



Diverging growth trends and climate sensitivities of individual pine trees after the 1976 extreme drought

Edurne Martinez del Castillo^{a,*}, Max C.A. Torbenson^a, Frederick Reinig^a, Oliver Konter^a, Emanuele Ziaco^a, Ulf Büntgen^{b,c,d,e}, Jan Esper^{a,c}

^a Department of Geography, Johannes Gutenberg-University Mainz, Mainz, Germany

^b Department of Geography, University of Cambridge, Cambridge, United Kingdom

^c Global Change Research Institute of the Czech Academy of Sciences (CzechGlobe), Brno, Czech Republic

^d Department of Geography, Faculty of Science, Masaryk University, Brno, Czech Republic

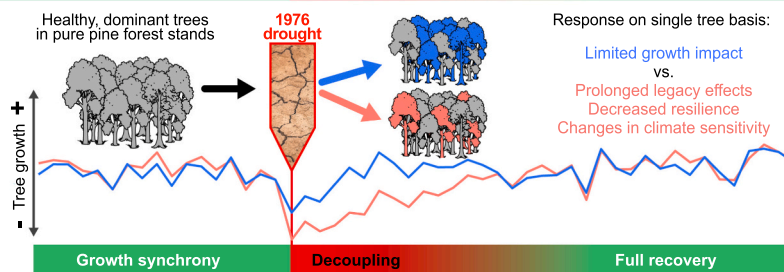
^e Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland

HIGHLIGHTS

- Growth responses of individual trees to the 1976 drought event were analyzed.
- A varying proportion of trees showed exceptionally prolonged legacy effects.
- Affected trees showed stronger growth reduction and lower drought resilience.
- Those trees exhibit significant changes in their climate sensitivity to temperatures.

GRAPHICAL ABSTRACT

Extreme droughts cause diverse long-term growth impacts on individual *Pinus sylvestris* trees



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ABSTRACT

Summer droughts are affecting the productivity and functioning of central European forests, with potentially lasting consequences for species composition and carbon sequestration. Long-term recovery rates and individual growth responses that may diverge from species-specific and population-wide behaviour are, however, poorly understood. Here, we present 2052 pine (*Pinus sylvestris*) ring width series from 19 forest sites in south-west Germany to investigate growth responses of individual trees to the exceptionally hot and dry summer of 1976. This outstanding drought event presents a distinctive test case to examine long-term post-drought recovery dynamics. We have proposed a new classification approach to identify a distinct sub-population of trees, referred to as “temporarily affected trees”, with a prevalence ranging from 9 to 33 % across the forest stands. These trees exhibited an exceptionally prolonged growth suppression, lasting over a decade, indicating significantly lower resilience to the 1976 drought and a 50 % reduced capacity to recover to pre-drought states. Furthermore, shifts in resilience and recovery dynamics are accompanied by changing climate sensitivities, notably an increased response to maximum temperatures and summer droughts in post-1976 affected pines. Our findings underscore the likely interplay between individual factors and micro-site conditions that contribute to divergent tree responses to droughts. Assessing these factors at the individual tree level is recommended to advancing our

* Corresponding author.

E-mail address: emartine@uni-mainz.de (E. Martinez del Castillo).

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understanding of forest responses to extreme drought events. By analyzing sub-population growth patterns, our study provides valuable insights into the impacts of summer droughts on central European forests in context of increasing drought events.

1. Introduction

The ongoing climate change has accelerated even more than previously projected, thereby increasing the intensity and frequency of extreme droughts globally (IPCC, 2021). Prolonged dry periods can fundamentally change ecological boundary conditions and may induce abrupt forest transformations comprising multiple and uncertain successional pathways, knock-on effects such as wildfires, insect outbreaks, and could even lead to regional species extinction (Feyen et al., 2020). The forest productivity in central Europe has been significantly impacted by historical droughts, with extensive research highlighting a pervasive decline or deterioration in overall forest growth attributed to the occurrence of severe dry conditions during specific years such as 1948 (Dulamsuren et al., 2022) or 1976 (Heer et al., 2018; Vitali et al., 2017), and even further in the past (Büntgen et al., 2010). The severity of droughts and their ecological and socio-economic impacts have increased over the past decades (Allen et al., 2010; Trnka et al., 2016) and are expected to continue progressing towards the end of this century (Spinoni et al., 2018).

The year 1976 represents a critical drought event in Central Europe. It has been documented as the greatest summer drought during the 20th century in central Europe (Samaniego et al., 2013; Zink et al., 2016), and ranked as the second lowest year in a central European water balance reconstruction covering the past 2000 years (Torbensohn et al., 2023). The 1976 drought reached its peak in May and continued throughout the summer (Spinoni et al., 2015), causing severe effects on central European forests and probably initiating one of the most remarkable phenomena of forest decline, collectively called *Waldsterben* (Schütt and Cowling, 1985). Given its large-scale implications as well as the possibility of studying recovery effects over >40 years, the 1976 drought event represents a unique test case to investigate post-drought recovery and growth patterns in tree rings.

The assessment of drought impacts on forest productivity and composition has become one of the main concerns for ecologists and managers (Hammond et al., 2022; Senf and Seidl, 2021; Norman et al., 2016). There is growing evidence that drought affects tree growth patterns (Cailleret et al., 2017; Kannenberg et al., 2019), forest composition (Taccoen et al., 2022), mortality rates (Allen et al., 2015; Gazol and Camarero, 2022; Hammond et al., 2022), and carbon uptake capacity (Brodrribb et al., 2020). Tree resilience analyses may help assessing the impacts of extreme droughts on forest stands (DeSoto et al., 2020; Lloret et al., 2011) by contributing to a comprehensive understanding of the forest response to a given event. Resilience indices have been widely applied given their simple, yet highly efficient quantification of tree responses to previous disturbances (Schwarz et al., 2020), allowing to describe the “recovery” and “resistance” to extreme events as complementary (van der Maaten-Theunissen et al., 2021). Such analyses are classically performed and referred to on a stand basis, providing insight into forest health and stand recovery (e.g. Bottero et al., 2021; Castagneri et al., 2022; Ovenden et al., 2021; Vitali et al., 2017). However, the implications of extreme droughts on forest stands are multifaceted, and uncertainties still remain about the influence on individual tree growth (Gazol et al., 2020b; Vilonen et al., 2022) and the processes determining post-drought recovery trajectories (Anderegg et al., 2016; Bose et al., 2021; Camarero et al., 2021).

The capacity for growth recovery following a drought event depends on a variety of factors. External drivers include climatic factors as the duration and intensity of the drought (Bose et al., 2020; Gazol and Camarero, 2022), and post-drought water limitations (Kannenberg et al., 2020). Forest management practices such as thinning can strongly

influence the forest responses, with positive effects on tree growth, faster recoveries and decreased drought sensitivity through changes in water use efficiency (Manrique-Alba et al., 2020; Sohn et al., 2013; Tonelli et al., 2023). Likewise, site-specific features such as elevation, stand density, competition, slope, soil characteristics, and water table depth (Kannenberg et al., 2019; Zalloni et al., 2019) influence stand recovery. The impacts of drought and competition on forest growth are difficult to tease apart due to their complex interactions (Gleason et al., 2017), which can be exacerbated if there are sudden changes in the intensity of competition, such as those produced by the weakening and death of neighbouring trees (Gavinet et al., 2020; Magalhães et al., 2021).

Drought vulnerability may also differ between gymnosperms and angiosperms (Gazol et al., 2018), or even between species (Anderegg et al., 2015b; Gazol et al., 2020b). At the tree level, individual responses can be influenced by multiple factors including genetic characteristics, life stages, and life history, whereas modulating physiological mechanisms include varying hydraulic functioning and stomatal regulation (Chen et al., 2022), which may all influence a tree’s capacity to resist and recover from drought (Klein, 2015; Sass-Klaassen et al., 2016). The susceptibility of drought-affected trees to various biotic factors (e.g. insect infestation, pathogen infestation) can prolong the recovery period and often lead to the death of individuals (Jactel et al., 2012). The structure of xylem and sapwood, affecting tree ring width, and thus plant-water dynamics at the tree level (Li et al., 2022), is also altered by drought. Narrow rings are commonly formed during such events and may limit photosynthetic activity by reducing water supply to the crown (Peltier and Ogle, 2020). Hence, the impact of water stress on tree functioning can last for several years causing lagged effects beyond the actual drought, constraining the potential for tree growth recovery, which is generally referred to as drought legacy effect (Anderegg et al., 2015b; Kannenberg et al., 2020).

The complex nature of external and internal factors determining post-drought recovery, together with individual sensitivity to long-term climate variability and extreme events over time (Carrer, 2011; Peltier and Ogle, 2020), implies that drought impact is heterogeneous within a stand and likely tree-specific (e.g. Zang et al., 2014). Considering other individual determinants (e.g. soil characteristics, micro-topography or access to light), some trees can be expected to exhibit higher drought vulnerability and climate sensitivity compared to neighbouring ones. The quantification of individual tree responses to drought within a forest stand and shifts of climate-growth relationships remain sparse but is needed for the assessment of species vulnerability at the population level. From both an ecological and management perspective, understanding the complex and individualized responses of trees to drought is crucial for making informed decisions about forest conservation, restoration, and sustainable management (Castagneri et al., 2022). This information is also needed to establish reliable tree-growth models to improve predictions of the impact of drought both subsequent to such events including forest productivity and carbon assimilation trajectories (Godoy-Veiga et al., 2021; Vilonen et al., 2022).

We hypothesize that individual trees that are now similar may have had different responses in the past to intense drought events and may have reacted as two different subpopulations, currently indistinguishable. Accordingly, we investigate growth patterns, tree resilience, and climate sensitivity of a *Pinus sylvestris* tree-ring network in south-west Germany following the 1976 drought. Analyzing distinct subpopulations based on individual tree level growth reactions provides unique insights into the growth responses after extreme drought events. This tree-centered approach outlines varying short-to-long-term impacts

of major droughts within the European network as well as on a regional scale and enhances our understanding of magnitude and temporal extent of the *Pinus sylvestris* response to drought.

2. Materials and methods

2.1. Tree-ring and climate data

We compiled a *Pinus sylvestris* tree-ring database in south-western Germany of 19 sites sampled between 2011 and 2020, ranging from 100 to 700 m a.s.l (Fig. 1). At each site, only healthy trees with no external signs of damages from any disturbance were cored, from mono-specific pine forests. The sampling strategy was consistent throughout these sites, focused on analyzing the growth of the dominant trees in each forest, therefore trees similar in size, social status and tree architecture were selected and sampled. The total number of trees per site varies between 27 and 124, with a mean of 54. The mean age of the trees across the forest stands is 133 years, with a minimum of 87 and a maximum of 184 years (Supplementary Table 1).

From each tree, two cores were extracted at breast height and crossdated using standard dendrochronological procedures (Fritts, 1972). In total, 2052 tree-ring width series were detrended by calculating ratios from fitted negative exponential functions to remove exclusively long-term age-related trends. We used an Expressed Population Signal (EPS) threshold of 0.85 to determine the strength of the

population signal of our chronologies, as it is a threshold commonly used in dendrochronology to consider them reliable and suitable for climate reconstruction purposes (see more details in Buras, 2017). Additionally, we calculated the interseries correlation (r_{bar}) to assess covariance, and computed the relative deviations between consecutive rings for a given tree to estimate sensitivity (sens; Supplementary Table 1). Basal area increments (BAI) were computed using the *bai.out* function of the *dplr* R package (Bunn, 2008).

Monthly precipitation and maximum temperature data from 1901–2016 were extracted from grid points closest to each site using the CHELSAcruts database (spatial resolution of 30 arc sec, details in Karger and Zimmermann, 2018). As an indicator of drought conditions, we used the Standardized Precipitation Evapotranspiration Index (SPEI, Vicente-Serrano et al., 2010), which takes into account the difference between precipitation and potential evapotranspiration, from 1901 to 2018 at a spatial resolution of 0.5° (SPEIbase v.2.6, Beguería et al., 2020). Seasonal means from April–June (AMJ) and July–September (JAS) (i.e. SPEI03 from June and September) from 1901–2018 were considered for the climate-growth analysis, covering the growing season of *Pinus sylvestris* (Martínez del Castillo et al., 2016).

2.2. Statistical analysis

We evaluated growth responses following the 1976 drought at the individual tree level by calculating the average tree-ring width indices

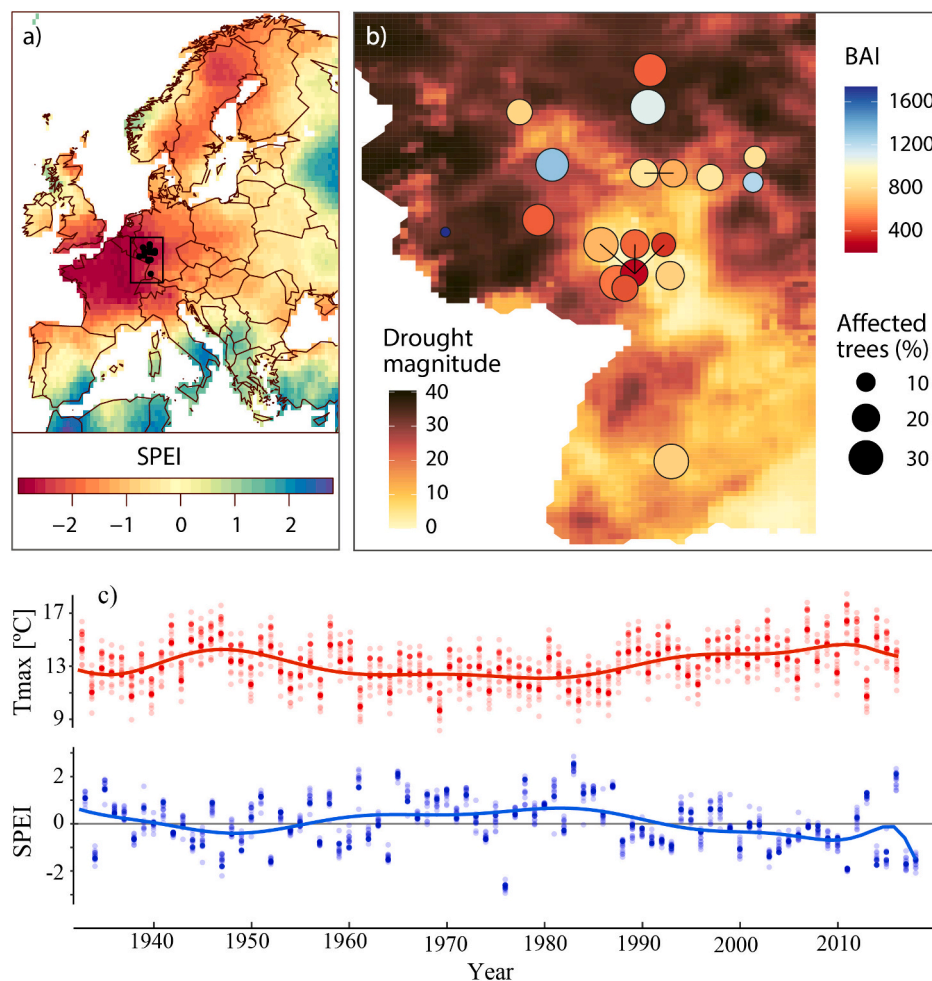


Fig. 1. Climate and tree-ring network. **a**, Tree-ring network in SW Germany (black dots) and June–August SPEI during 1976 across Europe (SPEIbase v.2.6, Beguería et al., 2020). **b**, April–October soil drought magnitude in 1976 in SW Germany derived from the Dürremonitor Deutschland (ufz.de.), darker colors indicate drier conditions. Colour code and symbol size specify mean Basal Area Increment (BAI) from 1930 to 2020 and percentages of temporarily affected trees respectively. **c**, Time-series and smoothed line of April–June Maximum Temperatures and SPEI, respectively, each dot representing one site.

(TRWi) per tree. At each forest stand, trees showing relatively reduced growth during five consecutive years after the drought from 1977 to 1981 were classified as “temporarily affected” (TA) while the remaining were classified as “control” trees. The growth was considered reduced when TRWi values were lower than the 50th percentile (Q2) of all trees within a forest stand during a particular calendar year. Growth values of TA trees had to be below Q2 in each year from 1977 to 1981 to exceed the average period considered in the literature for regular drought recovery (e.g., <4 years in Bose et al., 2020; Gazol et al., 2020a; Sánchez-Salguero et al., 2018; Tonelli et al., 2023; Vilonen et al., 2022).

The resilience components described by Lloret et al. (2011) were calculated to evaluate tree growth responses to drought, using the *pointRes* R-package (van der Maaten-Theunissen et al., 2021). The selected indices including (i) resistance, (ii) relative resilience, (iii) recovery period, and (iv) relative growth reduction were calculated using BAI as a measure of growth over four years before and after the drought event (van der Maaten-Theunissen et al., 2021). Resilience growth indices do not always consider the disturbance impact, the recovery rate, and post-drought climate with respect to reference conditions, yet have been widely used to assess post-drought responses (Schwarz et al., 2020; Vilonen et al., 2022). The resistance index (i) indicates the capacity of trees to buffer drought stress and continue growing after a drought event, by quantifying the difference between BAI during the dry year and the mean BAI of the preceding years, whereas the relative resilience (ii) evaluates the capacity of trees to recover to pre-drought growth values, weighted by the growth reduction experienced during drought. The recovery period (iii) indicates the number of years needed to reach the pre-drought growth averages. In Schwarz et al. (2020), the average growth reduction (iv) was introduced and defined, reflecting the total growth reduction divided by the length of the recovery period.

Climate-growth relationships were tested using response function analyses performed to all TRWi timeseries considering the CHLSA grid point climate data. Correlations were calculated over 3-month-aggregation periods, starting on April (AMJ) and July (JAS) covering the entire species' growing season (Delpierre et al., 2019; Martínez del Castillo et al., 2016). Correlation coefficients between tree growth and raw climatic variables were calculated considering TA and control site-chronologies and monthly/seasonal climate means. A consideration of the standardization of climatic variables in correlation computations is recommended as it can change and improve the climate-growth correlations (Ols et al., 2023). However, in this case correlations yielded similar results, indicating minimal influence of detrending climate data on the primary focus of this study. To evaluate the consistency of responses over time, we computed the response function coefficients from 1930 to 1976 and from 1976 to ending year of each time series and evaluated the significance in the correlation change with a Fisher test. Additionally, the Euclidean distance between the paired correlations (before/after 1976) of each site was calculated. All statistical analyses were performed in the R environment (v. 4.2.2), namely packages *dplR* (Bunn, 2008), *pointRes* (van der Maaten-Theunissen et al., 2021) and *lme4* (Bates et al., 2015).

3. Results

3.1. Patterns of tree growth

The percentage of temporarily affected trees (TA) varied across the studied sites, ranging from 9 % to 33 %, according to the prolonged growth suppression following the drought event (Fig. 1), resulting in 194 TA trees and 842 control trees. The percentage of TA trees is negatively related to local maximum temperatures, but not with other site-related variables such as drought intensity, elevation, precipitation, or tree size (Supplementary Fig. 1). Mean BAI noticeably differed among the 19 study sites, ranging from 400 to 1700 mm², yet the differences were unrelated to mean climatic conditions and/or elevation. No age bias was detected in the groups of trees, within each forest, TA

individuals were of the same age cohort as the control trees (Supplementary Table 2).

The growth trends and interannual variability of TA trees were similar to control trees until 1970 but differed thereafter, reaching the maximum difference four years after the 1976 event (Fig. 2). The growth decline was substantial during the drought year in both groups but persisted for more years in TA trees, exceeding a decade until growth rates became similar again after approximately 15 years. Since 1991, the mean growth patterns of both sub-populations converged and did not differ thereafter, including subsequent drought events e.g. in 1996 and 2006.

The growth patterns observed between these two groups of trees was generally consistent among sites, except for site-specific nuances (Supplementary Fig. 2). Site-by-site analyses revealed that two sites (EDO02 and EDP07) experienced a more severe decline in 1978. Other four sites (EDO02, EDO03, EDP05, and KD001) exhibited divergent growth patterns already before the event, including TA trees indicating lower growth rates, presumably affected by the prior drought events (Spinoni et al., 2015), such as 1964 or 1948 in case of EDO03. In EDN00 and EDP07, the TA trees displayed slightly higher growth rates before 1976 for decades. Despite the heterogeneity of the forests studied, most of them showed significant growth deviations between the identified tree groups only from 1976 onwards (Supplementary Fig. 3). After, the growth differences between TA and control trees started to decrease, being undistinguishable in half of the sites after 8 years and in all stands by year 2000.

3.2. Tree responses to drought

Tree growth was significantly reduced in all sites in response to the 1976 drought, compared with the mean growth of the previous 40 years (Fig. 2, *t*-test *p* value < 0.001) or previous 4 years (Fig. 3a, *T*-test *p* value = 0.0037). The mean BAI of 1935–1975 period was 721 mm² for control trees and 696 mm² for TA trees, and decreased to 404 mm² and 271 mm² respectively in 1976. Control trees were growing at slightly higher rates than TA trees but both groups experienced a strong growth reduction, with decreases ranging from 25 to 50 %. As expected due to the splitting criteria, the 1976 drought had significantly stronger effect on TA trees, with reductions averaging 39 % compared with the previous 4 years (Fig. 3a). On average, the recovery period of control trees was close to two years, whereas in TA trees the period was substantially longer, almost the double (Fig. 3b). Generally, TA trees showed a significantly lower post-drought resilience (Fig. 3c) but no large differences in resistance scores (Fig. 3d).

Both tree groups exhibited consistent climate sensitivity patterns, with comparable magnitude and directional responses (Supplementary Fig. 4), regardless of whether the climatic variables were standardized. Late spring (AMJ) and late summer (JAS) were selected to highlight the climate sensitivity changes as they exhibited the most distinct signals. Correlations during pre- (1930–1975) and post-drought (1977–2020) periods reveal a shift in climate response at most sites, particularly in the TA trees (Supplementary Fig. 4). The control trees were significantly affected by the dry conditions during late spring (AMJ) in eight sites before 1976, and only three sites maintained this relationship thereafter (Fig. 4a). The remaining sites either lost the signal, whereas five new sites that were not previously sensitive to drought became more responsive to late spring conditions. However, the majority of TA trees shifted towards a negative relationship with drought conditions, being five sites negatively correlated with late spring SPEI. The majority of site chronologies (control and TA) did not display statistically significant correlations with SPEI for the late summer period (JAS).

In case of the temperature signal, four out of nineteen control site chronologies showed a significant correlation with maximum temperatures in late spring before the event, being three of them negatively correlated (Fig. 4b, Supplementary Fig. 4). After the event, more sites became temperature sensitive in both directions, with four positively

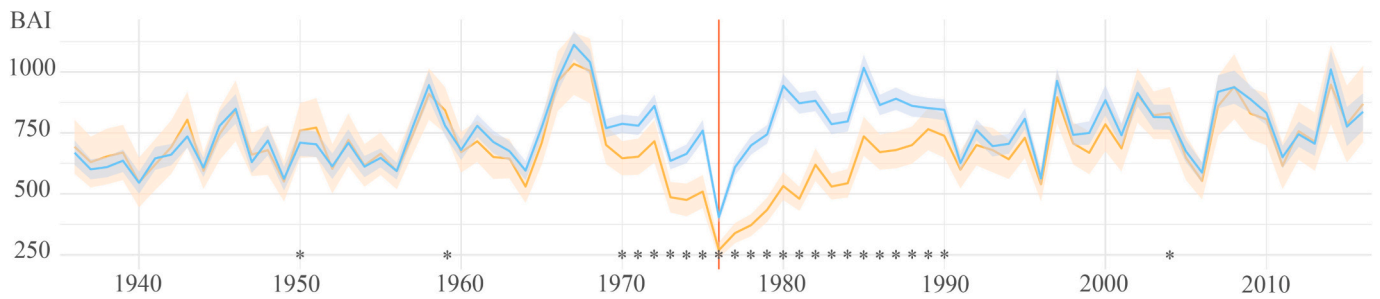


Fig. 2. Basal Area Increment (BAI, mm²) trajectories before, during, and after the 1976 drought of TA trees (orange) and control trees (blue). Dashed areas represent 95 % confidence intervals of mean BAI per year. Significant differences in mean growth between groups were tested with paired two-sided Student’s *t*-test ($p < 0.001$) and highlighted using asterisks. Red vertical line indicates the drought event in year 1976.

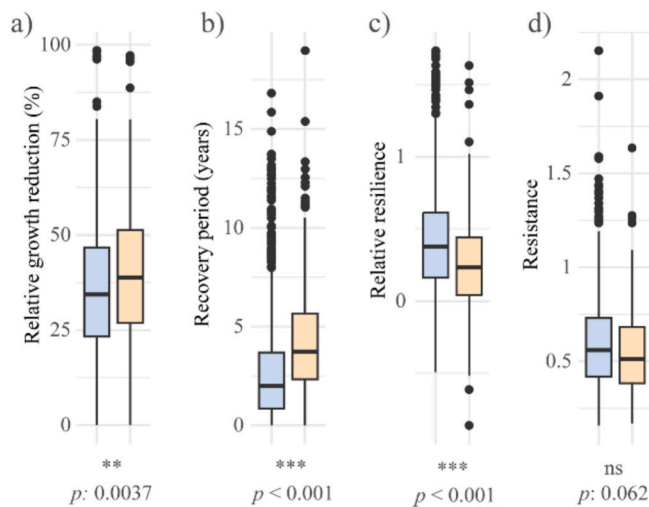


Fig. 3. Components of tree resilience in response to the 1976 drought. Comparison of (a) growth reduction, (b) recovery period, (c) resilience, and (d) resistance of temporarily affected (orange) vs control trees (blue). Asterisks below boxplots indicate significance between the mean groups’ values, based on Student *t*-test *p*-values ($p > 0.05$ not significant (ns), $p \leq 0.05$ as *, $p \leq 0.01$ as **, and $p \leq 0.001$ as ***. $n = 1056$).

and five negatively correlated. The relationship with temperature was not as strong during late summer, with only one site being temperature-sensitive before the event. However, TA trees exhibited a substantial change in the climatic signal before being impacted by the drought, with most of sites (i.e., eleven) becoming temperature-sensitive in late spring and seven sites in late summer.

The observed changes in correlation reveal information about which climatic variables became or ceased to be significant for tree growth, while the Euclidean distance of those changes indicates whether or not they were significant (Fig. 5). The influence of a climatic variable may become statistically significant only in the second period, but such a change in correlation may not statistically be significant. Changes in climate sensitivity between the pre- and post-1976 periods were most pronounced for late spring variables in the TA trees. These trees experienced significant changes in correlation with temperature, SPEI or both variables at 17 of the 19 sites. A common directional shift towards a greater positive influence of temperature and a negative relationship with SPEI is recorded. The magnitude of these changes is not significant during late summer in most cases, however, as only five of the 19 sites show such changes. In comparison, the control trees show only very few significant changes and do not follow a common pattern.

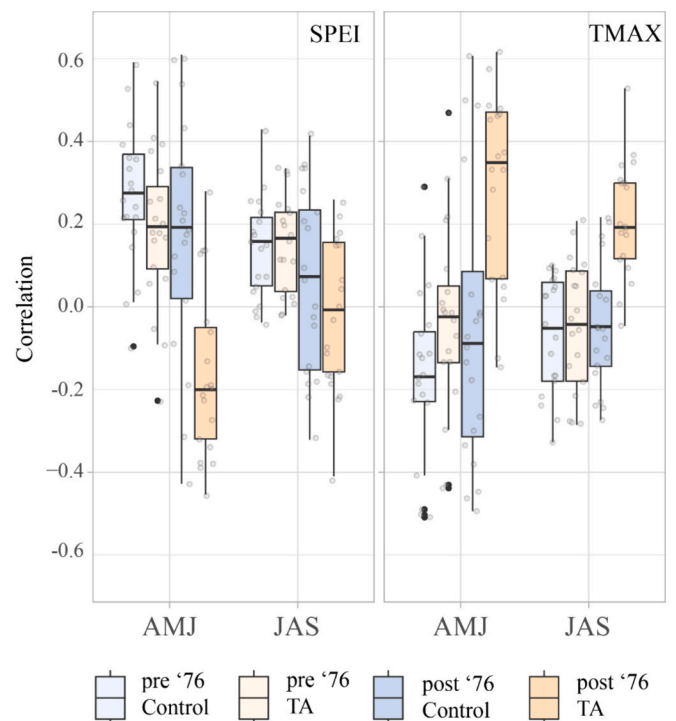


Fig. 4. Correlations between tree growth (TRWi) and a) SPEI and b) maximum temperature before and after 1976 for TA (orange) and control trees (blue). The month aggregations shown are April–May–June (AMJ) and July–August–September (JAS). Each box with whiskers represents the site-level variability of climate sensitivity, as it depicts the distribution of the climate–growth correlations calculated separately for the TA/control site stands. Individual-site correlations are shown as grey dots.

4. Discussion

The rationale of this study is to improve our understanding of the long-term impacts of major drought events on forests, considering and quantifying individual tree growth responses within forest stands. To this end, we classified trees into two groups based on growth patterns displayed during half a decade after 1976, and analyzed pre- and post-drought growth trajectories, resilience components, and changes in their climate sensitivity. Our results demonstrate that trees of similar size, age, and social status displayed different growth responses to the 1976 drought and a varied proportion of them experienced prolonged drought impacts. Whilst the social status and tree architecture were not affected by the climatic disturbance in the long term, the effect on growth differed significantly among trees over an extended period. Our results suggest that trees displaying retarded recovery to drought could be considered distinct sub-populations for certain purposes (e.g.

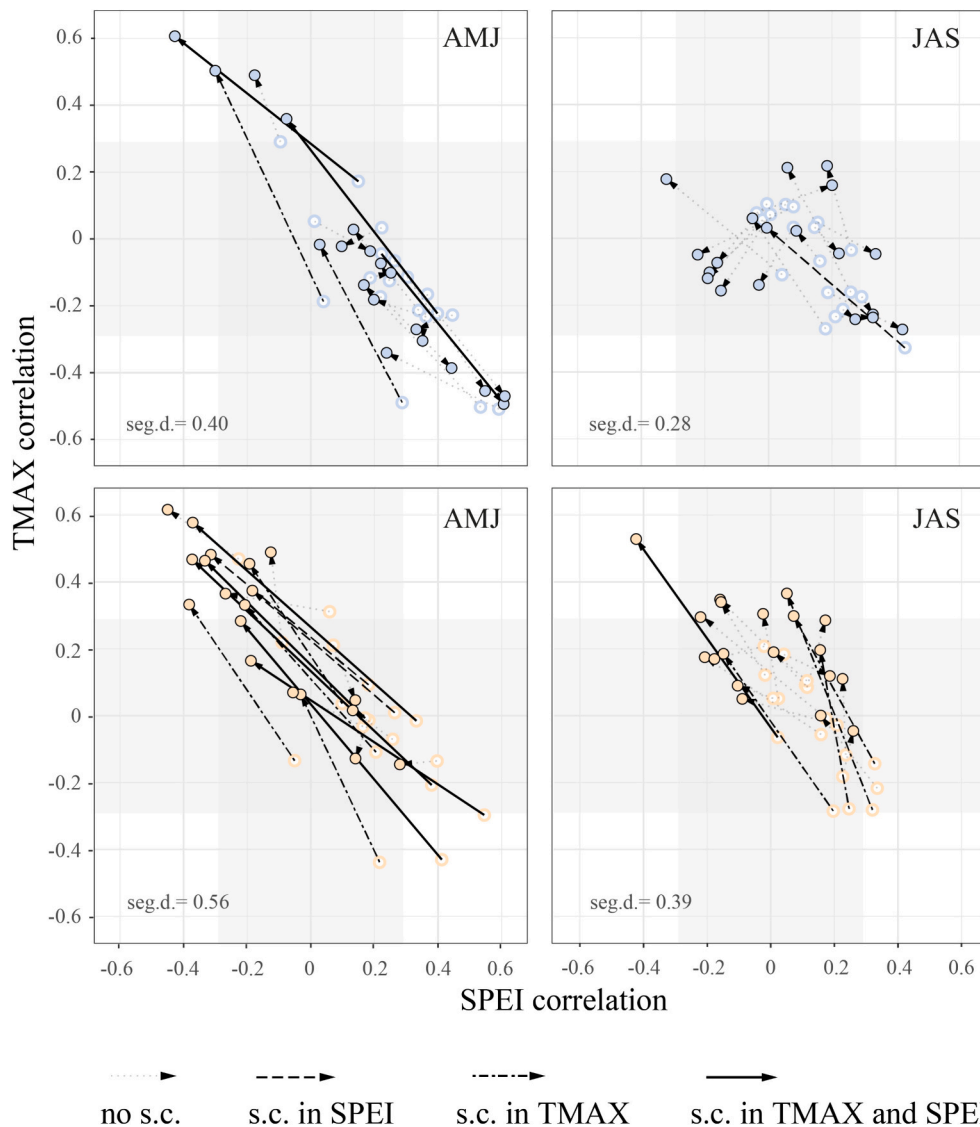


Fig. 5. Temporal changes of climate sensitivity before and after the 1976 event of temporally affected trees (orange) compared to control trees (blue) across sites. White dots represent the correlation with maximum temperature and SPEI from 1930 to 1975 (45-year period), and coloured dots from 1977 to 2020 (up to 43 years, depending on the chronology ending date). The arrows represent the relative shift in climate sensitivity. Shaded areas indicate non-significant correlation with climate. Significant changes between periods (assessed using a Fisher test ($p < 0.01$)), and the mean Euclidian distance (seg.d.) between the paired correlations are shown.

disturbance analyses or climate reconstructions), given their altered growth dynamics and altered response to local climate.

4.1. Tree responses to drought

Despite the site-specific differences detailed in the results, we demonstrate that stronger and longer drought legacy effects are common for only a proportion of trees within a forest stand. The percentage of trees displaying distinct growth responses across the region varies, but this variability is not directly linked to the intensity of drought experienced at each site during 1976, nor to the total amount of precipitation (Supplementary Fig. 1). However, warmer sites had a lower number of TA trees. *Pinus sylvestris* is a highly plastic species, exhibiting wide ranges in secondary growth, wood formation timing (Martínez del Castillo et al., 2016), anatomical traits (Martín et al., 2010), and water use efficiency capacity (Fernández-de-uña et al., 2017), and may have physiologically adapted to local conditions by displaying higher hydraulic safety margins at warmer sites. Individual trees with a vulnerable hydraulic structure are more likely to exhibit larger legacy effects,

as has been proven for different species by Anderegg et al. (2015a, b). Individual genetic adaptation to warmer or dryer conditions could also be possible (Moran et al., 2017), as varying proportions of trees within conifer populations were shown to exhibit specific and unique adaptations (George et al., 2015; Klisz et al., 2016) and might be possible for this species.

Although some sites showed reduced growth in TA trees even before the event, the growth patterns and interannual variability were similar between the two groups of trees until the drought event, but differed thereafter. Most sites displayed divergent growth patterns after the 1976 event, whereas other major droughts that occurred before (i.e., 1949 or 1964) and thereafter (i.e., 1991, 1996, or 2006) did not elicit similar responses in the same trees that were identified to be temporarily affected after 1976. This difference indicates that the individuals which are most affected would be event-dependent, and in this specific case, the effects are truly temporal, as no cumulative effects from repeated stress or disturbances were observed in the majority of cases. These results are consistent with the notion that dominant individuals within forests may exhibit differential responses to climate extremes, owing to

differences in their physiological status (e.g., non-structural carbohydrates, Peltier and Ogle, 2020) at the onset of a perturbation. Moreover, these individuals may undergo specific adaptations in their responses to recurrent stress before experiencing subsequent similar disturbances (i.e. the priming process, described in Hilker and Schmittling, 2019). These adaptations could avoid potential negative impacts from cumulative or compound events on tree functioning, which could ultimately lead to tree dieback (Gazol and Camarero, 2022).

The individual tree responses can be strongly affected by excess mortality within the forest stand, producing drastic changes in competition that would directly affect the recovery patterns (Castagneri et al., 2022) and therefore, the resistance and resilience capacity (Sohn et al., 2013). TA trees may have experienced reduced competition from adjacent trees, which would increase individual climate–growth sensitivity (D'Amato et al., 2013; Sánchez-Salguero et al., 2015), although if competition decreases, individuals would have more light and resources and consequently experience growth boosts on the following years. The unknown level of individual competence that each tree had before and after the drought may introduce uncertainty in these results, yet there is evidence of greater explanatory power of drought on tree growth compared to competition during dry periods (Gleason et al., 2017). The persistent growth reduction beyond five post-drought years points to extended drought legacy effects in TA trees. While the recovery pattern in TA trees is site-specific, lagged negative effects after the drought were substantial and persisted up to 15 years. Legacy effects are known to vary tremendously among species, likely due to the physiological and ecological mechanisms that cause these lags in drought recovery (Gazol et al., 2020a; Li et al., 2023). Even within species, differences in site conditions (Bottero et al., 2021; Castagneri et al., 2022; Leifsson et al., 2023), drought characteristics (Gao et al., 2018; Kannenberg, 2019) or recurrence (Anderegg et al., 2020) can cause variability in the legacy effects. Despite those differences, most of the studies report recovery periods lasting up to four years (Bose et al., 2021; DeSoto et al., 2020; Li et al., 2023; Peltier and Ogle, 2020; Vilonen et al., 2022), which is relatively short compared with our results for TA trees (but consistent with the control trees). A larger number of TA trees could indicate a higher sensitivity of a particular species to drought in a given region but also mask the capacity of the majority of trees to recover if all trees are considered as a whole.

The divergence of recovery responses between the two groups of trees seems to show different post-drought alterations in the carbon allocation strategy. Although decreased radial growth driven by carbon depletion (Oberhuber et al., 2011) or hydraulic damage (Anderegg et al., 2015a, b; Kannenberg et al., 2019) brought on by the drought can take months or years to recover from, shifts in carbon allocation patterns can last longer and persist over multiple years (Fernández-de-uña et al., 2017). The subsequent recovery of radial growth recovery can only begin once the foliage and the roots and mycorrhizal networks have been repaired and expanded, shifting allocation patterns back to compensate radial growth losses (Gessler et al., 2020; Kannenberg et al., 2020). Also, tree size was strongly linked to the recovery period ($r = 0.7$, Supplementary Fig. 1) of TA trees, indicating slower drought-induced reallocation of growth in bigger trees, as shown in Pretzsch et al., 2014.

Given the proposed procedure to classify trees, a weakened capacity to return to pre-drought growth levels (i.e., relative resilience) and a subsequent retarded growth recovery was reported for TA trees. While these characteristics are often associated with increased mortality risk (DeSoto et al., 2020) and decreased resistance to successive droughts (Bose et al., 2020), this was not observed in our TA trees. Conversely, recent research on ecological stress memory have suggested that slow recovery trajectories after antecedent stress were linked to improved resistance to subsequent stress, while rapid post-stress recovery was found to be less effective (Mu et al., 2022). Trees with a transitory growth depression triggered by climate stress were found to have long-term gains in ecological stress memory, and therefore slow post-stress recovery rates suggest improved drought resistance (Camarero, 2023;

Mu et al., 2022) and acclimation response (Gessler et al., 2020). Our results in TA trees revealed that long-lasting growth reductions are fully compatible with long-term survival and full growth recovery and not always lead to tree death.

4.2. Post-drought shifts in climate sensitivity

The trees' capacity to record climatic variability in its growth is driven by natural ontogenetic dynamics and influenced by diverse events and changes during their lifetime (Carrer, 2011). Likewise, drought disturbances can lead to physiological and physical processes altering the way trees respond to climate, leading to temporal variation in growth-climate sensitivity (Peltier and Ogle, 2020). Such temporal variations have been evaluated using moving window approaches with a common window of 30 years (Carrer, 2011; Wilmking et al., 2020). However, changes in tree growth response to climate variables can also occur abruptly, following distinct disturbances, leading to altered correlation between TRW and climate (Peltier and Ogle, 2020). Recent studies document the widespread legacies of drought in tree growth, which serve as strong evidence for variable growth-climate sensitivity (Anderegg et al., 2015b; Leifsson et al., 2023). However, climate sensitivity changes within a forest stand after drought disturbances have not been explored and can yield contrasting results (Fig. 5).

The shifts in climate sensitivity have been broadly discussed under different terms (e.g. the non-stationarity assumption (Wilmking et al., 2020), the divergence problem (Büntgen et al., 2021; Esper and Frank, 2009), or the homeostatic/dynamic sensitivity (Peltier and Ogle, 2020), and growth responses of trees to climatic or environmental drivers are unlikely linear and stable over time. Such changes after disturbances (e.g., droughts) have been reported but not analyzed for responses of individual tree. Our approach to define the climate growth relationships of pine sub-populations within forests stands confirm our hypothesis on climatic sensitivity changes of individual TA trees. These trees displayed a significant climatic signal weakening following the drought event and growth appears to be driven by other variables thereafter. For most sites, significant shifts occurred in the correlation coefficients, trending in the same direction. The most notable change in climate sensitivity occurred in late spring towards positive relationship with maximum temperatures. Previous positive relationships with SPEI disappeared, and several sites began to respond negatively, showing reduced growth under wet conditions, which is unusual for this species (Camarero et al., 2021; Gazol et al., 2020b). The lower temporal variability observed in the control trees caused, in some cases, climatic variables to lose significance in the second period, although the changes were not statistically significant, supporting the conclusion of more persistent climate signals. Within the context of new conceptual hypotheses on climate sensitivity of trees defined by Peltier and Ogle (2020), neighbouring trees may exhibit both homeostatic and dynamic sensitivities simultaneously, with the control trees exhibiting homeostatic sensitivity and the TA trees a dynamic sensitivity.

4.3. The individual-tree approach

Our current understanding of forest drought resilience is necessarily limited by the relative paucity of studies analyzing trees individually (Sass-Klaassen et al., 2016). Numerous studies and meta-analysis are based on the analysis of tree-ring data but analyzed at the forest-stand level (e.g. Bose et al., 2021; Castagneri et al., 2022; DeSoto et al., 2020; Gazol et al., 2018). Our results suggest this approach might overlook the prolonged effects of drought on individual trees, potentially leading to biased conclusions even when tree selection appears to be homogenous. Besides the well-known sampling biases inherent to dendrochronology, such as the 'slow-grower survivor bias', the 'big tree selection bias' or the 'pre-dead suppression bias' (Bowman et al., 2013), we identified a 'temporarily affected trees bias' that could increase uncertainties when interpreting forest ability to cope to droughts, even in

'ad hoc' sampling designs. Tree susceptibility to drought has been observed to be higher in large and old trees (Bennett et al., 2015; Trouillier et al., 2019), which could increase drought legacy effects in trees selected using standard dendrochronological sampling approaches (Klesse et al., 2018). At the same time, other analyses focusing on forest dynamics, forest productivity, growth trends or climate response, often rely on common responses of trees of the same social class, age and size (Nehrbass-Ahles et al., 2014), but results may be altered if droughts or other disturbances cause a prolonged and delayed recovery in varying proportions of trees. The proposed approach of classifying and grouping trees into sub-populations based on individual growth patterns could be a way to avoid the identified bias and provide increasingly reliable estimates of forest responses.

Furthermore, the alteration of the ring width sensitivity to climate depends on the individual drought impact on tree growth dynamics. The individual-tree growth analysis revealed two temporal but distinct sub-populations of trees that exhibited statistically significant differences in their relationship with climate when analyzed over 30-year periods. As the results were consistent across the regional tree-ring network, it can be assumed that this situation may occur throughout the species' distribution, and likely in other tree species. We suggest that disentangling the effects of major perturbances at the individual tree level on mid-term growing patterns and climate sensitivity is a useful strategy that may change or improve the interpretation of certain analyses. Shifts in growth-climate sensitivities could be conceptualized as an emergent indicator for potentially unobserved impacts of past disturbances on trees. Individual trees (rather than stand-level averages) should be the focus in this case, given their potentially idiosyncratic responses to their own unique disturbance histories (Peltier et al., 2022). As refining the prediction of forest and trees responses to climatic variability is becoming fundamental in the context of ongoing and future climate change, comprehensive investigations based on individual tree responses can improve our understanding of forest responses to climate disturbances.

5. Conclusions

The 1976 drought was a tipping-point for *Pinus sylvestris* populations in Central Europe as it preceded substantial changes in the growth dynamics of single trees, particularly temporarily affected individuals. Our results indicate that tree growth changes in response to drought can significantly differ within a forest stand. We detected a strong and prolonged legacy effect of drought on tree growth in certain trees, with higher drought-induced growth reductions and associated vulnerability. Likewise, trees showed contrasting climate sensitivities, with significant changes to the climatic drivers of growth among tree groups, with the ring-width series of temporarily affected trees more likely to show a non-stable climatic signal over time. These key transitions in growth responses to climate could not be obtained from the classical stand-level analyses, but were only possible by evaluating trees individually. Detailed information on individual responses to drought stress is therefore crucial for understanding future carbon-assimilation patterns, detailed drought legacy effects, and realistic climate sensitivities of trees, especially in areas of increasing drought occurrences. Quantifying the processes that mediate the uncertainty of tree drought responses to climate will be important for modelling forest performance in a warmer and dryer future.

CRedit authorship contribution statement

Eduarne Martínez del Castillo: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Max C.A. Torbenson:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Frederick Reinig:** Writing – review & editing, Visualization, Methodology, Investigation. **Oliver Konter:** Writing – review &

editing, Resources. **Emanuele Ziaco:** Writing – review & editing. **Ulrich Büntgen:** Writing – review & editing. **Jan Esper:** Writing – review & editing, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The author declares no conflict of interest.

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.2024.174370>.

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