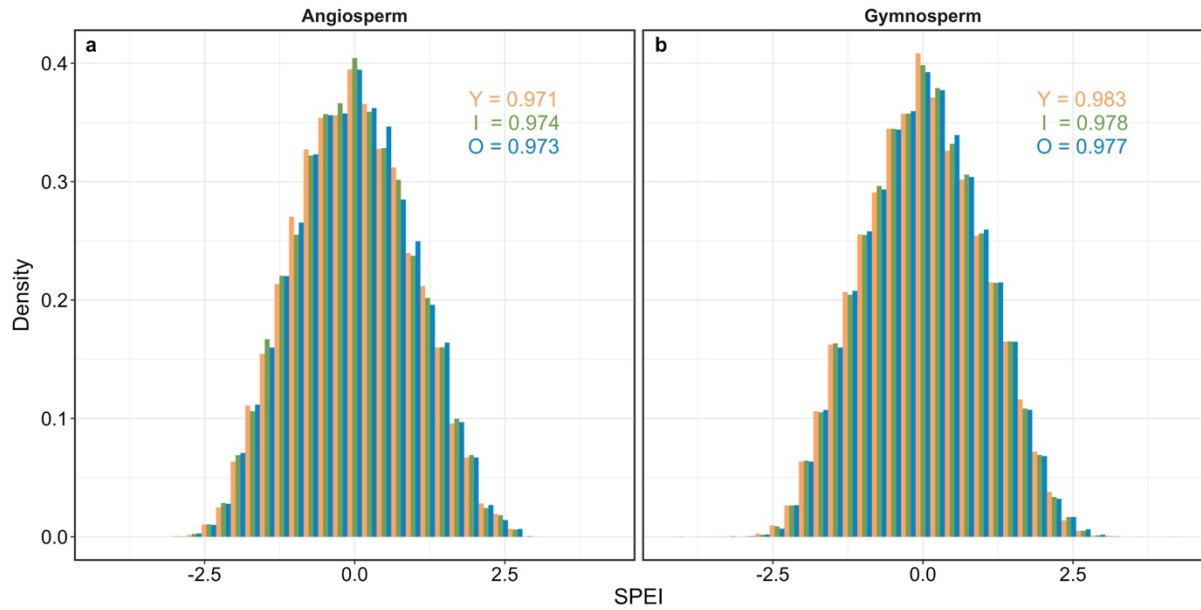
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Extended Data Fig. 5: Comparison of *Quercus alba* drought responses at 18 sites between (a) composite chronology with mean stand age and (b) individual series with individual tree age approach using the same dataset as in Au et al. 2020¹⁶. Hence, 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.



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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.



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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.

731 **Extended Data Table 1:** Fixed effect estimates, standard error (SE), and degree of freedom
 732 (df) of the linear mixed model for predicting percentage of growth reduction in response to
 733 individual tree age.
 734

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

735

736 **Extended Data Table 2:** Age cutoffs for 119 species of tree taxa angiosperm (A) and
737 gymnosperm (G) based on species-specific age distributions that separate young, intermediate
738 and old age cohorts. Q1 indicates the cutoff age of the first quartile while Q3 indicates the
739 cutoff age of the third quartile. Min and Max indicate the minimum and maximum age of each
740 canopy-dominant species within the dataset. Species codes PISP, JUSP, PCSP represent
741 miscellaneous or unknown species from the *Pinus*, *Juniperus* and *Picea* genera, respectively.
742

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

745 **Extended Data Table 3:** The maximum, mean, median, and minimum age of young,
 746 intermediate, and old age cohort of angiosperm and gymnosperm.
 747

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

748

749 **Extended Data Table 4:** Generalized additive mixed-effect model summary for angiosperms
 750 and gymnosperms, including effective degrees of freedom (edf), referenced degrees of freedom
 751 (Ref. df), F statistics, and corresponding p-values.
 752

Smooth terms	Angiosperms				Gymnosperms			
	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

753

754 **Extended Data Table 5:** Difference of mean estimate of log-transformed resistance and
 755 relative resilience between age cohorts within angiosperms and gymnosperms for non-drought
 756 and normal conditions by Tukey Honest Significant Differences. The numbers with
 757 parentheses are the mean estimate under normal conditions. Numbers in bold indicate
 758 significant difference in mean estimate ($\alpha = 0.05$).
 759

	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)

760
761

762 Data availability

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

766

767 Code availability

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

770

771 References

- 772 1. Bonan GB. Forests and climate change: forcings, feedbacks, and the climate benefits
 773 of forests. *Science* 2008, **320**(5882): 1444-1449.
 774
- 775 2. Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-
 776 Römermann M, *et al.* Forest microclimate dynamics drive plant responses to warming.
 777 *Science* 2020, **368**(6492): 772-775.
 778
- 779 3. De Frenne P, Zellweger F, Rodriguez-Sanchez F, Scheffers BR, Hylander K, Luoto M,
 780 *et al.* Global buffering of temperatures under forest canopies. *Nature Ecology &*
 781 *Evolution* 2019, **3**(5): 744-749.
 782
- 783 4. Anderegg WR, Kane JM, Anderegg LD. Consequences of widespread tree mortality
 784 triggered by drought and temperature stress. *Nature climate change* 2013, **3**(1): 30-36.
 785
- 786 5. Allen CD, Breshears DD, McDowell NG. On underestimation of global vulnerability
 787 to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*
 788 2015, **6**(8): 1-55.
 789

- 790 6. Novick KA, Ficklin DL, Stoy PC, Williams CA, Bohrer G, Oishi AC, *et al.* The
791 increasing importance of atmospheric demand for ecosystem water and carbon fluxes.
792 *Nature Climate Change* 2016, **6**(11): 1023-1027.
793
- 794 7. Ciais P, Reichstein M, Viovy N, Granier A, Ogée J, Allard V, *et al.* Europe-wide
795 reduction in primary productivity caused by the heat and drought in 2003. *Nature* 2005,
796 **437**(7058): 529-533.
797
- 798 8. Phillips OL, Aragão LE, Lewis SL, Fisher JB, Lloyd J, López-González G, *et al.*
799 Drought sensitivity of the Amazon rainforest. *Science* 2009, **323**(5919): 1344-1347.
800
- 801 9. Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, *et al.* Forest
802 disturbances under climate change. *Nature climate change* 2017, **7**(6): 395-402.
803
- 804 10. Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, *et al.* Global
805 convergence in the vulnerability of forests to drought. *Nature* 2012, **491**(7426): 752-
806 755.
807
- 808 11. Anderegg WR, Konings AG, Trugman AT, Yu K, Bowling DR, Gabbitas R, *et al.*
809 Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*
810 2018, **561**(7724): 538-541.
811
- 812 12. Anderegg WR, Trugman AT, Badgley G, Konings AG, Shaw J. Divergent forest
813 sensitivity to repeated extreme droughts. *Nature Climate Change* 2020, **10**(12): 1091-
814 1095.
815
- 816 13. Zhang T, Niinemets Ü, Sheffield J, Lichstein JW. Shifts in tree functional composition
817 amplify the response of forest biomass to climate. *Nature* 2018, **556**(7699): 99-102.
818
- 819 14. Engelbrecht BM, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, *et al.*
820 Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 2007,
821 **447**(7140): 80-82.
822
- 823 15. Lenoir J, Gégout J-C, Marquet P, De Ruffray P, Brisse H. A significant upward shift in
824 plant species optimum elevation during the 20th century. *Science* 2008, **320**(5884):
825 1768-1771.
826
- 827 16. Au TF, Maxwell JT, Novick KA, Robeson SM, Warner SM, Lockwood BR, *et al.*
828 Demographic shifts in eastern US forests increase the impact of late-season drought on
829 forest growth. *Ecography* 2020, **43**(10): 1475-1486.
830
- 831 17. Schwalm CR, Anderegg WR, Michalak AM, Fisher JB, Biondi F, Koch G, *et al.* Global
832 patterns of drought recovery. *Nature* 2017, **548**(7666): 202-205.
833
- 834 18. Lindenmayer DB, Laurance WF, Franklin JF. Global decline in large old trees. *Science*
835 2012, **338**(6112): 1305-1306.
836
- 837 19. McDowell NG, Allen CD, Anderson-Teixeira K, Aukema BH, Bond-Lamberty B,
838 Chini L, *et al.* Pervasive shifts in forest dynamics in a changing world. *Science* 2020,
839 **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

- 940 47. Cook ER, Kairiukstis LA. *Methods of dendrochronology: applications in the*
941 *environmental sciences*. Springer Science & Business Media, 2013.
942
- 943 48. Cook ER, Peters K. The smoothing spline: a new approach to standardizing forest
944 interior tree-ring width series for dendroclimatic studies. 1981.
945
- 946 49. Fritts H. *Tree rings and climate*. London, New York, San Francisco.: Academic Press;
947 1976.
948
- 949 50. Wilson R, Anchukaitis K, Briffa KR, Büntgen U, Cook E, D'arrigo R, *et al*. Last
950 millennium northern hemisphere summer temperatures from tree rings: Part I: The long
951 term context. *Quaternary Science Reviews* 2016, **134**: 1-18.
952
- 953 51. Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV, Underwood
954 EC, *et al*. Terrestrial Ecoregions of the World: A New Map of Life on Earth A new
955 global map of terrestrial ecoregions provides an innovative tool for conserving
956 biodiversity. *BioScience* 2001, **51**(11): 933-938.
957
- 958 52. Holmes R. Program COFECHA user's manual. *Laboratory of Tree-Ring Research, The*
959 *University of Arizona, Tucson* 1983.
960
- 961 53. Palmer JG, Cook ER, Turney CS, Allen K, Fenwick P, Cook BI, *et al*. Drought
962 variability in the eastern Australia and New Zealand summer drought atlas (ANZDA,
963 CE 1500–2012) modulated by the Interdecadal Pacific Oscillation. *Environmental*
964 *Research Letters* 2015, **10**(12): 124002.
965
- 966 54. Cook ER, Anchukaitis KJ, Buckley BM, D'Arrigo RD, Jacoby GC, Wright WE. Asian
967 monsoon failure and megadrought during the last millennium. *Science* 2010, **328**(5977):
968 486-489.
969
- 970 55. Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW. Long-term aridity
971 changes in the western United States. *Science* 2004, **306**(5698): 1015-1018.
972
- 973 56. Cook ER, Seager R, Heim Jr RR, Vose RS, Herweijer C, Woodhouse C. Megadroughts
974 in North America: Placing IPCC projections of hydroclimatic change in a long-term
975 palaeoclimate context. *Journal of Quaternary Science* 2010, **25**(1): 48-61.
976
- 977 57. Cook ER, Seager R, Kushnir Y, Briffa KR, Büntgen U, Frank D, *et al*. Old World
978 megadroughts and pluvials during the Common Era. *Science advances* 2015, **1**(10):
979 e1500561.
980
- 981 58. Morales MS, Cook ER, Barichivich J, Christie DA, Villalba R, LeQuesne C, *et al*. Six
982 hundred years of South American tree rings reveal an increase in severe hydroclimatic
983 events since mid-20th century. *Proceedings of the National Academy of Sciences* 2020,
984 **117**(29): 16816-16823.
985
- 986 59. Stokes M, Smiley T. 1968: An introduction to tree-ring dating. Chicago: University of
987 Chicago Press. 1968.
988

- 989 60. Lockwood BR, Maxwell JT, Robeson SM, Au TF. Assessing bias in diameter at breast
990 height estimated from tree rings and its effects on basal area increment and biomass.
991 *Dendrochronologia* 2021: 125844.
992
- 993 61. Locosselli GM, Brienen RJ, de Souza Leite M, Gloor M, Krottenthaler S, de Oliveira
994 AA, *et al.* Global tree-ring analysis reveals rapid decrease in tropical tree longevity with
995 temperature. *Proceedings of the National Academy of Sciences* 2020, **117**(52): 33358-
996 33364.
997
- 998 62. Rozas V, DeSoto L, Olano JM. Sex-specific, age-dependent sensitivity of tree-ring
999 growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytologist* 2009,
1000 **182**(3): 687-697.
1001
- 1002 63. Carrer M, Urbinati C. Age-dependent tree-ring growth responses to climate in *Larix*
1003 *decidua* and *Pinus cembra*. *Ecology* 2004, **85**(3): 730-740.
1004
- 1005 64. Gazol A, Camarero J, Anderegg W, Vicente-Serrano S. Impacts of droughts on the
1006 growth resilience of Northern Hemisphere forests. *Global Ecology and Biogeography*
1007 2017, **26**(2): 166-176.
1008
- 1009 65. Li X, Piao S, Wang K, Wang X, Wang T, Ciais P, *et al.* Temporal trade-off between
1010 gymnosperm resistance and resilience increases forest sensitivity to extreme drought.
1011 *Nature Ecology & Evolution* 2020, **4**(8): 1075-1083.
1012
- 1013 66. Pardos M, Del Río M, Pretzsch H, Jactel H, Bielak K, Bravo F, *et al.* The greater
1014 resilience of mixed forests to drought mainly depends on their composition: Analysis
1015 along a climate gradient across Europe. *Forest Ecology and Management* 2021, **481**:
1016 118687.
1017
- 1018 67. Vicente-Serrano SM, Beguería S, López-Moreno JI. A multiscalar drought index
1019 sensitive to global warming: the standardized precipitation evapotranspiration index.
1020 *Journal of climate* 2010, **23**(7): 1696-1718.
1021
- 1022 68. Wood SN. *Generalized additive models: an introduction with R*. CRC press, 2017.
1023
- 1024 69. Rollinson CR, Alexander MR, Dye AW, Moore DJ, Pederson N, Trouet V. Climate
1025 sensitivity of understory trees differs from overstory trees in temperate mesic forests.
1026 *Ecology* 2021, **102**(3): e03264.
1027
- 1028 70. Lloret F, Keeling EG, Sala A. Components of tree resilience: effects of successive low-
1029 growth episodes in old ponderosa pine forests. *Oikos* 2011, **120**(12): 1909-1920.
1030
- 1031 71. Li X, Piao S, Wang K, Wang X, Wang T, Ciais P, *et al.* Reply to: Disentangling biology
1032 from mathematical necessity in twentieth-century gymnosperm resilience trends.
1033 *Nature Ecology & Evolution* 2021, **5**(6): 736-737.
1034
- 1035 72. Zheng T, Martínez-Vilalta J, García-Valdés R, Gazol A, Camarero JJ, Mencuccini M.
1036 Disentangling biology from mathematical necessity in twentieth-century gymnosperm
1037 resilience trends. *Nature ecology & evolution* 2021: 1-3.
1038

- 1039 73. Bates D, Mächler M, Bolker B, Walker S. Fitting Linear Mixed-Effects Models Using
1040 lme4. *Journal of Statistical Software* 2015, **67**(1): 1 - 48.
1041
1042 74. Long JA. jtools: Analysis and presentation of social scientific data. R package version
1043 2.2.0. 2022.
1044
1045 75. Mazerolle MJ. AICcmodavg: Model selection and multimodel inference based on AIC.
1046 R package version 2.3-1. 2020.
1047
1048

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1055 **Author Contributions**

1056 T.F.A. and J.L. conceived and designed the study with all authors providing input. J.T.M., J.L.,
1057 M.P.D., T.L., and Z.C. contributed data. T.F.A. performed analyses with contribution from
1058 S.M.R. and J.L. All authors discussed, interpreted results, drew conclusions and wrote the
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1060

1061 **Competing interests**

1062 The authors declare no competing interests.
1063

1064 **Corresponding author**

1065 Correspondence and requests for materials should be addressed to Tsun Fung Au.