Revealing legacy effects of extreme droughts on tree growth of oaks across the Northern Hemisphere

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HIGHLIGHTS

- We examined the legacy effects of droughts in deciduous *Quercus* species.
- Repetitive droughts resulted significant negative legacy effects.
- Mediterranean oaks were more negatively affected by repetitive droughts.
- Sites showing positive correlations to winter temperature showed no growth depression after drought.
- Growth sensitivity to climate and species-specific traits were related to the size of legacy effects.

GRAPHICAL ABSTRACT
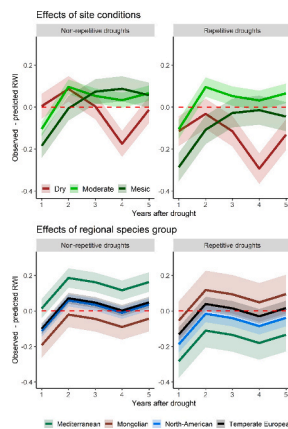
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ABSTRACT

Forests are undergoing increasing risks of drought-induced tree mortality. Species replacement patterns following mortality may have a significant impact on the global carbon cycle. Among major hardwoods, deciduous oaks (*Quercus* spp.) are increasingly reported as replacing dying conifers across the Northern Hemisphere. Yet, our knowledge on the growth responses of these oaks to drought is incomplete, especially regarding post-drought legacy effects. The objectives of this study were to determine the occurrence, duration, and magnitude of legacy effects of extreme droughts and how that vary across species, sites, and drought characteristics. The legacy effects were quantified by the deviation of observed from expected radial growth indices in the period 1940–2016. We used stand-level chronologies from 458 sites and 21 oak species primarily from Europe, north-eastern America, and eastern Asia. We found that legacy effects of droughts could last from 1 to 5 years after the drought and were more prolonged in dry sites. Negative legacy effects (i.e., lower growth than expected) were more prevalent after repetitive droughts in dry sites. The effect of repetitive drought was stronger in Mediterranean oaks especially in *Quercus faginea*. Species-specific analyses revealed that *Q. petraea* and *Q. macrocarpa* from dry sites were more negatively affected by the droughts while growth of several oak species from mesic sites increased during post-drought years. Sites showing positive correlations to winter temperature showed little to no growth depression after drought, whereas sites with a positive correlation to previous summer water balance showed decreased growth. This may indicate that although winter warming favors tree growth during droughts, previous-year summer precipitation may predispose oak trees to current-year extreme droughts. Our results revealed a massive role of repetitive droughts in determining legacy effects and highlighted how growth sensitivity to climate, drought seasonality and species-specific traits drive the legacy effects in deciduous oak species.

1. Introduction

Drought-induced tree mortality is increasing globally, with major consequences for the structure and functioning of forests and their ecosystem services (Allen et al., 2015; Hammond et al., 2022; Hartmann et al., 2022). Abrupt tree mortality during and after droughts can alter community composition towards the dominance of drought-tolerant tree and shrub species (Batllori et al., 2020; Etzold et al., 2019). In temperate regions, deciduous oaks (*Quercus* spp.) can tolerate relatively extreme droughts because of their deep-penetrating root systems and strong stomatal control, allowing them to maintain relatively high predawn water potentials during drought (Abrams, 1990; Madrigal-González et al., 2017). Further, deciduous oaks are usually ring-porous species producing large vessels in the early growing season, allowing for increased hydraulic conductivity and stomatal conductance (Martínez-Sancho et al., 2017; Peters et al., 2023), but such xylem is very vulnerable to frost- and drought-induced xylem cavitation (Sperry et al., 1994). Several recent studies reported a growing dominance of deciduous oak species after drought-induced mortality events mainly affecting conifers (Galiano et al., 2010; Rigling et al., 2013; Vilà-Cabrera

et al., 2013), albeit oaks may also experience increased defoliation (Michel et al., 2022) and dieback in response to severe dry spells (Camarero et al., 2021; Druckenbrod et al., 2019). Since drought-stressed trees are vulnerable to secondary pathogens (Haavik et al., 2015), drought-pathogen interactions can play a critical role in oak tree performance (Wood et al., 2018) and post-drought recovery. Performance and sensitivity of tree species during post-drought conditions will play an important role under future climatic conditions with increased frequency of extreme climate events and are predicted to have a lasting effect on ecosystem dynamics (Müller and Bahn, 2022) and associated changes in carbon storage and cycle (Schwalm et al., 2017; Trugman et al., 2018). Therefore, there is an urgent need to understand how previously drought-exposed trees would respond to future drought events to better mitigate potential adverse effects (Bose et al., 2020; Gessler et al., 2020).

Post-drought growth recovery can be a result of species- or population-related response patterns (Kannenberg et al., 2019b; Peltier and Ogle, 2019), and persistent functional adjustments during and after droughts can induce acclimation to future droughts (Zweifel et al., 2020). Such an acclimation process is characterized as ecological legacy

(Vilonen et al., 2022), which can significantly alter the responses of trees even several years after the drought event (Anderegg et al., 2015b; Ovenden et al., 2021; Wu et al., 2018). The alteration of tree growth due to legacies of past drought could occur through different sets of mechanisms (Bose et al., 2022; Marqués et al., 2022; Ogle et al., 2015). For example, drought could induce crown dieback (Klesse et al., 2022) or damage to water transport system (Anderegg et al., 2015a). The repair of damaged organs after drought could occur at the expense of biomass growth (Kannenberg et al., 2019b), which could result in negative drought legacies on radial growth (Anderegg et al., 2015b; Huang et al., 2018). The negative legacy effect on growth can endure several years depending on post-drought climatic conditions, the magnitude of drought-induced damages, and species-specific recovery capacities (Ruehr et al., 2019). For example, based on a global analysis of tree-ring series, pine species experienced more persistent negative legacy effects of drought than oaks (Anderegg et al., 2015b). Furthermore, the magnitude of these negative legacy effects was found to be higher in dry sites compared to mesic sites. Moreover, Huang et al. (2018) reported that negative legacy effects were more pervasive when droughts occurred in the dry compared to the wet season. Studying two widely distributed deciduous oak species across a latitudinal gradient in Europe, Bose et al. (2021b) identified slow recovery to spring droughts in *Q. petraea* but not in *Q. robur*. The later species even grew better during the 2nd and 3rd post-drought years compared to pre-drought years, indicating a positive legacy effect. The switch from negative to positive legacy effects can occur through changes in tree-to-tree competition within a forest stand (Cavin et al., 2013). The changes in competition may occur through drought-induced mortality or growth decline of drought-sensitive species or individuals favoring the growth of drought-tolerant species or individuals capable of taking water from deeper soil layers (Ripullone et al., 2020). These findings suggest that the magnitude of drought legacy effects vary between drought-tolerant and -intolerant species. However, we currently lack a large global-scale synthesis on drought tolerant species, especially how their responses evolve during the post-drought years and whether they show positive legacy effects i.e., higher growth than expected due to droughts.

Deep-rooted deciduous oaks are widely distributed in dry and mesic sites (Abrams, 1990) and considered drought tolerant (Arend et al., 2011; Dickson and Tomlinson, 1996). In north-eastern America, *Q. rubra, Q. montana, Q. stellata, and Q. velutina* showed little to no-legacy effects of droughts (Kannenberg et al., 2019a), though projections of future oak abundance are reputed to considerably decrease in the U.S. (Novick et al., 2022). Those ring-porous species can recover quickly by developing new xylem (because they keep only a small number of tree rings active and therefore significantly change the quality of their hydraulics every year). In contrast, the diffuse-porous species need a longer time to repair (if possible at all) drought-induced hydraulic damages since they maintain a higher number of tree rings in the sapwood area and usually have longer leaf lifespans (Zweifel and Sterck, 2018). In the Mediterranean region, *Q. pubescens* showed a progressive decline in resistance to extreme droughts in northern Spain (Camarero et al., 2021; González de Andrés et al., 2021), while drought-induced growth decline and tree mortality have been reported for *Q. pubescens*, *Q. frainetto*, and *Q. faginea* in Southern Italy and Eastern Spain (Colangelo et al., 2017; Corcuera et al., 2004; Ripullone et al., 2020). Studying a *Q. robur* population mixed with *Pinus sylvestris* and *Picea abies* in southern Germany, Zang et al. (2012) reported a faster recovery of *Q. robur* compared to two other species. This result for *Q. robur* is consistent with those reported by Steckel et al. (2020) and Bose et al. (2021b). However, the later study showed a weaker recovery potential in *Q. petraea* than *Q. robur*. In a mixed-species forest, *Q. petraea* was not significantly affected by droughts but benefited from the release of competition through drought-induced mortality of neighboring *Fagus sylvatica* (Cavin et al., 2013). Overall, the existing literature on deciduous oaks is primarily based on local to regional studies and indicates drought tolerance but also shows their

vulnerability under extreme drought conditions. This inconsistencies in literature need to be addressed by examining the responses at a larger spatial scale and considering many oak species.

We used a network of tree-ring chronologies of deciduous oak species from 458 stands covering 21 species and a large part of their distribution in North America, Europe, and Asia. Our main objective was to determine the occurrence, duration, and magnitude of legacy effects on tree growth induced by extreme droughts. Specifically, we asked: (i) do legacy effects occur in deciduous oaks and at which extent? (ii) are legacy effects more prominent in dry than mesic sites irrespective of species? (iii) do legacy effects vary by drought seasonality, drought repetitiveness and by species, and can species-specific traits explain this? and (iv) do legacy effects of extreme droughts in deciduous oaks depend on long-term growth-climate sensitivity? We hypothesized that post-drought growth legacies are mainly negative, and their absolute magnitude peaks one year after drought, particularly in dry sites.

2. Methods

2.1. Study area

The study area spans from 122.03° W to 145.85°E and includes a latitudinal band from 32.21°N to 59.36°N (Fig. 1), where oak forests are located in temperate and sub-tropical (e.g., Mediterranean) ecosystems. Across the study sites, the climate varies largely (Salinger, 2005), with mean annual temperatures, total annual precipitation sum, and climatic water balance (precipitation-potential evapotranspiration, P-PET) for the years 1986–2015 ranging between 0.88 and 18.93 °C (mean 9.75 °C), 338 and 2133 mm (mean 833 mm), and − 36.28 and 131.0 mm (mean 15.08 mm), respectively. While temperatures increased by 0.85 °C during 1986–2015 compared to the period 1956–1985, precipitation and climatic water balance remained relatively stable.

2.2. Ring width data

We compiled tree-ring width data (RW) of 21 deciduous *Quercus* species from 12,744 trees located in 458 sites in North America, Europe, and Eastern Asia (Fig. 1), covering a period approximately from 1940 to 2016. The RW data were obtained from the International Tree-Ring Data Bank (http://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring) in November 2022 (n = 117), from Bose et al. (2021b) (n = 106), and from additional sites provided by the authors (n = 239). Based on the geographic distribution (Fig. 1) and their climatic envelope (Fig. SM1), the 21 oak species were grouped as North American oaks, temperate European oaks, Mediterranean oaks, and Mongolian oaks (Table SM1). To reduce trends related to tree age and size, we detrended the raw ring-width (RW) series using a 30-year cubic smoothing spline with a 50 % frequency cut-off (Cook and Kairiukstis, 1990). This detrending method retains 99 % of the variance at 5 years and 50 % of the variance at 15 years (Cook and Kairiukstis, 1990). We chose cubic spline method due to difference in age of the sampled trees. Although removing the effects of past forest management on tree-ring width chronologies is difficult with existing method, Esper et al. (2012) showed minor effects of harvesting on the climate-growth relationships in temperate forests. We then averaged the individual level residual series of ring-width indices (RWI) to obtain site-level standard chronologies.

2.3. Climate data and identification of droughts

We obtained site-specific climate data from the CHELSA V1.2 timeseries (Climatologies at high resolution for the earth's land surface areas) for each site using the latitude and longitude coordinates (Karger et al., 2017). Monthly precipitation sums and monthly mean, maximum, and minimum air temperatures from January to December were obtained for the period 1940–2016. We then calculated the climatic water
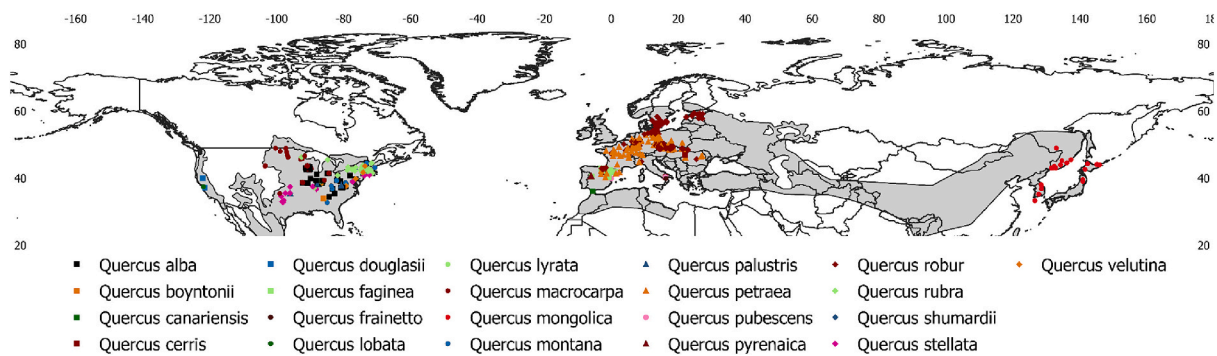
Fig. 1. Location of oak sites from where tree-ring width data was collected. Shaded areas represent the distribution of deciduous oak species across the Northern Hemisphere.

balance (CWB) at monthly, seasonal, and annual scales. The CWB represents precipitation minus potential evapotranspiration (PET). The PET was obtained using the *Thornthwaite* function of the R package SPEI (Begueria and Vicente-Serrano, 2013). Seasonal climatic variables were computed by averaging (temperature) or summing (precipitation) monthly values (winter: December–February; spring: March–May; summer: June–August; and autumn: September–November). We identified extreme drought events at annual as well as at three seasonal scales (i.e., previous winter (December–February), current spring (March–May), and current summer (June–August)). CWB measures absolute climate water balance and were chosen to characterize drought as it better captures the absolute water availability (Zang et al., 2019) and was also used by previous studies (Anderegg et al., 2015b; Bose et al., 2021b). CWB that exceeded 1.5 standard deviations towards negative values were used to define an extreme drought "event". The list of years when the extreme drought events occurred at annual and/or seasonal scales is presented in Table SM2 in the supplementary materials. We characterized each of those identified drought as (i) whether it has a repetitive drought (i.e., repetitive within the 5-year period post of a drought), termed as "*has repetitive drought*", (ii) whether it is a repetitive drought termed as "*is repetitive drought*" and (iii) whether there were no other droughts within the 5-year post of the drought event, termed as a "*single drought*". We characterized those three variables as binary variables (i.e., 0 or 1). The variable "*is repetitive drought*" was not significant for any of the analyses performed (see below), therefore excluded from the analyses. The variable "*single drought*" was correlated with "*has repetitive drought*" and not considered in the final analyses.

2.4. Quantification of legacy effects

We quantified the legacy effects of droughts as a departure of observed tree growth (RWI) from expected growth (based on the relationship between RWIs and climate) (Anderegg et al., 2015b). Considering the availability of climatic information from 1940 to 2016, we quantified legacy effects of all droughts occurred in this period. For each site, we first identified the most important climatic variable (i.e., CWB) based on the linear relationship between growth indices (RWI) and CWB. For that purpose, we considered monthly, seasonal, and annual CWB from previous year to current year growing season. For each site, the most important climatic variable (i.e., CWB) was then used to predict tree growth after each drought event. The difference between the observed and the predicted post-drought growth indices was used to determine the legacy effect. We determined legacy effects for a five-year period after the drought event. We compared the trend of observed and predicted growth irrespective of species (Fig. SM2) as well as separately for major species (Fig. SM3).

2.5. Statistical analyses

We used linear-mixed effect models (Zuur et al., 2009) for detecting the effects of predictor variables on legacy effects. The values of the legacy effects were standardized for better quantifying the effect size of predictor variables and comparing effect sizes across predictor variables. The modelling was performed using the function *lme* of the R package *nlme* (Pinheiro et al., 2014; Pinheiro and Bates, 2000; R Development Core Team, 2022). For predictor variables, we considered site types (dry, moderate, and mesic), regional species groups (Mongolian oak, temperate European oaks, Mediterranean oaks and North American oaks), elevation, latitude, longitude, drought intensity, drought types (i. e., "*has repetitive drought*"), site-specific growth sensitivity types (sensitive and non-sensitive) and years since droughts. We considered the additive and two-way interactions of those variables. We developed statistical models incorporating different combinations of additive and interaction effects of the variables mentioned above and selected the best model based on the Akaike Information Criterion corrected for small sample sizes (AICc) (Mazerolle, 2011).

Similar to Anderegg et al. (2015b), site type was assigned by long-term precipitation averages including dry, moderate and mesic sites associated with total annual precipitation (TAP) sums <600 mm, 601–999 mm, and > 1000 mm, respectively. The sites were also categorized as sensitive (i.e., when tree radial growth correlates significantly with any CWB seasonal, monthly, or annual i.e., by $p < 0.05$) and non-sensitive sites. Multiple droughts nested within a site and multiple sites nested within a species group were considered as random effect variables.

For species-specific analysis, we merged moderate and mesic sites as the results from earlier analyses showed no difference between them. The analysis was performed separately for the seven species (*Q. petraea, Q. robur, Q. faginea, Q. mongolica, Q. macrocarpa, Q. alba,* and *Q. rubra*) with at least 20 sites, including the same model structure as before.

We also examined whether there was a significant relationship between species-specific drought legacy effects and selected functional traits representing the leaf and wood economics spectra (Chave et al., 2009; Wright et al., 2004) including maximum height, specific leaf area (SLA), mass-based leaf N concentration, sapwood density, and the xylem tension causing 50 % loss of hydraulic conductivity (P50). These species-specific traits were obtained from Liu et al. (2019). We also considered relationships with species shade and drought tolerance indices developed by Niinemets and Valladares (2006). The functional traits data were not available for all species. Therefore, the analyses were limited to only those species (i.e., *Q. alba, Q. frainetto, Q. petraea, Q. robur, Q. rubra,* and *Q. stellata*) where the data was available. For each species, we summed the legacy effect values of 1–5-post drought years and termed as "integrated legacy effects" similar to Anderegg et al. (2015b). We then used linear regression to detect relationship between integrated legacy effects and species-specific functional traits.

For detecting the role of drought timing or seasonality (Bose et al., 2021b; D'Orangeville et al., 2018; Huang et al., 2018), we first quantified the legacy effects of all seasonal droughts (Table SM2) occurred in the study period (1940–2016) following the same methods explained above. We considered three seasons including the previous winter, current spring, and current summer. The legacy effects were then modelled as a function of site types, seasons, regional species groups, and years since droughts and the same random effect structure (explained earlier).

3. Results

Repetitive droughts caused significant negative legacy effects (i.e.,

lower growth than expected) in radial growth in dry (TAP 350–598 mm) and mesic sites (TAP >1000 mm) but not in moderate sites (TAP 600–1000 mm) (Table SM3 and Fig. 2A). The negative legacy effects of repetitive droughts were not fully recovered in dry sites and the size of negative legacy effects was larger in dry sites compared to other mesic sites but not initial two-years after droughts (Fig. 2A). However, negative legacy effects turned to positive (i.e., higher growth than expected) both in mesic and moderate sites during 3–5-years after the non-repetitive extreme droughts. Contrary to moderate and mesic sites, the initial non-significant legacy effects turned to negative legacy effects in dry sites from the 3rd year after the non-repetitive extreme droughts.

We detected significant negative effect of repetitive droughts irrespective of site-specific growth-climate sensitivity (Table SM4).
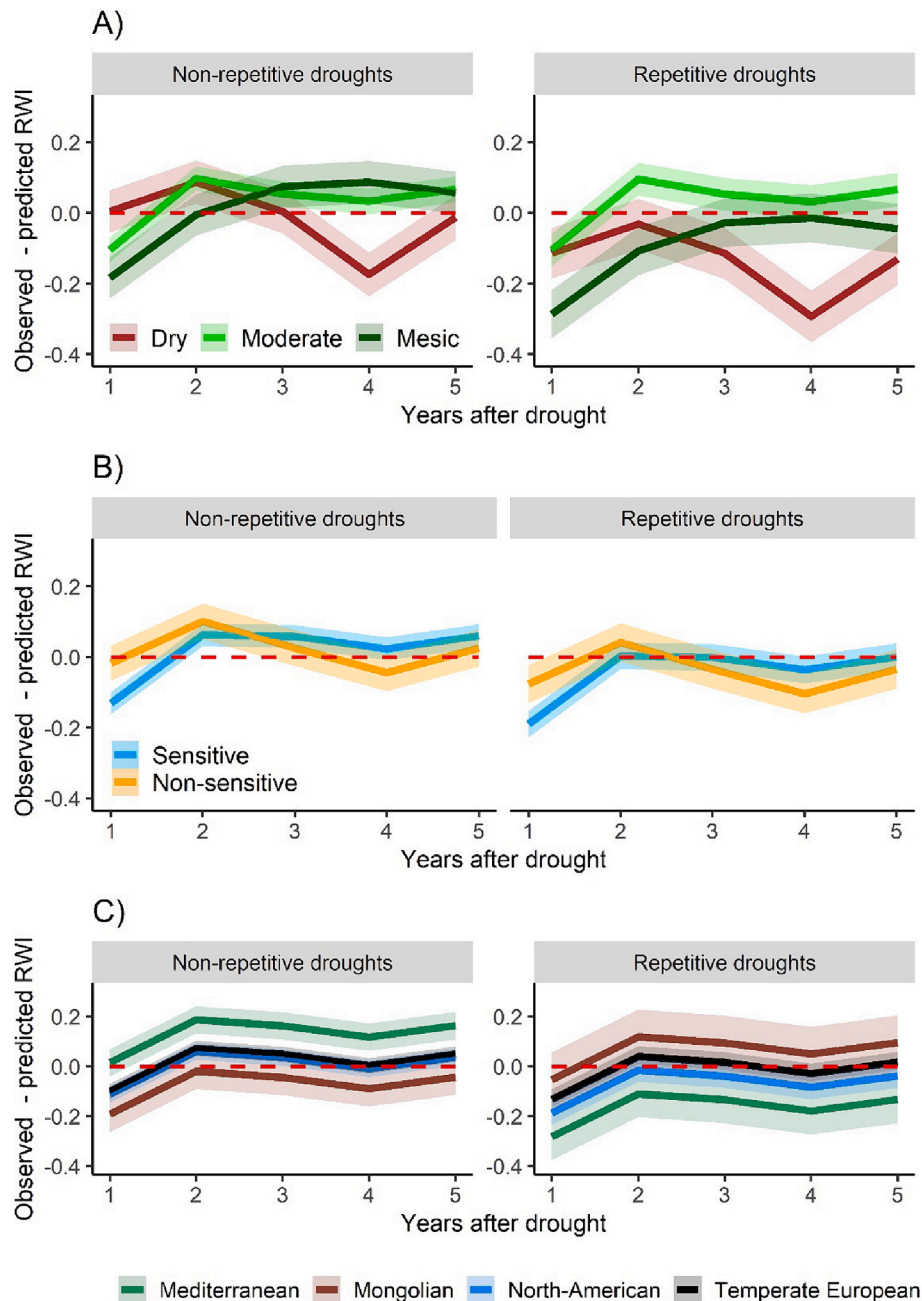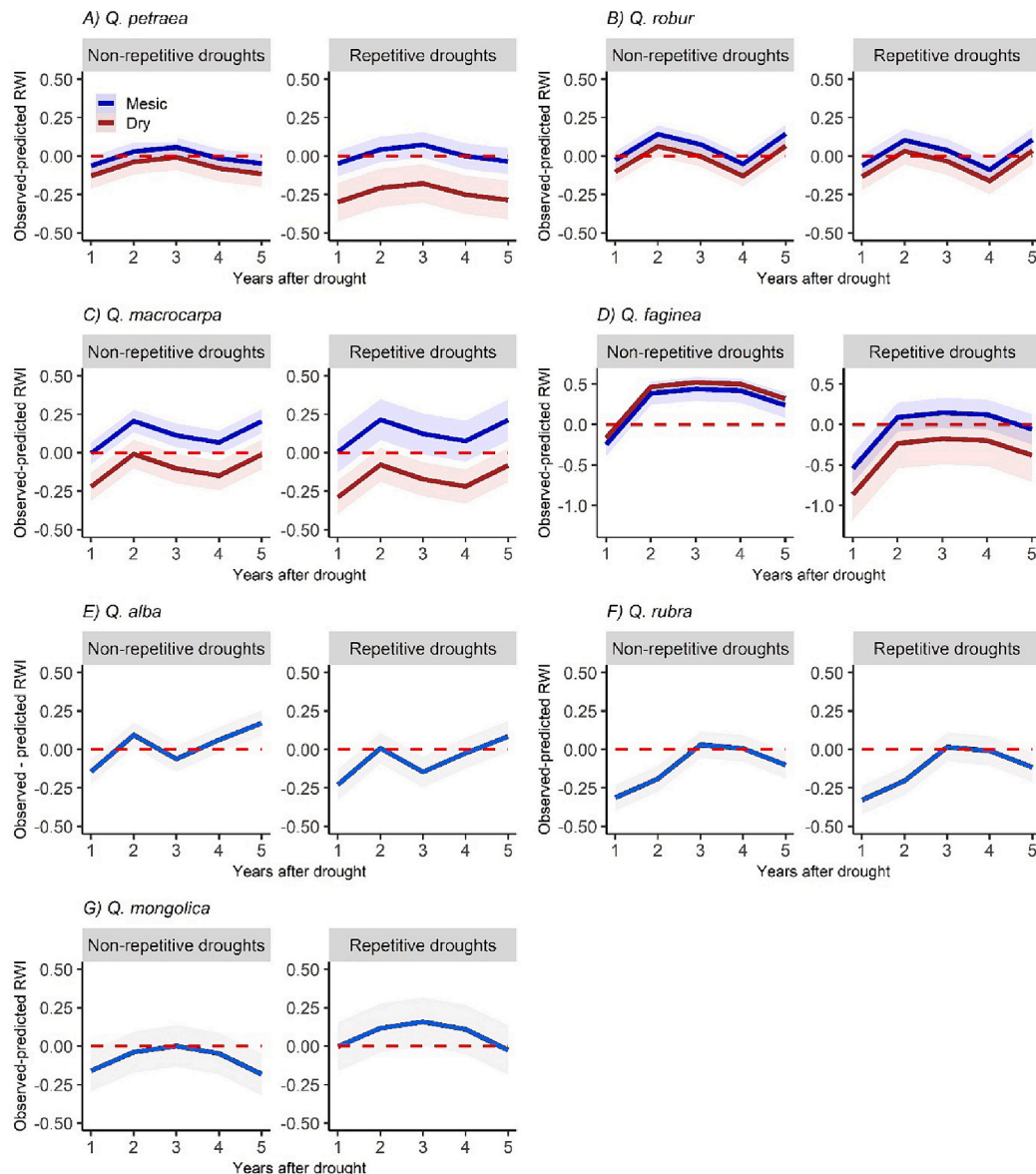

Fig. 2. Mean legacy effects of droughts for 1 to 5 years (x axes) under the presence and absence of repetitive drought events. (A) Legacy effects across dry (annual precipitation <600 mm), moderate (600–1000 mm), and mesic sites (>1000 mm), (B) Legacy effects observed across sensitive (tree growth significantly correlated with the climatic water balance) and non-sensitive sites, and (C) Legacy effects across four species groups based on regions of distribution. The red dashed line indicates no difference between observed and predicted growth and shaded areas in all panels represent the mean ± standard error.

Significant negative legacy effects were observed only in sensitive sites (where growth significantly correlated with CWB), and that occurred only in the first year after the drought event (Fig. 2B and Table SM4). The negative legacy effects then turned to positive and stayed positive from 2 to 5 years after the droughts.

Repetitive droughts caused significant negative legacy effects in Mediterranean oaks and such negative legacy effects were not fully recovered during 1–5-year post-drought period (Fig. 2C). However, non-repetitive droughts resulted significant positive legacy effects in Mediterranean oaks and not in other species group (Fig. 2C). Negative legacy effects were found in temperate European, North American, and Mongolian oaks, but only in the 1st year after the extreme droughts (Fig. 2C). The frequency of negative legacy effects was lower compared to positive legacy effects except in the first year after the drought event (Fig. SM4).

Species-specific analysis revealed that repetitive droughts had significant effects in determining legacy effects of *Q. petraea* and *Q. faginea* but not of other species (Fig. 3). *Q. petraea, Q. macrocarpa,* and *Q. faginea*

could not fully recover the growth in dry sites after repetitive droughts for the entire 1–5 years post-drought period. However, we observed positive legacy effects in mesic sites for *Q. petraea*, and *Q. macrocarpa* (Fig. 3). Significant difference between mesic and dry sites were observed only for *Q. macrocarpa*. The differences between mesic and dry sites were tested only for four species (*Q. macrocarpa, Q. petraea, Q. robur,* and *Q. faginea)* because of insufficient number of observations for other species. Significant negative legacy effects that occurred during 1–2 years after the extreme droughts were fully recovered for *Q. faginea* and *Q. rubra*. We did not observe significant changes in legacy effects over 1–5 years after the drought event for *Q. robur* and *Q. mongolica*. The magnitude of positive legacy effects was higher for *Q. faginea* as compared to other species after non-repetitive droughts (Fig. 3). When we integrated the legacy effects of 1–5 years by species, we detected significant relationship between integrated legacy effects and P50, SLA, and nitrogen mass, although the species-specific trait data was available for only six oak species (Fig. 4).

Fig. 3. Mean legacy effects of repetitive and non-repetitive droughts for different deciduous oak species. The analyses were performed separately for each species with at least 20 observations (i.e., number of sites). All sites of *Q. alba, Q. rubra,* and *Q. mongolica* were from mesic regions and therefore the effect of site type was not considered in the analysis for those three species. Legacy effects were quantified as the difference between observed and predicted growth (unitless index) after extreme climatic drought. The red dashed line indicates no difference between observed and predicted growth, and shaded areas in all panels represent the mean ± standard error.
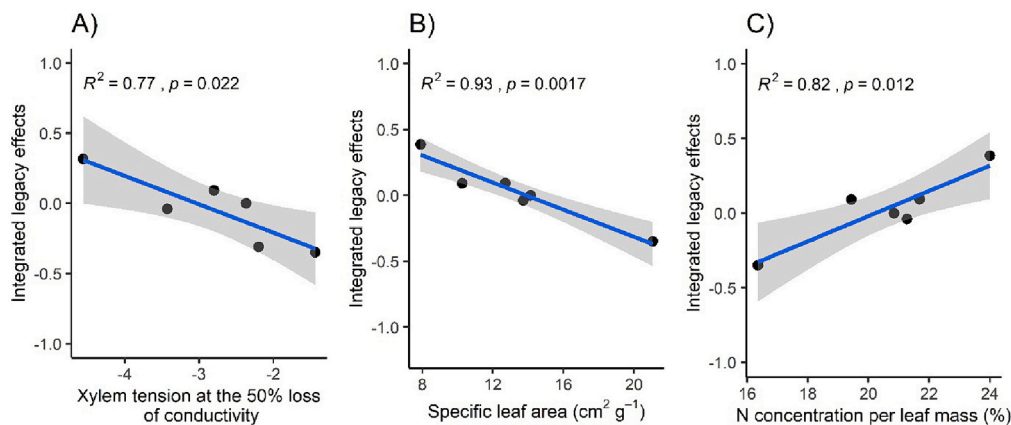
Fig. 4. Relationship between integrated legacy effects (integrated of legacies from 1 to 5 years after drought) and species-specific traits. In plot (A), the P50 units are MPa and the P50 data was available for *Q. alba, Q. frainetto, Q. petraea, Q. robur, Q. rubra,* and *Q. stellata*. The data for specific leaf area and N concentration were available for *Q. alba, Q. faginea, Q. petraea, Q. robur, Q. stellata,* and *Q. velutina*. Shaded areas in all panels represent the mean ± standard error.

We found a strong positive relationship between the legacy effect and growth sensitivity to past-year winter temperature (Fig. 5A) and a negative relationship between the legacy effect and growth sensitivity to past-year summer water balance (Fig. 5B). These analyses revealed a switch from positive to negative legacy effects in dry sites while negative to positive legacy effects in mesic sites over the 5 years after the extreme droughts (Fig. 5A). This switch has also been identified in Mediterranean oaks which showed negative legacy effects during the first year after the extreme droughts followed by positive legacy effects during

later years (Fig. 5B). The effects of mean annual temperature on legacy effects also switched from negative to positive during 1–5 years after the extreme droughts (Fig. SM5).

In mesic sites, significant negative legacy effects of winter droughts were found and lasted 1–4 years after the drought event while significant positive legacy effects of winter droughts were found in dry sites (Fig. 6A). Contrary to winter droughts, significant negative legacy effects of spring and summer droughts occurred in dry sites and lasted 1–5 years after the droughts. The size of negative legacy effects of winter
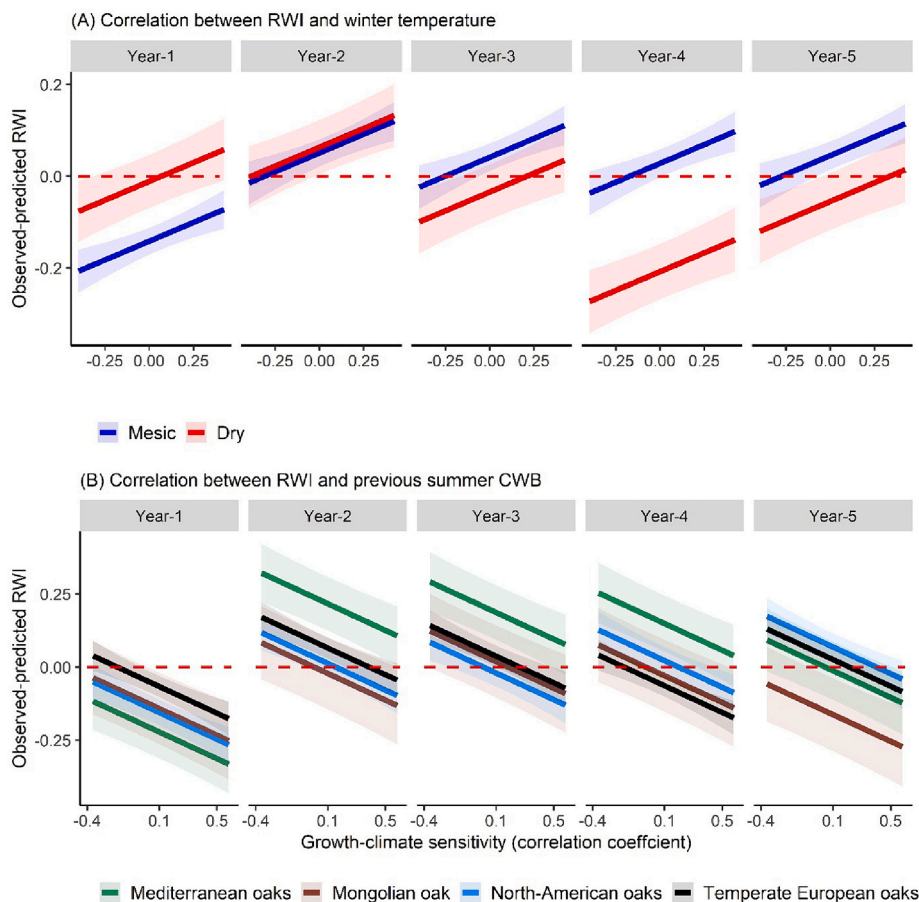
Fig. 5. Mean drought legacies during 1–5-year following extreme droughts as (A) a function of site type and growth-climate sensitivity to winter temperature and as (B) a function of regional species group and growth-climate sensitivity to previous summer climatic water balance (CWB). RWI is the ring-width index.
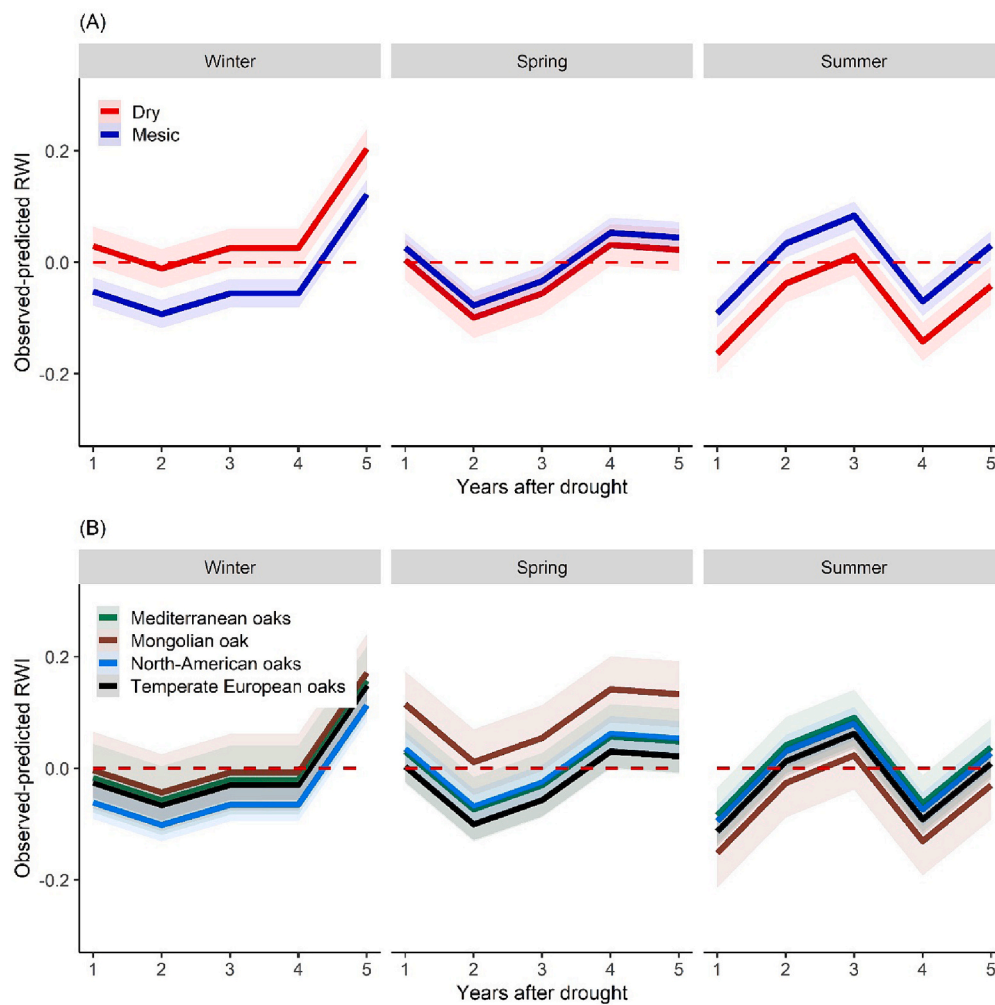
Fig. 6. Mean legacy effects of seasonal droughts across (A) site type and (B) regional species groups. Three seasons were considered including previous winter (previous year December – current February), current spring (March–May) and current summer (June–August). Legacy effects were quantified as the difference between observed and predicted growth (unitless index) after extreme climatic drought. Red dashed line indicates no-difference between observed and predicted growth (RWI, ring-width index) and shaded areas in all panels represent the mean $\pm$ standard error.

droughts was larger in North American oaks compared to the other species groups (Fig. 6B). We observed non-significant differences among temperate European, Mediterranean, and Mongolian oaks when responding to winter droughts. Temperate European oaks were more negatively affected by spring droughts as the negative legacy effects were larger compared to other species groups. Spring droughts induced positive legacy effects in Mongolian oaks. Contrary to spring droughts, Mongolian oaks were more negatively affected by summer droughts compared to other species groups (Fig. 6B).

4. Discussion

While prior research has assessed the enduring impacts of severe droughts on tree species' radial growth at various geographical levels (Anderegg et al., 2015b; Bose et al., 2021b; Huang et al., 2018; Kannenberg et al., 2019a; Peltier et al., 2016; Wu et al., 2018), our study provides a first empirical confirmation for deciduous oak species, typically seen as resilient species to extreme drought events. We acknowledge that the spatial coverage of our data set is limited largely to temperate and Mediterranean biomes, although it encompasses substantial variation in climatic conditions within these regions. We showed that the magnitude and the direction (positive or negative) of legacy effects in deciduous oaks largely depend on species-specific functional traits, drought repetitiveness, drought seasonality, growth sensitivity to

the previous year climate, and site type related to long-term precipitation averages. Our results revealed significantly different post-drought growth trajectories between oak trees growing in mesic vs dry sites. We detected a strong legacy effect of droughts especially when occurred in successive years on tree growth of deciduous oaks. The legacy effects occurred even when climatic conditions return to normal. Given that tree growth is a central component of carbon storage often correlated with productivity and that oaks are a major (forest) component, these legacy effects have the potential to contribute to the inter-annual variability of ecosystem-level carbon cycling and long-term carbon storage.

Negative legacy effects were more pronounced in dry sites where the annual precipitation was <600 mm compared to mesic sites (TAP >1000 mm) and when trees experienced repetitive droughts. Although several studies in the past identified the roles of repetitive droughts (e.g., Anderegg et al., 2020; Serra-Maluquer et al., 2018), our study is the first effort that examined the roles of repetitive droughts for determining the legacy effects of extreme droughts. We indeed found significant negative legacy effects of repetitive droughts especially in dry sites and in Mediterranean oaks. Compared to Mediterranean oaks (e.g., *Q. faginea*) other species were not significantly vulnerable to repetitive droughts as showed by our species-species analyses (Fig. 3). It is important to mention that approximately 20 % of our identified droughts were repetitive, therefore not all sites and species experienced repetitive droughts (Table SM6).

Although the size of negative legacy effects was larger in mesic sites during the 1st post-drought year a faster recovery or even positive legacies were observed in mesic sites compared to dry sites. Overall, the frequencies of positive legacy effects were higher during 1–5 years after the extreme droughts; however, the size of the positive legacy effects varied across species, drought seasonality, drought repetitiveness, and site-specific growth sensitivity to climatic variables. The positive legacy effects were mostly observed in the Mediterranean and temperate European oak species after non-repetitive droughts (Fig. 2). In the Mediterranean, deep root systems, thicker leaves, and deciduousness enable deciduous oaks to maintain relatively high pre-dawn water potentials in leaves and high water-use efficiency during droughts (Abrams, 1990; Granda et al., 2018). For example, *Q. pubescens* growing in Southern France under extremely dry conditions showed early leaf senescence to avoid cell damage and maintained water potentials above critical thresholds (Damesin and Rambal, 1995). A similar finding was observed for *Q. petraea* at a dry site where oaks maintained water transport, photosynthesis and growth by using stem water reserves (Neuwirth et al., 2021). The greater frequencies of positive legacy effects of extreme droughts in deciduous oaks might have resulted from a release in competition among trees within a forest stand, where mortality or growth decline of drought-sensitive species may favor the growth of deep-rooted deciduous oak species (Ripullone et al., 2020). In addition, dominant and co-dominant trees were selected for our study and these larger trees could also benefit from the growth decline of the companion-suppressed neighboring trees. In the UK, Cavin et al. (2013) reported that *Q. petraea* increased its growth rate by 20 % in the period immediately following a drought, which was due to the release of competition as a result of growth decline and mortality of the competing *F. sylvatica*. The decline in competitiveness of companion species over deciduous oaks during and after droughts has also been identified by other studies in recent years (e.g., Dorado-Liñán et al., 2017; Jourdan et al., 2020; Rubio-Cuadrado et al., 2018; Scharnweber et al., 2011; Weber et al., 2008).

Under xeric conditions, deciduous oaks maintained higher osmolyte concentrations and reduced stomatal size compared to evergreens to avoid tissue loss. While studying 12 oak species, Ramírez-Valiente et al. (2020) showed that growth was not reduced even when deciduous oaks lowered hydraulic conductivity and leaf size under drought. This is also in line with findings of the European-wide crown conditions surveys under ICP Forests revealing that temperate and Mediterranean oaks species showed the smallest (or even no significant) increase in mean defoliation from 2002 to 2021 among all inspected tree species (Michel et al., 2022). Ring-porous oak species transport the main share of water in the outermost ring allowing them to recover quickly from drought damage by developing new xylem tissues in the following year after drought (Zweifel and Sterck, 2018). In contrast, in mixed species stands, diffuse-porous species, which use multiple rings for effective water transport, need several years to fully replace damaged vessels (Alla and Camarero, 2012). We also observed compensatory growth responses (i.e., positive legacy effects) after growth decline, which is consistent with previous studies (Anderegg et al., 2015b; Bose et al., 2021b; Huang et al., 2018). The transition from negative to positive legacy effects may occur from drought-induced tree mortality, which relieves surviving individuals from competition (Hajek et al., 2022). This particular positive growth response can, however, also be a physiological reaction of trees, given the higher amount of ray parenchyma tissues (and therefore xylem non-structural carbohydrates) of angiosperms as compared to gymnosperms (Morris et al., 2016), to compensate for losses during periods of stress (Gessler et al., 2020; Trugman et al., 2018).

Our analyses have shown that the legacy effects of extreme droughts observed for dry and mesic sites and across regional-species groups depend on the growth-climate sensitivity. This relationship is shown when we relate the legacy effects with growth-climate sensitivity for previous winter temperature and previous summer water balance (Fig. 6). Anderegg et al. (2015b) also observed a direct link between the

magnitudes of legacy effects and growth-climate sensitivity in the semi-arid regions of the northern hemisphere. In our study, higher growth sensitivity to winter temperature was positively related to the size of legacy effects, indicating that future warming in winter will favor the growth of trees (even with droughts). In contrast, the correlation coefficient of growth with previous summer CWB was negatively associated with the size of legacy effects, which may indicate that higher precipitation in previous summer can predispose oak trees to more negative growth responses to extreme droughts in current summer. This can be interpreted as a memory effect due to structural overshoot, i.e., the development of high shoot-to-root ratios in response to favourable climate conditions, which could predispose to drought damage (Jump et al., 2017; Zweifel et al., 2020). Comparable structural overshoot due to high early spring water availability and consequently increased drought susceptibility in the summer of the same year has been observed for *F. sylvatica* (Leuschner, 2020) and for *Q. ilex* (Misson et al., 2010).

Seasonality of drought occurrence (D'Orangeville et al., 2018; Huang et al., 2018) was also important in determining the size and temporal patterns of legacy effects in deciduous oak species. The drought that occurred in previous winter induced negative legacy effects in mesic sites but zero to positive legacy effects in dry sites. Oak trees growing in relatively mesic sites are probably taller and associated with a faster growth tendency which may require higher water availability during the winter compared to slow-growing, shorter trees growing in dry sites (Harvey et al., 2020). The temperate European oak species group is associated with *Q. robur* and *Q. petraea* and was sensitive to spring droughts which have also been reported by Vanhellemont et al. (2019) and Bose et al. (2021b). Although Mediterranean and North American oaks were not significantly different from temperate European oaks in terms of their responses to spring droughts, the size of negative legacy effects was larger for temperate European oaks indicating their vulnerability to drought damage. In contrast to these species spring droughts increased the growth of Mongolian oaks resulting in positive legacies. This difference may be related to the wetter summers experienced by Mongolian oaks in eastern Asia and related to the monsoon.

Despite spatial variations among or even within bioclimatic regions, we found clear differences in drought legacy effects among regional species groups. This indicates that regional climatic conditions (Fig. SM1), species traits, and possible local adaptation of oak populations (cf. Du et al., 2020) could play an important role in determining the type (positive or negative) and magnitude of legacy effects. Among seven species, only *Q. petraea, Q. faginea* and *Q. macrocarpa* from dry sites did not fully recover from the negative legacy effects after repetitive droughts over the 1–5 years post-drought period. The higher sensitivity of *Q. petraea* to extreme droughts has also been observed in earlier studies (Bose et al., 2021b; Camarero et al., 2021; Cochard et al., 1992).

The P50 and SLA were significantly associated with the size of legacy effects, although data was available for only six species. Our analyses showed that oak species associated with higher P50 showed lower legacy effects of extreme droughts. These results may indicate that the repair of damaged organs including the water transport system and leaf area after drought occurred at the expense of radial growth in oaks from more mesic sites. Greater damage to those tree organs might have stagnated the growth of deciduous oaks and resulted in negative legacy effects of extreme droughts as reported by Anderegg et al. (2015b). We also found that higher N concentration in leaf biomass was positively associated with legacy effects indicating that higher N in leaf biomass can foster the recovery process by enhancing photosynthesis rate and carbon uptake and can even result in positive legacy effects after drought. However, Ouyang et al. (2023) recently reported that higher soil N before drought could predispose *Q. petraea* seedlings to drought-induced mortality as N promotes disproportionally higher above-ground biomass (i.e., structural overshoot) making seedlings vulnerable to hydraulic failure (Gessler et al., 2017). In the present study, it is evident that larger oak trees are benefiting from higher leaf N during the post-

drought recovery phases, but future research should investigate long-term relationships between post-drought resilience and nutrient use efficiency by trees (e.g., Wang et al., 2023).

Tree-ring based studies are biased by design towards trees that survived droughts (Nehrbass-Ahles et al., 2014). Stand-level analysis could provide additional insights on whether and how legacy effects vary across trees of different sizes, stand structures, and located in pure or mixed stands (Au et al., 2022; Teets et al., 2018; Weigel et al., 2023) and whether droughts disproportionately lower the growth of smaller trees while benefiting the growth of their larger counterparts or vice versa (Bose et al., 2021a; Forrester, 2019). Long-term monitored soil water information could improve the quantification of drought indices and identification of extreme drought years (Meusburger et al., 2022) and could provide additional insights into whether deciduous oaks are indeed utilizing water from deep soil layers during and after drought events (Ripullone et al., 2020). In addition, how drought-pathogen interactions influence drought impacts and recovery in deciduous oaks needs to be included as they have a considerable potential to modify legacy effects (Haavik et al., 2015).

Considering the increased frequency of extreme droughts in Europe (Spinoni et al., 2018) and elsewhere in the world (Spinoni et al., 2014), our results provide novel insights that repetitive droughts can significantly enlarge negative legacy effects (i.e., significantly lowering the radial growth than expected) in deciduous oak species which are considered tolerant to extreme drought events. These results have important implications for future ecosystem-scale drought resilience and carbon balance as deciduous oaks are often suggested to mix with drought sensitive species for increasing the ecosystem-level resistance and resilience to droughts (Steckel et al., 2020). However, when drought has not been occurred in successive years, oak trees showed strong recovery potential especially in mesic sites. In addition, not all species of deciduous oaks were affected by repetitive droughts (Fig. 3). Therefore, site conditions and selection of oak species is crucial for mixed-species plantation. For example, *Q. robur* was not affected by repetitive droughts and even showed positive legacy effects after the droughts.

Overall, our results showed that deciduous oak species have a strong recovery potential after drought events but not when drought occurs in successive years. Recovery trajectories over time since drought plausibly vary between dry and mesic sites. The switch from negative to positive legacy effects occurred in a shorter time in mesic sites compared to dry sites and was dependent upon mean annual temperature and climate-growth sensitivity. The legacy effects lasted longer in dry and climatically non-sensitive sites. However, dry sites were not sensitive to winter droughts but to spring or summer droughts. This indicates that in addition to site aridity drought seasonality determines the size and prevalence of legacy effects of extreme droughts in deciduous oak species.

CRediT authorship contribution statement

Arun K. Bose: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jiri Doležal:** Writing – review & editing, Validation, Resources, Data curation. **Jan Altman:** Writing – review & editing, Validation, Data curation. **Daniel Ziche:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Elisabet Martínez-Sancho:** Writing – review & editing, Formal analysis, Data curation. **Christof Bigler:** Writing – review & editing, Validation, Data curation. **Michele Colangelo:** Writing – review & editing, Validation, Data curation. **Isabel Dorado-Liñán:** Writing – review & editing, Validation, Data curation. **Igor Drobyshev:** Writing – review & editing, Validation, Data curation. **Sophia Etzold:** Writing – review & editing, Validation, Methodology. **Patrick Fonti:** Writing – review & editing, Validation, Methodology, Data curation. **Arthur Gessler:** Writing – review & editing, Validation, Funding acquisition, Conceptualization. **Tomáš Kolář:** Writing – review & editing, Validation, Data curation. **Eva Koňasová:** Writing – review & editing, Validation, Data curation. **Kirill Aleksandrovich Korznikov:** Writing – review & editing, Validation, Data curation. **François Lebourgeois:** Writing – review & editing, Validation, Data curation. **Manuel Esteban Lucas-Borja:** Writing – review & editing, Validation. **Annette Menzel:** Writing – review & editing, Validation, Methodology, Data curation. **Burkhard Neuwirth:** Writing – review & editing, Validation, Data curation. **Manuel Nicolas:** Writing – review & editing, Data curation. **Alexander Mikhaylovich Omelko:** Writing – review & editing, Data curation. **Neil Pederson:** Writing – review & editing, Validation, Data curation. **Any Mary Petritan:** Writing – review & editing, Validation, Data curation. **Andreas Rigling:** Writing – review & editing, Validation, Funding acquisition, Data curation. **Michal Rybníček:** Writing – review & editing, Validation, Data curation. **Tobias Scharnweber:** Writing – review & editing, Validation, Methodology, Data curation. **Jens Schröder:** Writing – review & editing, Validation, Data curation. **Fernando Silla:** Writing – review & editing, Validation, Data curation. **Irena Sochová:** Writing – review & editing, Validation, Data curation. **Kristina Sohar:** Writing – review & editing, Validation, Data curation. **Olga Nikolaevna Ukhvatkina:** Writing – review & editing, Validation, Data curation. **Anna Stepanovna Vozmishcheva:** Writing – review & editing, Validation, Data curation. **Roman Zweifel:** Writing – review & editing, Validation. **J. Julio Camarero:** Writing – review & editing, Validation, Supervision, Methodology, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the research reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.172049.

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