RESEARCH ARTICLE

Higher growth synchrony and climate change-sensitivity in European beech and silver linden than in temperate oaks

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Abstract

Aim: Climatic changes affect the growth dynamics of temperate trees, but these effects might differ between co-occurring ring- and diffuse-porous species as well as between mesic and xeric rear-edge populations. We explore whether recent climate warming has increased the climate sensitivity and within-stand synchrony of growth in these groups differently.

Location: The natural beech–oak ecotone in Western Romania at the dry margin of beech occurrence.

Taxa: Three ring-porous oak species (*Quercus petraea*, *Q. frainetto* and *Q. cerris)*, and diffuse-porous European beech (*Fagus sylvatica*) and silver linden (*Tilia tomentosa*).

Methods: We correlated tree-ring records with monthly and seasonal climate data (period 1940–2017). Regional growth synchrony was assessed through the analysis of inter-series correlation of growth within populations and among populations using mixed models.

Results: In all five species including two south-east European oak taxa and silver linden, water availability in summer was the most important climatic determinant of radial growth. This factor has gained in importance since the onset of rapid warming after 1980, while the impact of other climate factors in spring and summer has decreased. Within-population growth synchrony as a measure of overall climatic stress has increased, or remained stable, since 1980 in beech and silver linden, but has decreased in the oak species, matching declining growth trends in beech and linden and increasing (or stable) trends in the oaks.

Main Conclusions: The patterns of growth synchrony provide valuable information on tree species' drought susceptibility in efforts to select suitable tree species for climate change-adapted forestry. The climate vulnerability of beech is higher than that of the more drought-resistant oak species due to its marked summer-drought sensitivity of growth.

KEYWORDS
climate warming, climate–growth relationship, dendrochronology, drought, *Quercus cerris*, *Quercus frainetto*, *Quercus petraea*, radial growth, Romania, tree rings

1 | INTRODUCTION

Widespread occurrence of pre-senescent leaf fall, crown dieback and increased tree mortality have hit Central European forests during the extreme hot droughts of 2003, 2015 and 2018–2020, when heat, a high evaporative demand of the atmosphere and long rainless periods harmed especially fast-growing conifers such as Norway spruce, but hit also broadleaf trees like European beech (*Fagus sylvatica* L.) (Allen et al., 2015; Schuldt et al., 2020; Senf et al., 2020). It is almost certain that sensitive timber species will not maintain their productivity during the predicted warming trend until the end of the century and beyond, but our capacity to predict physiological stress responses of temperate forest trees is limited and knowledge of tree species' drought tolerance limits is still poor. The predicted annual temperature increase in Central Europe (Lee et al., 2021) is likely to shift the natural distribution limit of many tree species polewards and upwards to regions with cooler temperatures and higher precipitation (Lenoir et al., 2008; Sykes et al., 1996). For example, climate envelope models predict for the warmer and drier lowlands and lower montane belts of Central Europe a shift from beech-dominated forests to more drought-tolerant, thermophilic forest communities in the course of the 21st century (Fischer et al., 2019; Kramer et al., 2010).

The centre of the distribution range of European beech is located in central and southern Germany (Figure S1.1 in Appendix S1), where the species naturally would cover more than 2/3 of the area and is occurring from the lowlands to the montane belt in the mountains (Leuschner & Ellenberg, 2017). Toward southern and south-eastern Europe, hotter summers and higher climatic aridity are shifting the occurrence of beech forests toward higher elevations with cooler and moister climates (Czúcz et al., 2011; Fang & Lechowicz, 2006). In the mountains of south-eastern and southern Europe, beech forests at montane or lower montane elevation usually give way to oak-dominated forest communities at lower elevations, which are linked through a beech–oak ecotone with a mixture of these species (Horvat et al., 1975; Mayer, 1984). Various thermophilic deciduous oak species replace beech at its hot and dry distribution limit, in south-eastern Europe mainly *Quercus cerris* Liebl., *Q. frainetto* Ten., *Q. pubescens* L., and various taxa in the species aggregate of *Q. petraea* (Matt.) L. (Figure S1.1 in Appendix S1). They are accompanied by other broadleaf species with assumed higher drought tolerance such as *Carpinus betulus* L. and *C. orientalis* L., *Tilia cordata* L. and *T. tomentosa* Moench., and *Acer tataricum* L. At its south-eastern and southern distribution limit, beech often only persists in small refugia as in deep valleys or on north-exposed slopes with more humid local climate (Coldea et al., 2015; Hohnwald et al., 2020; Indreica et al., 2017). These rear-edge populations are well suited for analysing the adaptive capacity and growth response to climatic changes of beech in comparison to other more drought-tolerant species.

Beech is known to be more drought-sensitive than many co-occurring broadleaf tree species in Central Europe and it suffers from increasing climatic aridity in the course of climate warming especially at the species' drought- and heat-induced range limits (Brinkmann et al., 2016; Leuschner, 2020; Zang et al., 2014). This is visible in vitality losses at lower elevations, while vitality often increases at higher elevations (Dulamsuren et al., 2017; Kasper et al., 2022; Serra-Maluquer et al., 2019), and the distribution range may shift gradually in northern and upward direction (Peñuelas et al., 2008). Yet, some studies detected no differences in climate sensitivity of growth between dry marginal and more humid beech populations, which may highlight the species' potential for drought adaptation in dry-marginal populations (Hacket-Pain et al., 2016; Muffler et al., 2020; Tegel et al., 2014).

Dendrochronological and physiological evidence demonstrates that European temperate and submediterranean deciduous oak species are more drought-resistant than beech (Friedrichs et al., 2009; Härdtle et al., 2013; Kasper et al., 2022; Scharnweber et al., 2011) and several other broadleaf species such as linden and hornbeam (Fuchs et al., 2021; Köcher et al., 2009; Leuschner, 2020; Zang et al., 2014; Zimmermann et al., 2015). However, most comparative studies cover considerable differences in site conditions, but neglect potential shifts in climate sensitivity over time, in particular possible sensitivity changes after the onset of the rapid warming since the 1980s.

As a consequence of deteriorating climatic growing conditions, trees may show increasingly synchronous radial growth responses to environmental stress (Shestakova et al., 2016, 2018; Tejedor et al., 2020). Synchrony here stands for a common temporal variation in a trait among the individuals of a population, or among different species in an ecosystem, which may have implications for ecosystem functioning and stability (Schurman et al., 2019; Shestakova et al., 2016). To quantify the common stress response, we follow the approach of Tejedor et al. (2020) and use the so-called rbar statistic, which is per definition "the common inter-annual variability in tree growth within a defined group", to characterize tree growth synchrony (del Río et al., 2021). Growth synchrony can be assessed spatially by depicting regional to global similarities in growth variation, or temporarily by analysing the response to environmental changes over time. Furthermore, growth synchrony can be investigated at different taxonomical levels, that is, within populations of the same species or between species (Tejedor et al., 2020). In climate change research, high growth synchrony across populations or across species has been interpreted as an indicator of higher drought susceptibility, whereas lower synchrony was assessed as an indication of higher response diversity (Anderegg & HilleRisLambers, 2019; Camarero et al., 2015; Pretzsch et al., 2020; Shestakova et al., 2016). A number of studies have reported climate warming-related increases in growth synchrony during the last century, suggesting a causal link to climate change (del Río et al., 2021; Muffler et al., 2020; Shestakova et al., 2016).

In this study, we investigate the climate sensitivity of radial growth and within-population growth synchrony in five co-existing temperate broadleaf tree species, European beech (*F. sylvatica*), hereafter referred to as beech, silver linden (*T. tomentosa*; hereafter linden), and three central to south-east European deciduous oak species (*Q. petraea*, *Q. cerris* and *Q. frainetto*) in western Romania. In this region, the climate conditions are similar to the predicted conditions in the centre of the beech distribution range at the end of the century (Hohnwald et al., 2020;

Kasper et al., 2021). For establishing replicates at the landscape scale, we studied three transects across different forest communities with sufficient comparability in terms of thermal and hygric conditions, exposition, bedrock type, tree species composition and management history (Kasper et al., 2021, 2022; Öder et al., 2021). We analyse correlations between tree growth and climatic factors in the time interval 1940–2016 and split it into the two periods before the pronounced recent temperature increase from ca. 1980 onwards and thereafter. We compare the ring-porous oak species with diffuse-porous beech and silver linden, and further contrast the growth responses of mesic beech stands in a more subhumid climate with xeric beech stands, that is rear-edge populations surviving in local humid refugia beyond the drought and heat limit of beech. By selecting western Romania with an about 2.5 K higher annual mean temperature than in central Germany today, this study offers insights into potential responses of beech forests in the species' distribution centre under the Representative Concentration Pathway (RCP) warming scenarios 2.6–8.5 (Lee et al., 2021), which predict by 1.0–3.7°C warmer climates at the end of the century (Figure S1.2 in Appendix S1).
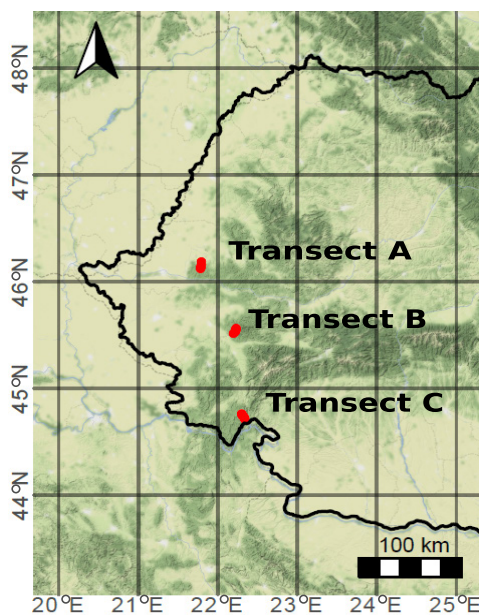
The following questions guided our research: (1) How do beech, silver linden and the three oak species differ in their climate sensitivity of growth? (2) Did the climate sensitivity of the five species change from the mid-20th century to the period with pronounced warming since the 1980s? (3) Do the five species differ in their within-population growth synchrony and how did the recent warming affect synchrony? (4) Do mesic and xeric (rear-edge) beech populations differ in their climate sensitivity and synchrony of the stress response?
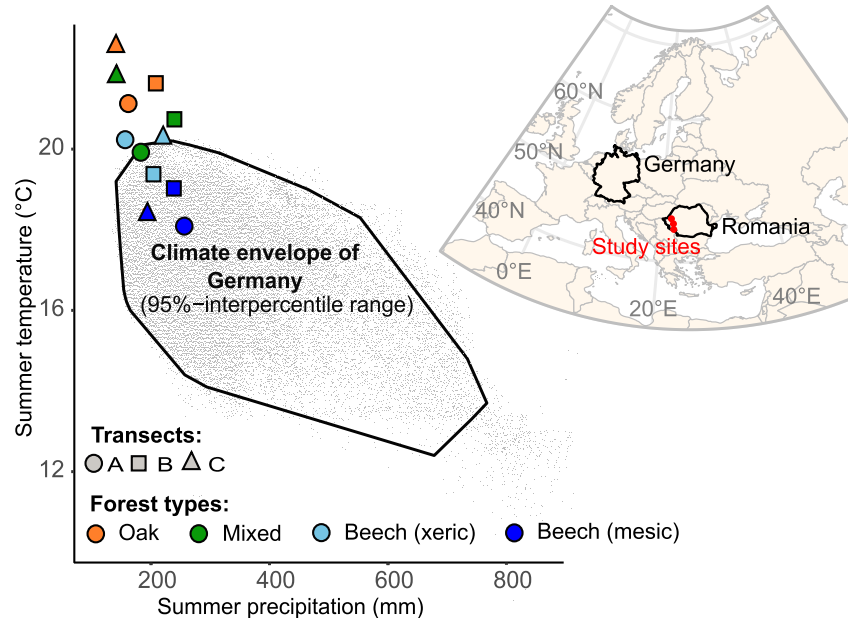
2 | MATERIALS AND METHODS

2.1 | Study region, physiography and transect selection

The study was conducted in western Romania on the foothills of the south-western Carpathians (Figure 1a). The climate is temperate sub-continental with warm summers and relatively cold winters and is considered as an analogue for the projected climate in the current centre of the distribution range of European beech in Central Germany around the 2080s. The current climate in the study region thus matches the projected climate in Germany toward the end of the 21st century, as demonstrated by plotting the current and future climates of European regions in an ordination space defined by winter cold, summer warmth and growing season precipitation (Figure S1.2 in Appendix S1, following Kölling & Zimmermann, 2014). Pronounced warming took place at all sites since about 1980, while mean summer precipitation (MSP) has fluctuated in the past decades without a clear trend (Figure S1.3 in Appendix S1). The climatic water balance in summer (precipitation – potential evapotranspiration) has decreased markedly since about 1980 at all sites (Figure S1.4 in Appendix S1; Kasper et al., 2022). Three elevation gradients in downhill direction from submontane/montane to colline elevation were established (Transects A, B and C, Figure 1b, Kasper et al., 2022), which sequentially cover humid beech-dominated forests at >500 m a.s.l., the humid-subhumid ecotone of mixed beech–hornbeam–oak forests at 350–600 m a.s.l.,

(a) Transects A-C in Western Romania

(b) Climate in forest types (transects A-C) vs. current climate in Germany

Transect A
Transect B
Transect C

100 km

Summer temperature (°C)

Climate envelope of Germany
(95%–interpercentile range)

Germany
Romania
Study sites

Summer precipitation (mm)

Transects:
○ A ☐ B △ C

Forest types:
● Oak ● Mixed ● Beech (xeric) ● Beech (mesic)

FIGURE 1 (a) Location of the study transects in the western Romanian Carpathians. (b) Summer climate conditions (June–August CHELSA gridded climate data, Karger et al., 2017, average of 1940–2016) in the study transects in comparison to the centre of beech distribution in Germany. Climate data were extracted for the mean locations of *F. sylvatica* forests in the mesic beech zone (elevation >550 m), "rear-edge" stands of *F. sylvatica* in the low-elevation xeric beech zone (elevation <400 m), *Q. petraea* and *T. tomentosa* in the ecotones (600 m > elevation >350 m) and *Q. cerris* and *Q. frainetto* in the thermophilic oak zone (elevation <350 m). Local maps are in Mercator projection, the map inset of Europe in azimuthal equal-area projection centred on the North Pole (South, 2011).

and finally the basal subhumid thermophilic oak-dominated forests at <350 m a.s.l., predominantly on south-west- to south-east-facing slopes (Hohnwald et al., 2020; Indreica et al., 2017; Kasper et al., 2021).

The dominant soils on base-poor bedrock are acidic but eutric Cambisols in all studied forests. The soil is covered at many places by an up to 100 cm thick loess layer (Kasper et al., 2021). All selected stands had roughly similar stem densities and thus comparable competition intensities, were of mature age (>60 years old), 21–33 m in height and had a closed canopy (Table S1.2 in Appendix S1 and Kasper et al., 2022). While subjected to occasional wood-cutting and low-intensity coppicing in the years before 1960, the forests were afterwards transferred to state-ownership. Previously coppiced stands were allowed to grow into high forests (Öder et al., 2021), and stands were lightly thinned (5%–15% of stand volume) from the pole-wood stage onwards until three quarters of the time till harvest had passed (Ashton & Kelty, 2018). Irregular salvage and sanitary loggings have been conducted at low intensity (removal of <5% of stand volume). No major harvest operations have occurred in the stands in the last 20 years (Öder et al., 2021).

All three transects were established on predominantly south-west- to south-east-facing slopes. *F. sylvatica* contributed with at least 85% to total stem numbers in the beech forests, while the thermophilic oak forests were dominated by the three oak species *Q. petraea*, *Q. cerris*, and *Q. frainetto*, which contributed >85% of the stem numbers (Table S1.2 in Appendix S1). The remaining stems were contributed by accompanying species such as *Tilia tomentosa*, *Carpinus betulus*, and *Acer campestre* L. In the ecotone, subhumid mixed beech-oak and hornbeam forests were present, with the oak species and beech each contributing with about 30% to total basal area (except for transect B) and the remaining stems mostly belonging to *T. tomentosa* and *Carpinus* species (Kasper et al., 2021, 2022).

2.2 | Species selection and wood core sampling

Five focal species were selected. *F. sylvatica* as the dominant species of the humid beech forests (mesic beech), *Q. petraea*, *Q. frainetto* and *Q. cerris* as dominants of the thermophilic submediterranean, xeric oak forests (oak), and again *Q. petraea* with *T. tomentosa* as co-occurring species in the subhumid mixed beech-oak-hornbeam forests that form the beech–oak ecotone (Figure 1b and Table S1.2 in Appendix S1). In addition, north-facing *F. sylvatica* stands were sampled in extra-zonal beech forests at colline elevation (<400 m a.s.l.; xeric beech) in close proximity to the basal thermophilic oak forest belt.

The wood core sampling in summer 2018 and 2019 resulted in 92 to 153 cores per tree species or forest type (beech mesic vs. xeric). We sampled in most cases dominant individuals of the upper canopy layer with DBH >40 cm (Table S1.2 in Appendix S1). The sample trees lacked signs of pre-senescent leaf abscission, canopy dieback, or other damage. Tree cores were extracted at breast height (1.3 m) with an increment borer (Haglöf) in the direction of least tension

wood, that is, perpendicular to any potential tilting direction. Cores with rotten segments were excluded from further analysis. As tree cores were sampled after the beginning of the growing season, the last incomplete annual ring was omitted in the analysis; hence, tree-ring series collectively ended in 2017. For assessing individual tree competition intensity, the Hegyi competition index (CI) was calculated (Hegyi, 1974) and tree age was approximated by counting the number of tree rings.

2.3 | Tree-ring data and climate sensitivity analysis

We cross-dated all tree-ring series (TRW, tree-ring width in mm) by relying on the coefficient of agreement ("Gleichläufigkeit" GLK; Eckstein & Bauch, 1969), the cross-dating index (CDI; Dobbertin & Grissino-Mayer, 2004) and Student's *t*-value (TVBP; Baillie & Pilcher, 1973). All ring series contributing to the chronologies had a GLK >65%, a CDI >2.0, and a TVBP >3.0 (Table S1.2 in Appendix S1). To obtain the detrended dimensionless ring width index (RWI), the individual TRW series were divided by the derived 30-year moving-average spline with frequency cut-off at 50%, with the first-order autoregression removed subsequently (pre-whitening). Master chronologies were calculated for each site and population as the mean value sample (Tukey's bi-weight robust mean) of individual tree-ring series (RWI) (Figure S1.5 in Appendix S1). As a quality indicator for these chronologies, we considered an expressed population signal (EPS) >0.85, which is an indicator of high growth coherence among neighbouring trees (Wigley et al., 1984). Sample sizes were considered sufficient for the period 1940–2017 (except for *T. tomentosa* in transect B: 1950–2017) for analysing climate sensitivity and growth synchrony.

Monthly and seasonal (winter: previous December–current February; spring: March–May; summer: June–August; autumn: September–November) temperature and precipitation time series of the period 1940–2016 for the studied forest stands were computed from high-resolution gridded climate data (30 arcsec, ~1 km²) that were downloaded from the CHELSA (CHELSAcruts) climate database (Karger et al., 2017). To investigate the effect of droughts, we calculated the Standardized Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) for 3-month time intervals at monthly and seasonal scales. Climate data were compiled for each individual tree before being averaged to population or transect means.

The effect of climate variables on annual radial increment (climate sensitivity) was assessed by correlating RWI chronologies with mean monthly temperature, the monthly precipitation sums, and drought exposure (3-month SPEI value), spanning the meteorological conditions from previous year's June to current year's September. This was done for the common observation period (1940–2016) and separately for the periods before (1940–1979; earlier period) and after the onset of the recent warming trend (1980–2016; later period) (Figure S1.3 in Appendix S1). We assessed the statistical significance at $p \leq 0.05$ in all analyses using a 1000-fold bootstrapping procedure in the R-package 'treeclim' v2.0.5.1 (Zang & Biondi, 2015).

2.4 | Growth synchrony

Synchronous inter-annual variability in tree-ring series is usually estimated through the mean inter-series correlation (rbar; 0: no synchrony to 1: totally synchronized growth dynamics) value, which is the average Pearson correlation among all tree-ring series within a given chronology (Wigley et al., 1984). We calculated running synchrony values (rbar) in a 20-year moving window using the R package 'dplR' v1.7.1 (Bunn, 2008). Significance of trends during the observation period was assessed using the Mann–Kendall trend test.

When computing synchrony values among different populations of a species, the associated random error structure, which may change over time, must be carefully selected. We followed the approach of Shestakova et al. (2016, 2018), using a mixed model approach ('DendroSync' v0.1.3 R package; Alday et al., 2018) to analyse spatial patterns of radial growth (RWI) synchrony in tree-ring networks at species level (and for beech mesic vs. xeric). First, mixed models allowing for different variance–covariance (VCOV) structures among grouping variables (homoscedastic vs. heteroscedastic versions) were estimated to select the best VCOV structure based on Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) (Burnham & Anderson, 2004). Species synchronicities were then estimated from the VCOV models, where synchrony values again range from 0 (no regional synchronization across populations) to 1 (total regional synchronization) (Alday et al., 2018; Shestakova et al., 2018). We also calculated moving averages in a 30-year window with individual fitting of the best VCOV model in lag periods of 5 years (del Río et al., 2021; Shestakova et al., 2016), where for each 5-year period the best VCOV model was selected following the above-mentioned criteria.

Means (±SD) are presented throughout the paper and differences between means depicted in the graphs and tables were tested for statistical significance with a Wilcoxon Rank test and with a t-test in case of pairwise comparisons. All statistical procedures were performed in R v4.0.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Climate sensitivity

Radial growth was limited by high summer temperatures in most species and transects (and additionally by high spring temperatures in transect A), while we found no hints on low-temperature limitation in winter and autumn (Figure 2; similar patterns are visible in Figure S1.6 in Appendix S1 which were derived from correlations with monthly climate data). Interestingly, negative temperature-growth correlations were generally weaker in the driest transect C (Figure 2). High summer precipitation enhances growth in all stands (except for Q. petraea in transect A and Q. frainetto in transect C), while spring precipitation was only sporadically influential (Q. frainetto (A and B), Q. cerris (A), T. tomentosa (A and B), and F. sylvatica xeric (A)), and winter and autumn precipitation variability had no effect (Figure 2). Previous year's summer

precipitation seemed to be less important for the three oak species than for F. sylvatica and T. tomentosa, especially in the driest transect C (Figure S1.6 in Appendix S1). Local variability in summer water availability (SPEI 3-months aggregation period) was the most limiting climate factor for stem growth in all species and all transects (except for Q. petraea in transect A), while spring SPEI was influential only in Q. cerris (transect A) and Q. frainetto (transects A and B), and autumn SPEI was only influential in F. sylvatica (transect B), Q. cerris (transect C) and Q. frainetto (transect B) (Figure 2). Previous year's SPEI of the summer months was not influential in Q. petraea, while it influenced Q. cerris and Q. frainetto and, in particular, F. sylvatica and T. tomentosa (Figure S1.6 in Appendix S1).

After the onset of recent warming at around 1980, most species (except for Q. frainetto in transects A and B) showed a weakening of the summer high-temperature signal (Figure 3). All species became more sensitive to higher summer precipitation with notable exceptions in the driest transect C, where the influence of summer precipitation declined in Q. cerris, Q. frainetto, and the xeric F. sylvatica stands (Figure 3; Figure S1.7 in Appendix S1). There was no consistent decline or increase of the summer SPEI signal across species and transects, whereas the influence of climate conditions in spring declined especially in beech and linden (Figure 3). Differences also existed between transects, with an overall increase of the influence of summer precipitation toward the later period in the moister transects A and B, but no consistent change over time in the driest transect C, and a reduced negative influence of summer temperature in the driest transect C, but less so in the moister transects A and B (Figure S1.7).

3.2 | Within-population growth synchrony

Growth synchrony (rbar) among the trees of a stand was in most species lowest in the moistest transect B. Overall, highest synchrony was recorded for Q. cerris and Q. petraea in the moderately moist transect A, while lowest rbar values were found for Q. petraea in the moistest transect B (Figure 4a). Compared to the other species, F. sylvatica was characterized by medium rbar values at both the mesic and xeric sites. The five species also differed in their synchrony change from the earlier to the later period (Figure 4b). Synchrony of F. sylvatica increased in transect A (mesic and xeric) and C (xeric) and declined for T. tomentosa in transect B (Figure 4b). All three oak species showed large declines in growth synchrony toward the later period in transects A and C; the synchrony of Q. cerris declined also in transect B (Figure 4b).

Within-stand synchrony (rbar) significantly increased for F. sylvatica in all transects (except transect B for xeric beech) and for T. tomentosa in transect A and C in the long term, which was linearly related to long-term increases in mean summer temperature (Figure 5). In both species, synchrony dropped temporarily in the 1970s, which coincided with temporarily high summer precipitation. When precipitation decreased again in the early 1980s (Figure S1.3), synchrony continuously increased (Figure 5). Both Q. frainetto and Q. petraea showed a significant synchrony decline in the drier transects A and C, and an increase in the moistest transect B. For Q. cerris, a significant decrease of growth synchrony was only observed in transect A (Figure 5). In
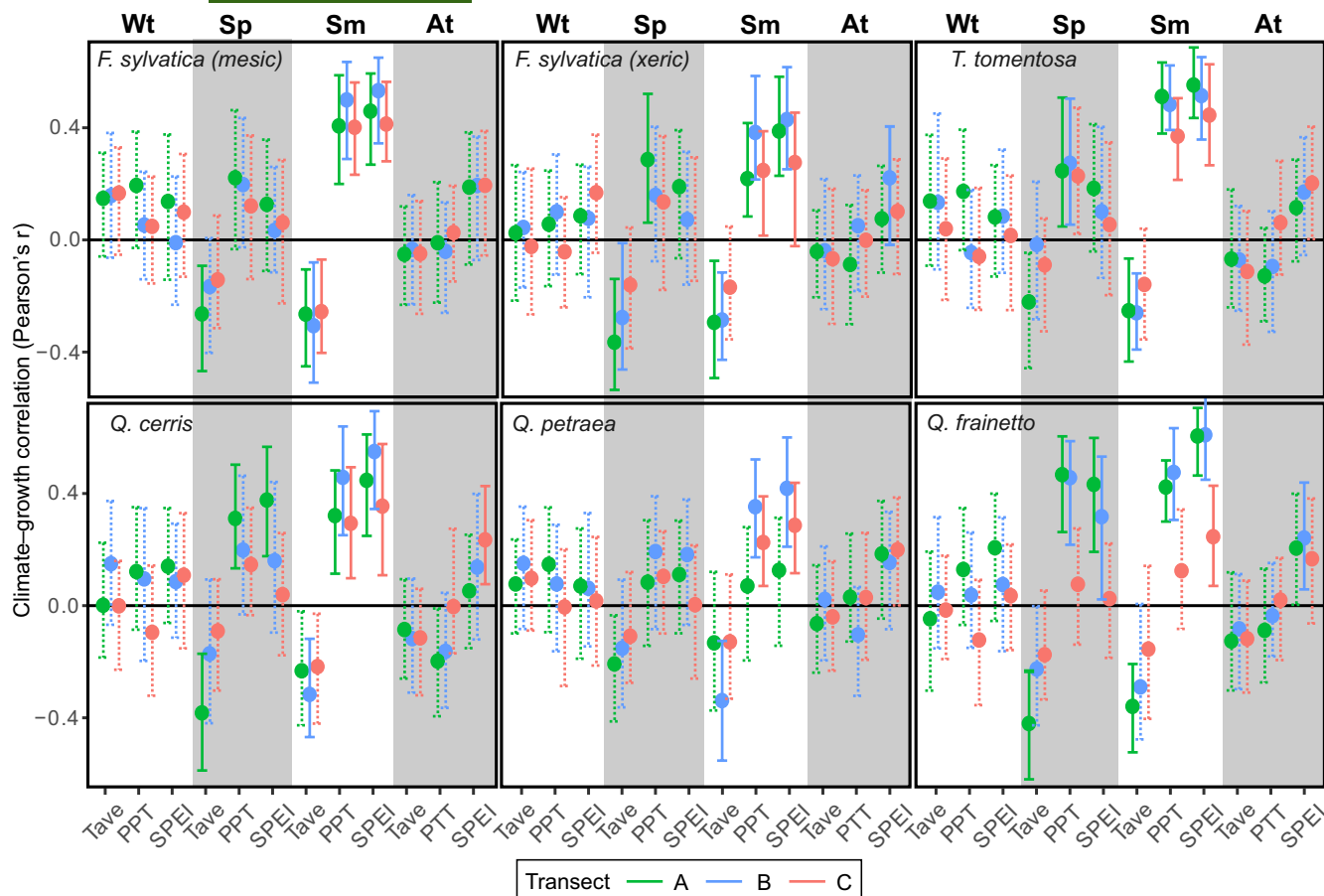
FIGURE 2 Climate–growth relationships (Pearson's r on the y-axis) for the correlation of tree-ring index chronologies with winter (Wt: Previous December–February), spring (Sp: March–May), summer (Sm: Jun–Aug) and autumn (At: September–November) averages/sums of climate variables (Tave – Average temperature, PPT – Precipitation sum, SPEI – Average Standardized Precipitation–Evapotranspiration Index) for the period 1940–2016 at the study transects A–C in the western Romanian Carpathians. Significant correlations are shown through solid whiskers for the 2.5% and 97.5% empirical 1000-fold bootstrapped confidence interval.

contrast to beech and silver linden, the synchrony within the oak populations of the two driest transects (A and C) was inversely related to mean summer temperature during the last decades (Figure 5).

### 3.3 | Between-species growth synchrony and temporal trends

The best variance–covariance (VCOV) models for assessing growth synchrony among the five species were homoscedastic unstructured models (mUN) that allowed for heterogeneous variances and co-variances. The obtained results were similar for RWI data with and without pre-whitening (Table S1.4 in Appendix S1), showing lower growth synchronicities in the *Quercus* species as compared to *F. sylvatica* (mesic and xeric) and *T. tomentosa* (Figure S1.8 in Appendix S1). Split into two periods (before and after the temperature increase), the results of the best VCOV models (Table S1.4 in Appendix S1) show a synchrony increase for *F. sylvatica* (mesic and xeric) and *T. tomentosa* in comparison to decreases in the *Quercus* species (Figure S1.8c in Appendix S1), again with similar results for non-pre-whitened RWI data (Figure S1.9a in Appendix S1). The best VCOV models for assessing temporal synchrony

trends for pre-whitened RWI data until 1975 were broad evaluation models (mBE), suggesting homogenous growth responses among the species (Figure 6b; Table S1.5 in Appendix S1). After 1975, homoscedastic unstructured models (mUN) showed the best fit, with bifurcations in synchrony patterns for each species. Following the VCOV models, synchrony then increases for *F. sylvatica* (mesic and xeric) and *T. tomentosa*, whereas it remains stable or decreases for the *Quercus* species (Figure 6b) with again similar results for non-pre-whitened RWI values (Figure S1.9b and Table S1.5 in Appendix S1).

4 | DISCUSSION

### 4.1 | Climatic drivers of radial growth in the five species

In agreement with our results from the beech–oak ecotone in Romania, low summer water availability and high summer temperatures have been identified as limiting factors for temperate Central and Southern European beech and oak forests in numerous other studies (Bose et al., 2021; Bosela et al., 2018; Fuchs
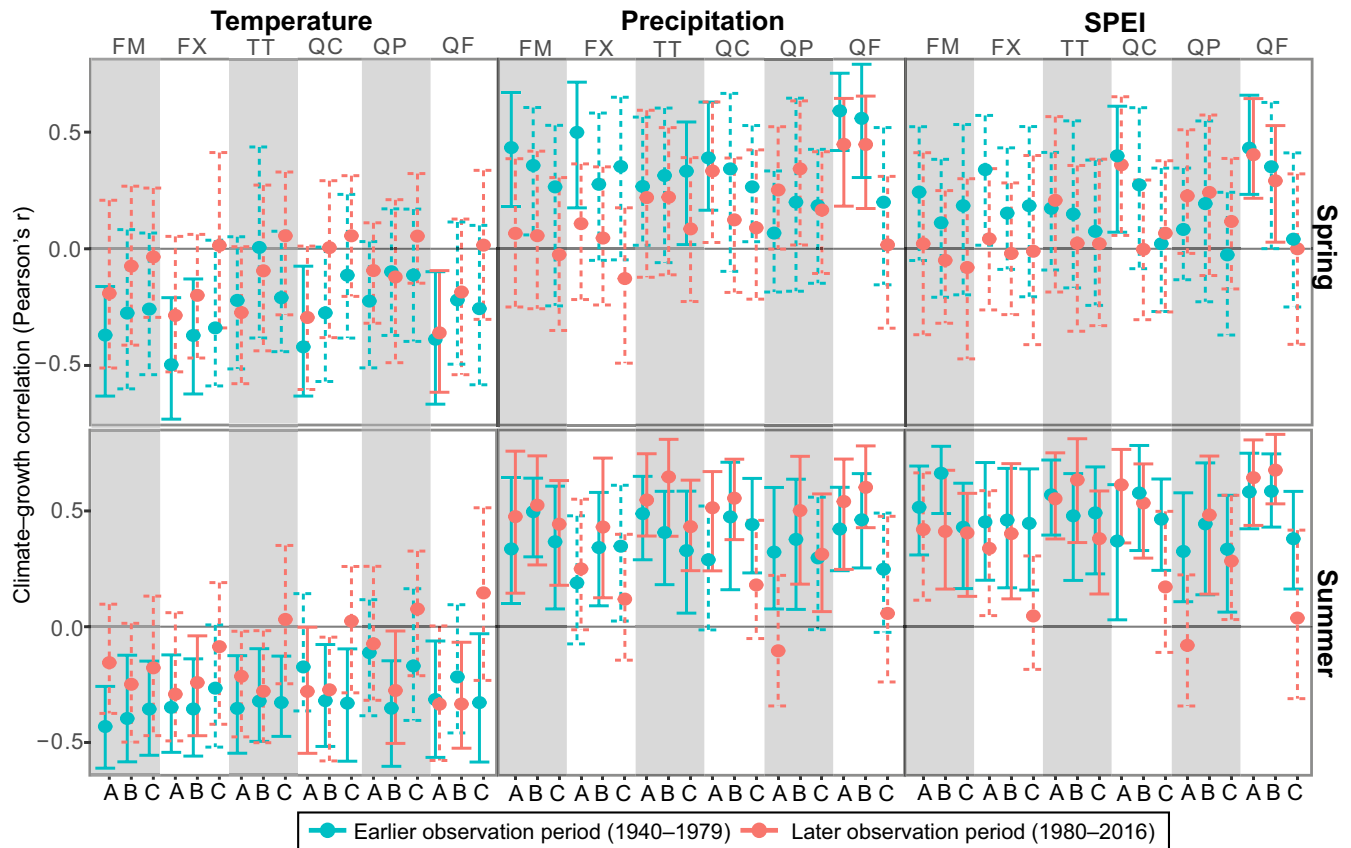
FIGURE 3 Shift of climate–growth correlations (Pearson's r on the y-axis) with spring (March–May) and summer (June–August) averages (temperature and SPEI) or sums (precipitation) of climate variables between the earlier observation period (1940–1979) and the recent climate warming (later) period (1980–2016). Significant correlations are shown through solid whiskers for the 2.5% and 97.5% empirical 1000-fold bootstrapped confidence interval. Species are abbreviated as: FM, *F. sylvatica* (mesic); FX, *F. sylvatica* (xeric); QC, *Q. cerris*; QF, *Q. frainetto*; QP, *Q. petraea*; TT, *T. tomentosa* at the study transects A–C in the western Romanian Carpathians. SPEI is the Standardized Precipitation–Evapotranspiration Index.
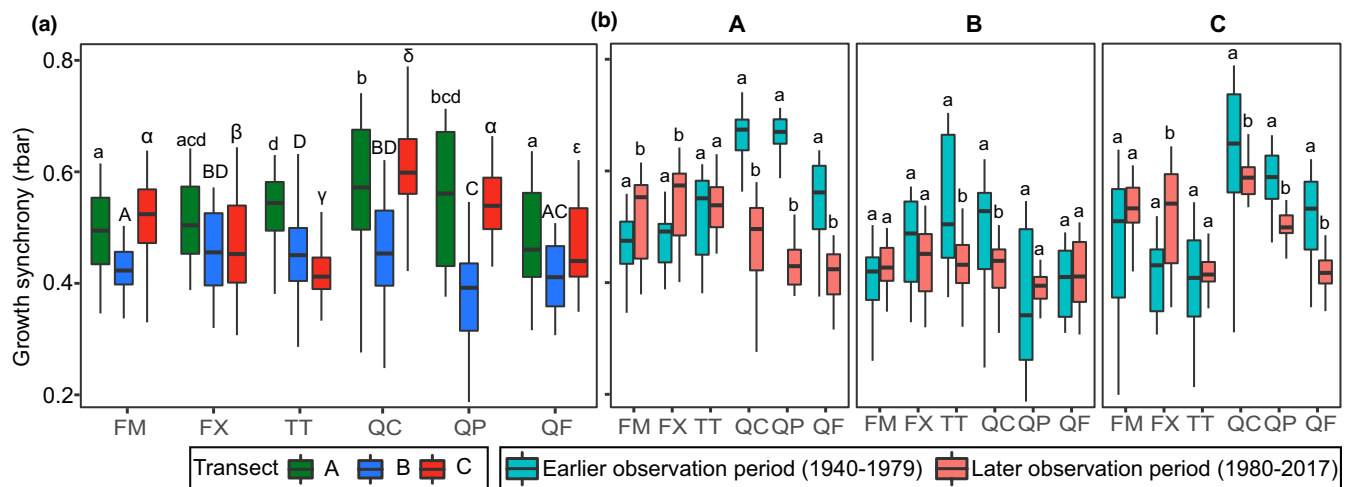
FIGURE 4 (a) Growth synchrony ("rbar": The mean correlation between all tree-ring index series in a chronology) for the five species (and two site types for beech) for the period 1940–2017 in the three transects in the western Romanian Carpathians. For each transect, significant differences between the species (and two site types for beech) are marked with different lowercase letters (transect A), uppercase letters (transect B), and Greek letters (transect C). (b) Growth synchrony (rbar) of the five species in the three transects in the earlier observation period before the onset of warming (1940–1979, light blue) and in the later period (1980–2017, red) during warming. Significant changes between the two periods are marked with different lowercase letters. Species are abbreviated as: FM, *F. sylvatica* (mesic); FX, *F. sylvatica* (xeric); QC, *Q. cerris*; QF, *Q. frainetto*; QP, *Q. petraea*; TT, *T. tomentosa*. Whiskers extend over the 5–95% confidence intervals.
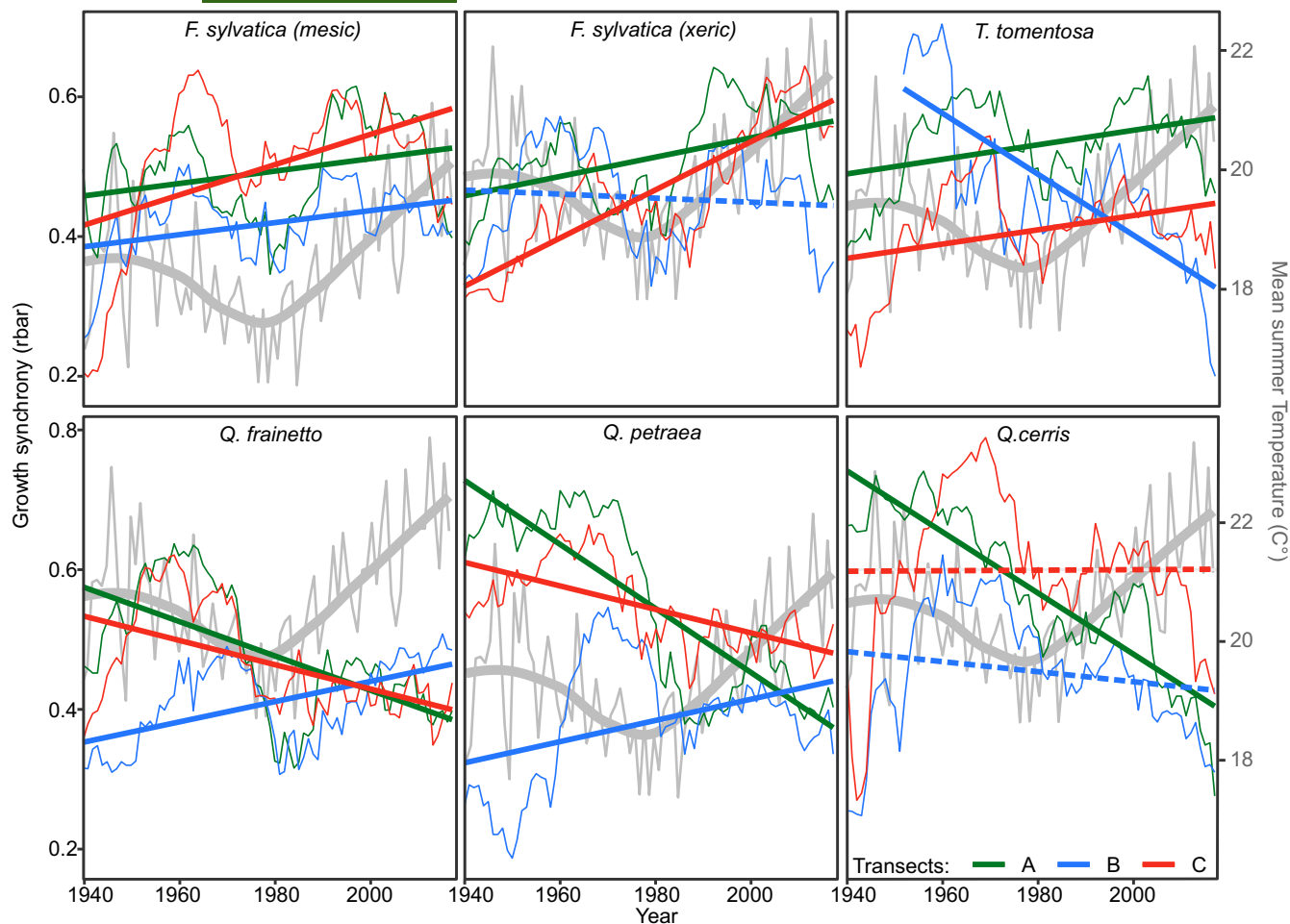
FIGURE 5 Change in growth synchrony ("rbar": The mean correlation between all tree-ring index series in a chronology) in the five species (and two site types for beech) in the three transects in the western Romanian Carpathians from 1940 to 2017 (in case of *T. tomentosa* in transect B: 1950–2017). Pooled over the three transects (A–C) per species on the second y-axis is the mean summer (June–August) temperature (raw data: Fine grey line and trends: Depicted through spline smoothing as thick grey line). Linear regression models predicting rbar depending on the calendar year were computed for every transect and species (and two site types for beech) and are depicted as solid lines, if a significant temporal trend was detected in a Mann-Kendall trend test. For detailed results of the Mann-Kendall trend tests see Table S1.3 in Appendix S1.

et al., 2021; Hacket-Pain et al., 2016). The key role for atmospheric and/or edaphic water limitation is further underpinned by the observation that the growth rates of all five species were generally lower in transect C with highest stress exposure than in the other transects and the generally more productive beech and linden suffered greater growth reductions than the oak species during the extreme dry years 2000, 2003 and 2012 (Kasper et al., 2022). In our study, the strong influence of local variability of the climatic water balance (SPEI) suggests that primarily atmospheric vapour pressure deficit (for which long-term stand-level data are missing), together with soil water availability during summer is controlling growth instead of temperature and precipitation alone (Fuchs et al., 2021; Kasper et al., 2022; Scharnweber et al., 2011). Physiological mechanisms leading to reduced stem growth during dry summers may include lowered carbon gain due to partial stomatal closure and turgor loss in stem cambial cells caused by

a reduction in the tree's hydraulic capacity (Bréda et al., 2006; Müller-Haubold et al., 2013; Salomón et al., 2022). Other factors leading to reduced stem growth could be enhanced C investment in the fine root system to compensate for increased root mortality during drought, as well as the formation of thicker pit membranes and a reduction of xylem conduit cross-sectional area to enhance hydraulic safety at the cost of hydraulic efficiency (Fonti et al., 2013; Fuchs et al., 2020; Hertel & Leuschner, 2002). Thus, smaller annual growth rings to increase hydraulic safety might alternatively be interpreted as an acclimation to drought rather than a response to drought-impairment of the tree's carbon and water relations (Bréda et al., 2006; Gessler et al., 2020; Lloret et al., 2011). Physiological measurements on hydraulic safety margins and the C and water balance of the trees would be needed to separate between active (adaptive) and passive (drought impairment) responses to water deficits.
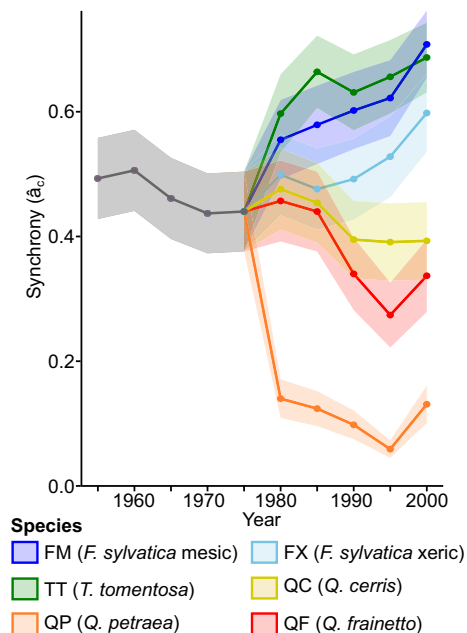
FIGURE 6 Temporal trends of synchrony estimates ("$\hat{a}_c$" ranging from 0 (no regional synchronization) to 1 (total regional synchronization) calculated with a mixed model approach, Alday et al., 2018) for the five species (and two site types of *F. sylvatica*) in the western Romanian Carpathians for pre-whitened ring-width index (RWI) chronologies calculated with the best-fit variance–covariance model for 30 year-wide moving intervals by 5-year steps over the period 1940–2017. The x-axis shows the central year of the moving time interval. Shadows are 1 standard error (SE).

The ring-porous oaks complete most of their radial growth during a short period during or after leaf-out, when large vessels are formed that allow high photosynthetic rates, while stored carbohydrates seem to play a smaller role than in diffuse-porous beech and linden (Di Filippo et al., 2007; Fuchs et al., 2021; Lebourgeois et al., 2005; Müller-Haubold et al., 2013). In accordance, our data show not only a minor influence of previous year's weather on the growth of oaks (all three species in transect C, and *Q. petraea* in all transects) but also support the evidence of a generally lower climate susceptibility of oak growth (Friedrichs et al., 2009; Mérian et al., 2011; Scharnweber et al., 2011). This is visible both in a higher drought resistance of oak radial growth to individual drought events and in a higher resilience to recover to pre-drought growth levels in comparison to beech and linden, as detected earlier in our stands (Kasper et al., 2022). Furthermore, *Q. petraea* seems to maintain a smaller fine root system than the other species and its fine roots apparently are less drought-sensitive (Fuchs et al., 2020; Hertel & Leuschner, 2002). Temporal shifts in the carbohydrate allocation to the root system might therefore be less important for *Q. petraea* than for the studied diffuse-porous species.

Drought stress in spring has been identified as the main climatic factor constraining the radial growth of temperate oaks due to their early onset of wood formation during bud burst in contrast

to the diffuse-porous species, which have a later onset of growth (Barbaroux & Bréda, 2002; Bose et al., 2021; Fuchs et al., 2021). In our study region with hot and dry summers, however, summer drought was in most cases at least equally, or even more, important for oak radial growth than spring water availability, suggesting that this picture may need adjustment in continental climates.

4.2 | Temporal changes in climate sensitivity

Our results demonstrate a marked decadal shift in the climate sensitivity of growth, confirming non-stationarity of climate responses as discussed by Wilmking et al. (2020). This bases on the observation of D'Arrigo et al. (2008) that high-latitude forests lose track of their temperature signal, because climate factors other than low temperatures have recently become more growth-limiting. In our study in the southeast European beech–oak ecotone, non-stationarity in climate-growth relationships was detected, although summer heat and drought, and not low temperatures, are the main growth-limiting climatic factors. Surprisingly, the summer heat limitation of tree growth weakened in the observation period in this region especially in beech and linden, despite a rising evaporative demand of the atmosphere with climate warming, in a similar manner as has been observed in some Central and Western European forests during the last decades (Fuchs et al., 2021; Mérian et al., 2011). Instead, summer water deficit and summer precipitation became more important growth-controlling factors over time especially in the diffuse-porous species, as has been observed in other studies on beech and also oak species at their dry limits (Bosela et al., 2018; Friedrichs et al., 2009; Roibu et al., 2020). Probably as a consequence of increasing limitation by summer water deficits, the influence of spring weather on growth has decreased. It appears that non-stationarity is greater in beech and linden than in the oaks, and higher sensitivity to summer water availability has partly replaced sensitivity to summer heat in the diffuse-porous species.

While tree age is known to affect climate-growth relationships, climate sensitivity of growth should rather stabilize when trees reach maturity (Carrer & Urbinati, 2004; Konter et al., 2016). Tree size may also affect climate sensitivity (Trouillier et al., 2019), as trees often become more sensitive to xylem embolism when growing tall (Olson et al., 2018; Ryan et al., 2006). Changes in dominance (Mérian & Lebourgeois, 2011) or competition intensity in the stand over time might also change climate sensitivity (Piutti & Cescatti, 1997; Rozas, 2001). Although we took great care to extract all cores from dominant, vital trees of the top canopy layer (Kraft classes 1 or 2) that were exposed to similar Hegyi-competition intensities across the study plots (except for one mesic beech stand in transect C), we naturally cannot precisely conclude on the competitive pressure the sample trees were exposed to in the past.

Surprisingly, the driest transect C showed the largest share (3 of 5) of species with recently declining precipitation signal in the tree-ring series. A plausible explanation is acclimation of the local tree

populations during the last decades to increasing water deficits in an already drought-limited environment (Bréda et al., 2006; Gessler et al., 2020; Lloret et al., 2011; Muffler et al., 2020). Possible mechanisms are increasingly deeper root penetration and increases in hydraulic safety through the production of smaller xylem conduits.

4.3 | Climate warming effects on growth synchrony

In temperate and boreal forests, increased climate variability or shifts in the climate sensitivity of growth have been found to be linked to increasing synchronization of tree growth patterns, suggesting the amplification of common climatic stressors for tree growth (del Río et al., 2021; Muffler et al., 2020; Shestakova et al., 2016). This happens when climatic conditions become more stressful, local factors such as competition intensity and small-scale edaphic conditions become less influential on tree growth, and the common ring width variance due to the effect of macroclimatic drivers increases (Shestakova et al., 2016; Tejedor et al., 2020). It is highly likely that the recent temporal increase in growth synchrony of more drought-sensitive beech and linden is attributable to the species' higher vulnerability to summer water deficits, as evidenced by both their recent simultaneous increase in precipitation sensitivity and growth synchrony in contrast to the oak species in our study area. Moreover, the more pronounced growth reductions in extreme drought years of beech and linden as compared to the oak species, as found in Kasper et al. (2022), is another strong hint of the former species' greater vulnerability. Shifting phenological patterns due to climate warming likely do not explain this recent synchrony divergence, as experimental warming of beech and oak saplings led to similar phenological responses in both genera (Fu et al., 2014; Zohner et al., 2019). The most plausible explanation is a better drought adaptation of the oaks. In support of this conclusion, we observed generally positive growth trends in the three oak species, but declining trends (notably in the transects A and C) in beech and linden since the 1980s (Kasper et al., 2022).

It is reasonable to expect that growth coherence in the more drought-sensitive tree species beech and linden will further increase with increasing climate variability and drought stress in the future. Since our Romanian study area was chosen as a climate analogue site for the projected climate change during this century in the distribution centre of beech (which is located in Germany), our findings of recently increasing growth synchrony together with the evidence of lower drought resilience (Kasper et al., 2022) suggest that central beech populations will suffer in the next decades more from increasing climate stress than the ring-porous oak species. Certainly, the genetic constitution differs between central beech populations in Germany and Romanian dry-marginal populations (Magri et al., 2006), which complicates extrapolating from Romania to Germany. In any case, central beech provenances were found to be less drought-adapted than dry-marginal populations (Thiel et al., 2014), suggesting that the results from Romania should underestimate rather than

exaggerate the expected growth response to future climate change in German beech forests.

Our results further suggest that the analysis of growth synchrony may represent a better measure for comparing the climate sensitivity of tree species than the more conventional analysis of climate-growth relationships, since the former may capture the joint influence of various climatic stressors on tree growth dynamics better. In fact, climate sensitivity analysis might fail to capture climate change-related stressors due to the 'divergence problem' (D'Arrigo et al., 2008) of shifting importance between different growth-influencing climate factors.

5 | CONCLUSIONS

From the start of rapid warming since the 1980s onwards, growth synchrony in the western Romanian beech–oak ecotone has increased in beech and, to a lesser extent, in silver linden, while marked decreases were observed in the three oak species. This can be interpreted as a sign of recently increasing climatic limitation of beech and linden vitality in contrast to the less affected oak species. We conclude that the analysis of climate change impacts on temperate forest growth, which often alter climate–growth relationships, may profit from the interpretation of growth synchrony patterns, as these patterns should provide an integrative picture of long-term change in the climate sensitivity of tree growth. Our results further suggest that water deficits in summer are a main determinant of the observed changes in synchrony, as water limitation was identified as key determinant of radial growth rates. Our results of climate warming-induced impairment of tree growth in the natural beech–oak ecotone of South-eastern Europe may support predictive modelling of the fate of Central European forests under advancing climate warming. Various lines of evidence suggest that productive but vulnerable species such as beech will face increasing risks of climate warming-induced vitality loss and possible future dieback also in some regions in the range centre, while the more drought-resistant oak species will be advantaged, if drought happens in summer and not in spring. To increase climate change resilience of forests, it may be wise to favour more stress-tolerant over high-yield timber species in vulnerable regions. The three studied oak species, which produce highly valued timber, would be a promising option for the transition to climate change-adapted forests.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available under the online data repository: *Göttingen Research Online data* provide by the Georg-August-University of Goettingen: DOI: https://doi.org/10.25625/HRJTV2

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REFERENCES

Alday, J. G., Shestakova, T. A., Resco de Dios, V., & Voltas, J. (2018). DendroSync: An R package to unravel synchrony patterns in tree-ring networks. *Dendrochronologia*, *47*, 17–22. https://doi.org/10.1016/j.dendro.2017.12.003

Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*(8), 129. https://doi.org/10.1890/ES15-00203.1

Anderegg, L. D. L., & HilleRisLambers, J. (2019). Local range boundaries vs. large-scale trade-offs: Climatic and competitive constraints on tree growth. *Ecology Letters*, *22*(5), 787–796. https://doi.org/10.1111/ele.13236

Ashton, M. S., & Kelty, M. J. (2018). *The practice of silviculture: Applied forest ecology* (10th ed.). Wiley.

Baillie, M. G. L., & Pilcher, J. R. (1973). A simple crossdating program for tree-ring research. *Tree-Ring Bulletin*, *33*, 7–14.

Barbaroux, C., & Bréda, N. (2002). Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiology*, *22*, 1201–1210.

Bose, A. K., Scherrer, D., Camarero, J. J., Ziche, D., Babst, F., Bigler, C., Bolte, A., Dorado-Liñán, I., Etzold, S., Fonti, P., Forrester, D. I., Gavinet, J., Gazol, A., de Andrés, E. G., Karger, D. N., Lebourgeois, F., Lévesque, M., Martínez-Sancho, E., Menzel, A., … Rigling, A. (2021). Climate sensitivity and drought seasonality determine post-drought growth recovery of *Quercus petraea* and *Quercus robur* in Europe. *Science of the Total Environment*, *784*, 147222. https://doi.org/10.1016/j.scitotenv.2021.147222

Bosela, M., Lukac, M., Castagneri, D., Sedmák, R., Biber, P., Carrer, M., Konôpka, B., Nola, P., Nagel, T. A., Popa, I., Roibu, C. C., Svoboda, M., Trotsiuk, V., Büntgen, U., & Büntgen, U. (2018). Contrasting effects of environmental change on the radial growth of co-occurring beech and fir trees across Europe. *Science of the Total Environment*, *615*, 1460–1469. https://doi.org/10.1016/j.scitotenv.2017.09.092

Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, *63*(6), 625–644. https://doi.org/10.1051/forest:2006042

Brinkmann, N., Eugster, W., Zweifel, R., Buchmann, N., & Kahmen, A. (2016). Temperate tree species show identical response in tree water deficit but different sensitivities in sap flow to summer soil drying. *Tree Physiology*, *36*(12), 1508–1519. https://doi.org/10.1093/treephys/tpw062

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, *26*(2), 115–124. https://doi.org/10.1016/j.dendro.2008.01.002

Burnham, K. P., & Anderson, D. R. (2004). *Model selection and multimodel inference*. Springer. https://doi.org/10.1007/b97636

Camarero, J. J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., & Vicente-Serrano, S. M. (2015). To die or not to die: Early warnings of tree dieback in response to a severe drought. *Journal of Ecology*, *103*(1), 44–57. https://doi.org/10.1111/1365-2745.12295

Carrer, M., & Urbinati, C. (2004). Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology*, *85*(3), 730–740. https://doi.org/10.1890/02-0478

Coldea, G., Indreica, A., & Oprea, A. (2015). *Les associations vegetales de Roumanie. Tome 3. Les associations forestieres et arbustives*. Presa Universitara Clujeana.

Czúcz, B., Gálhidy, L., & Mátyás, C. (2011). Present and forecasted xeric climatic limits of beech and sessile oak distribution at low altitudes in Central Europe. *Annals of Forest Science*, *68*(1), 99–108. https://doi.org/10.1007/s13595-011-0011-4

D'Arrigo, R., Wilson, R., Liepert, B., & Cherubini, P. (2008). On the 'divergence problem' in northern forests: A review of the tree-ring evidence and possible causes. *Global and Planetary Change*, *60*(3–4), 289–305. https://doi.org/10.1016/j.gloplacha.2007.03.004

del Río, M., Vergarechea, M., Hilmers, T., Alday, J. G., Avdagić, A., Binderh, F., Bosela, M., Dobor, L., Forrester, D. I., Halilović, V., Ibrahimspahić, A., Klopcic, M., Lévesque, M., Nagel, T. A., Sitkova, Z., Schütze, G., Stajić, B., Stojanović, D., Uhl, E., … Pretzsch, H. (2021). Effects of elevation-dependent climate warming on intra- and inter-specific growth synchrony in mixed mountain forests. *Forest Ecology and Management*, *479*(17–22), 118587. https://doi.org/10.1016/j.foreco.2020.118587

Di Filippo, A., Biondi, F., Čufar, K., de Luis, M., Grabner, M., Maugeri, M., Presutti Saba, E., Schirone, B., & Piovesan, G. (2007). Bioclimatology of beech (*Fagus sylvatica* L.) in the eastern Alps: Spatial and altitudinal climatic signals identified through a tree-ring network. *Journal of Biogeography*, *34*(11), 1873–1892. https://doi.org/10.1111/j.1365-2699.2007.01747.x

Dobbertin, M. K., & Grissino-Mayer, H. D. (2004). The bibliography of dendrochronology and the glossary of dendrochronology: Two new online tools for tree-ring research. *Tree-Ring Research*, *60*(2), 101–104. https://doi.org/10.3959/1536-1098-60.2.101

Dulamsuren, C., Hauck, M., Kopp, G., Ruff, M., & Leuschner, C. (2017). European beech responds to climate change with growth decline at lower, and growth increase at higher elevations in the center of its distribution range (SW Germany). *Trees*, *31*(2), 673–686. https://doi.org/10.1007/s00468-016-1499-x

Eckstein, D., & Bauch, J. (1969). Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. *Forstwissenschaftliches Centralblatt*, *88*(1), 230–250. https://doi.org/10.1007/BF02741777

Fang, J., & Lechowicz, M. J. (2006). Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. *Journal of Biogeography*, *33*(10), 1804–1819. https://doi.org/10.1111/j.1365-2699.2006.01533.x

Fischer, H. S., Michler, B., & Fischer, A. (2019). High resolution predictive modelling of potential natural vegetation under recent site conditions and future climate scenarios: Case study Bavaria. *Tuexenia*, *39*, 9–40. https://doi.org/10.14471/2018.39.001

Fonti, P., Heller, O., Cherubini, P., Rigling, A., & Arend, M. (2013). Wood anatomical responses of oak saplings exposed to air warming and soil drought. *Plant Biology*, *15*, 210–219. https://doi.org/10.1111/j.1438-8677.2012.00599.x

Friedrichs, D. A., Trouet, V., Büntgen, U., Frank, D. C., Esper, J., Neuwirth, B., & Löffler, J. (2009). Species-specific climate sensitivity of tree growth in central-West Germany. *Trees*, 23(4), 729–739. https://doi.org/10.1007/s00468-009-0315-2

Fu, Y. S. H., Campioli, M., Vitasse, Y., de Boeck, H. J., van den Berge, J., AbdElgawad, H., Asard, H., Piao, S., Deckmyn, G., & Janssens, I. A. (2014). Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 111(20), 7355–7360. https://doi.org/10.1073/pnas.1321727111

Fuchs, S., Hertel, D., Schuldt, B., & Leuschner, C. (2020). Effects of summer drought on the fine root system of five broadleaf tree species along a precipitation gradient. *Forests*, 11(3), 289. https://doi.org/10.3390/f11030289

Fuchs, S., Schuldt, B., & Leuschner, C. (2021). Identification of drought-tolerant tree species through climate sensitivity analysis of radial growth in central European mixed broadleaf forests. *Forest Ecology and Management*, 494, 119287. https://doi.org/10.1016/j.foreco.2021.119287

Gessler, A., Bottero, A., Marshall, J., & Arend, M. (2020). The way back: Recovery of trees from drought and its implication for acclimation. *New Phytologist*, 228(6), 1704–1709. https://doi.org/10.1111/nph.16703

Hacket-Pain, A. J., Cavin, L., Friend, A. D., & Jump, A. S. (2016). Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. *European Journal of Forest Research*, 135(5), 897–909. https://doi.org/10.1007/s10342-016-0982-7

Härdtle, W., Niemeyer, T., Assmann, T., Aulinger, A., Fichtner, A., Lang, A., Leuschner, C., Neuwirth, B., Pfister, L., Quante, M., Ries, C., Schuldt, A., & von Oheimb, G. (2013). Climatic responses of tree-ring width and δ13C signatures of sessile oak (*Quercus petraea* Liebl.) on soils with contrasting water supply. *Plant Ecology*, 214(9), 1147–1156. https://doi.org/10.1007/s11258-013-0239-1

Hegyi, F. (1974). A simulation model for managing jack pine stands. In J. Fries (Ed.), *Growth models for tree and stand simulation* (pp. 74–90). Royal College of Forestry.

Hertel, D., & Leuschner, C. (2002). A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus-Quercus* mixed forest. *Plant and Soil*, 239(2), 237–251. https://doi.org/10.1023/A:1015030320845

Hohnwald, S., Indreica, A., Walentowski, H., & Leuschner, C. (2020). Microclimatic tipping points at the beech–oak ecotone in the western Romanian Carpathians. *Forests*, 11(9), 919. https://doi.org/10.3390/f11090919

Horvat, I., Glavač, V., & Ellenberg, H. (1975). *Vegetation Südosteuropas, Band 4 von Geobotanica selecta*. Gustav Fischer. https://doi.org/10.1007/bf02854718

Indreica, A., Turtureanu, P. D., Szabó, A., & Irimia, I. (2017). Romanian Forest database: A phytosociological archive of woody vegetation. *Phytocoenologia*, 47(4), 389–392. https://doi.org/10.1127/phyto/2017/0201

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, 4, 170122. https://doi.org/10.1038/sdata.2017.122

Kasper, J., Leuschner, C., Walentowski, H., Petritan, A. M., & Weigel, R. (2022). Winners and losers of climate warming: Declining growth in *Fagus* and *Tilia* vs. stable growth in three *Quercus* species in the natural beech–oak forest ecotone (western Romania). *Forest Ecology and Management*, 506(12), 119892. https://doi.org/10.1016/j.foreco.2021.119892

Kasper, J., Weigel, R., Walentowski, H., Gröning, A., Petritan, A. M., & Leuschner, C. (2021). Climate warming-induced replacement of mesic beech by thermophilic oak forests will reduce the carbon storage potential in aboveground biomass and soil. *Annals of Forest Science*, 78(4), 220. https://doi.org/10.1007/s13595-021-01081-0

Köcher, P., Gebauer, T., Horna, V., & Leuschner, C. (2009). Leaf water status and stem xylem flux in relation to soil drought in five temperate broad-leaved tree species with contrasting water use strategies. *Annals of Forest Science*, 66(1), 101. https://doi.org/10.1051/forest/2008076

Kölling, C., & Zimmermann, L. (2014). Klimawandel gestern und morgen. Neue Argumente können die Motivation zum Waldumbau erhöhen. *LWF Aktuell*, 99, 27–31. https://doi.org/10.1155/2013/787250

Konter, O., Büntgen, U., Carrer, M., Timonen, M., & Esper, J. (2016). Climate signal age effects in boreal tree-rings: Lessons to be learned for paleoclimatic reconstructions. *Quaternary Science Reviews*, 142, 164–172. https://doi.org/10.1016/j.quascirev.2016.04.020

Kramer, K., Degen, B., Buschbom, J., Hickler, T., Thuiller, W., Sykes, M. T., & de Winter, W. (2010). Modelling exploration of the future of European beech (*Fagus sylvatica* L.) under climate change - range, abundance, genetic diversity and adaptive response. *Forest Ecology and Management*, 259(11), 2213–2222. https://doi.org/10.1016/j.foreco.2009.12.023

Lebourgeois, F., Bréda, N., Ulrich, E., & Granier, A. (2005). Climate-tree-growth relationships of European beech (*Fagus sylvatica* L.) in the French permanent plot network (RENECOFOR). *Trees*, 19(4), 385–401. https://doi.org/10.1007/s00468-004-0397-9

Lee, J.-Y., Marotzke, J., Bala, G., Cao, L., Corti, S., Dunne, J. P., ... Zhou, T. (2021). Future global climate: Scenario-based projections and near-term information. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, et al. (Eds.), *Climate change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change* (pp. 553–672). Cambridge University Press. https://doi.org/10.1017/9781009157896.006

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884), 1763–1768. https://doi.org/10.1126/science.1157704

Leuschner, C. (2020). Drought response of European beech (*Fagus sylvatica* L.)—A review. *Perspectives in Plant Ecology, Evolution and Systematics*, 47, 125576. https://doi.org/10.1016/j.ppees.2020.125576

Leuschner, C., & Ellenberg, H. (2017). *Vegetation ecology of Central Europe (revised and extended version of the 6th German edition). Life sciences*. Springer.

Lloret, F., Keeling, E. G., & Sala, A. (2011). Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, 120(12), 1909–1920. https://doi.org/10.1111/j.1600-0706.2011.19372.x

Magri, D., Vendramin, G. G., Comps, B., Dupanloup, I., Geburek, T., Gömöry, D., Latałowa, M., Litt, T., Paule, L., Roure, J. M., Tantau, I., Van Der Knaap, W. O., Petit, R. J., & de Beaulieu, J.-L. (2006). A new scenario for the quaternary history of European beech populations: Palaeobotanical evidence and genetic consequences. *New Phytologist*, 171, 199–221. https://doi.org/10.1111/j.1469-8137.2006.01740.x

Mayer, H. (1984). *Wälder Europas*. Gustav Fischer.

Mérian, P., Bontemps, J.-D., Bergès, L., & Lebourgeois, F. (2011). Spatial variation and temporal instability in climate-growth relationships of sessile oak (*Quercus petraea* [Matt.] Liebl.) under temperate conditions. *Plant Ecology*, 212(11), 1855–1871. https://doi.org/10.1007/s11258-011-9959-2

Mérian, P., & Lebourgeois, F. (2011). Size-mediated climate–growth relationships in temperate forests: A multi-species analysis. *Forest Ecology and Management*, 261(8), 1382–1391. https://doi.org/10.1016/j.foreco.2011.01.019

Muffler, L., Weigel, R., Hacket-Pain, A. J., Klisz, M., Maaten, E., Wilmking, M., Kreyling, J., & Maaten-Theunissen, M. (2020). Lowest drought sensitivity and decreasing growth synchrony towards the dry

distribution margin of European beech. *Journal of Biogeography*, *47*, 1910–1921. https://doi.org/10.1111/jbi.13884

Müller-Haubold, H., Hertel, D., Seidel, D., Knutzen, F., & Leuschner, C. (2013). Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: A transect study in mature forests. *Ecosystems*, *16*(8), 1498–1516. https://doi.org/10.1007/s1002 1-013-9698-4

Öder, V., Petritan, A. M., Schellenberg, J., Bergmeier, E., & Walentowski, H. (2021). Patterns and drivers of deadwood quantity and variation in mid-latitude deciduous forests. *Forest Ecology and Management*, *487*(10), 118977. https://doi.org/10.1016/j.foreco.2021.118977

Olson, M. E., Soriano, D., Rosell, J. A., Anfodillo, T., Donoghue, M. J., Edwards, E. J., León-Gómez, C., Dawson, T., Martínez, J. J. C., Castorena, M., Echeverría, A., Espinosa, C. I., Fajardo, A., Gazol, A., Isnard, S., Lima, R. S., Marcati, C. R., & Méndez-Alonzo, R. (2018). Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(29), 7551–7556. https://doi.org/10.1073/pnas.1721728115

Peñuelas, J., Hunt, J. M., Ogaya, R., & Jump, A. S. (2008). Twentieth century changes of tree-ring δ13 C at the southern range-edge of *Fagus sylvatica*: Increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. *Global Change Biology*, *14*(5), 1076–1088. https://doi.org/10.1111/j.1365-2486.2008.01563.x

Piutti, E., & Cescatti, A. (1997). A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. *Canadian Journal of Forest Research*, *27*(3), 277–284. https://doi.org/10.1139/x96-176

Pretzsch, H., Grams, T., Häberle, K. H., Pritsch, K., Bauerle, T., & Rötzer, T. (2020). Growth and mortality of Norway spruce and European beech in monospecific and mixed-species stands under natural episodic and experimentally extended drought. Results of the KROOF throughfall exclusion experiment. *Trees*, *34*(4), 957–970. https://doi.org/10.1007/s00468-020-01973-0

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Roibu, C.-C., Sflecă, V., Mursa, A., Ionita, M., Nagavciuc, V., Chiriloaei, F., Lesan, I., & Popa, I. (2020). The climatic response of tree ring width components of ash (*Fraxinus excelsior* L.) and common oak (*Quercus robur* L.) from Eastern Europe. *Forests*, *11*(5), 600. https://doi.org/10.3390/f11050600

Rozas, V. (2001). Detecting the impact of climate and disturbances on tree-rings of *Fagus sylvatica* L. and *Quercus robur* L. in a lowland forest in Cantabria, northern Spain. *Annals of Forest Science*, *58*(3), 237–251. https://doi.org/10.1051/forest:2001123

Ryan, M. G., Phillips, N., & Bond, B. J. (2006). The hydraulic limitation hypothesis revisited. *Plant, Cell and Environment*, *29*(3), 367–381. https://doi.org/10.1111/j.1365-3040.2005.01478.x

Salomón, R. L., Peters, R. L., Zweifel, R., Sass-Klaassen, U. G. W., Stegehuis, A. I., Smiljanic, M., Poyatos, R., Babst, F., Cienciala, E., Fonti, P., Lerink, B. J. W., Lindner, M., Martinez-Vilalta, J., Mencuccini, M., Nabuurs, G.-J., van der Maaten, E., von Arx, G., Bär, A., Akhmetzyanov, L., ... Steppe, K. (2022). The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests. *Nature Communications*, *13*(1), 28. https://doi.org/10.1038/s41467-021-27579-9

Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C., & Wilmking, M. (2011). Drought matters – Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. In North-Eastern Germany. *Forest Ecology and Management*, *262*(6), 947–961. https://doi.org/10.1016/j.foreco.2011.05.026

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., Gharun, M., Grams, T. E. E., Hauck, M., Hajek, P., Hartmann, H., Hiltbrunner, E., Hoch, G., Holloway-Phillips, M., Körner, C., Larysch, E., Lübbe, T., Nelson, D. B., ... Kahmen, A. (2020). A first assessment of the impact of the extreme 2018 summer drought on central European forests. *Basic and Applied Ecology*, *45*, 86–103. https://doi.org/10.1016/j.baae.2020.04.003

Schurman, J. S., Babst, F., Björklund, J., Rydval, M., Bače, R., Čada, V., Janda, P., Mikolas, M., Saulnier, M., Trotsiuk, V., & Svoboda, M. (2019). The climatic drivers of primary *Picea* forest growth along the Carpathian arc are changing under rising temperatures. *Global Change Biology*, *25*(9), 3136–3150. https://doi.org/10.1111/gcb.14721

Senf, C., Buras, A., Zang, C. S., Rammig, A., & Seidl, R. (2020). Excess forest mortality is consistently linked to drought across Europe. *Nature Communications*, *11*(1), 660. https://doi.org/10.1038/s4146 7-020-19924-1

Serra-Maluquer, X., Gazol, A., Sangüesa-Barreda, G., Sánchez-Salguero, R., Rozas, V., Colangelo, M., Gutiérrez, E., & Camarero, J. J. (2019). Geographically structured growth decline of rear-edge iberian *Fagus sylvatica* forests after the 1980s shift toward a warmer climate. *Ecosystems*, *22*(6), 1325–1337. https://doi.org/10.1007/s10021-019-00339-z

Shestakova, T. A., Gutiérrez, E., Kirdyanov, A. V., Camarero, J. J., Génova, M., Knorre, A. A., Linares, J. C., Resco de Dios, V., Sánchez-Salguero, R., & Voltas, J. (2016). Forests synchronize their growth in contrasting Eurasian regions in response to climate warming. *Proceedings of the National Academy of Science of the United States of America*, *113*(3), 662–667. https://doi.org/10.1073/pnas.1514717113

Shestakova, T. A., Gutiérrez, E., & Voltas, J. (2018). A roadmap to disentangling ecogeographical patterns of spatial synchrony in dendrosciences. *Trees*, *32*(2), 359–370. https://doi.org/10.1007/s0046 8-017-1653-0

South, A. (2011). Rworldmap: A new R package for mapping global data. *The R Journal*, *3*(1), 35–43. http://journal.r-project.org/archi ve/2011-1/RJournal_2011-1_South.pdf

Sykes, M. T., Prentice, I. C., & Cramer, W. (1996). A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography*, *23*(2), 203–233.

Tegel, W., Seim, A., Hakelberg, D., Hoffmann, S., Panev, M., Westphal, T., & Büntgen, U. (2014). A recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress. *European Journal of Forest Research*, *133*(1), 61–71. https://doi.org/10.1007/s10342-013-0737-7

Tejedor, E., Serrano-Notivoli, R., Luis, M., Saz, M. A., Hartl, C., St. George, S., Büntgen, U., Liebhold, A. M., Vuille, M., & Esper, J. (2020). A global perspective on the climate-driven growth synchrony of neighbouring trees. *Global Ecology and Biogeography*, *29*(7), 1114–1125. https://doi.org/10.1111/geb.13090

Thiel, D., Kreyling, J., Backhaus, S., Beierkuhnlein, C., Buhk, C., Egen, K., Huber, G., Konnert, M., Nagy, L., & Jentsch, A. (2014). Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. *European Journal of Forest Research*, *133*(2), 247–260. https://doi.org/10.1007/s10342-013-0750-x

Trouillier, M., van der Maaten-Theunissen, M., Scharnweber, T., Würth, D., Burger, A., Schnittler, M., & Wilmking, M. (2019). Size matters—A comparison of three methods to assess age- and size-dependent climate sensitivity of trees. *Trees*, *33*(1), 183–192. https://doi.org/10.1007/s00468-018-1767-z

Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index. *Journal of Climate*, *23*(7), 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Wigley, T. M. L., Briffa, K. R., & Jones, P. D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Applied Meteorology*, *23*(2), 201–213. https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2

Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A., Biermann, C., Gurskaya, M., Hallinger,

M., Lange, J., Shetti, R., Smiljanic, M., & Trouillier, M. (2020). Global assessment of relationships between climate and tree growth. *Global Change Biology*, 26(6), 3212–3220. https://doi.org/10.1111/gcb.15057

Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., & Menzel, A. (2014). Patterns of drought tolerance in major European temperate forest trees: Climatic drivers and levels of variability. *Global Change Biology*, 20(12), 3767–3779. https://doi.org/10.1111/gcb.12637

Zang, C. S., & Biondi, F. (2015). Treeclim: An R package for the numerical calibration of proxy-climate relationships. *Ecography*, 38(4), 431–436. https://doi.org/10.1111/ecog.01335

Zimmermann, J., Hauck, M., Dulamsuren, C., & Leuschner, C. (2015). Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in central European mixed forests. *Ecosystems*, 18(4), 560–572. https://doi.org/10.1007/s10021-015-9849-x

Zohner, C. M., Rockinger, A., & Renner, S. S. (2019). Increased autumn productivity permits temperate trees to compensate for spring frost damage. *New Phytologist*, 221(2), 789–795. https://doi.org/10.1111/nph.15445

BIOSKETCH

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SUPPORTING INFORMATION

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