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Climate-driven growth dynamics and trend reversal of *Fagus sylvatica* L. and *Quercus cerris* L. in a low-elevation beech forest in Central Italy

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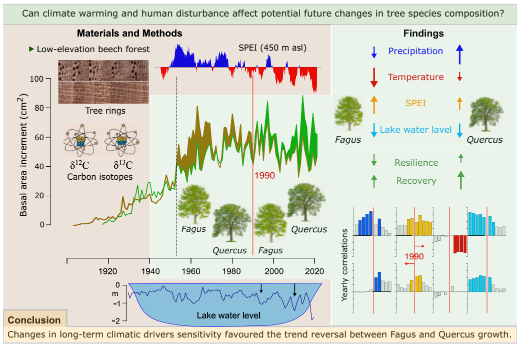
HIGHLIGHTS

- In *Fagus sylvatica*, the negative effect of temperatures has highly intensified after the ‘90s.
- Changes in long-term climatic drivers sensitivity favoured *Quercus cerris* growth.
- Tree growth correlated with the nearby lake water-level fluctuations but reduced after the 90s.
- The post-extreme droughts growth recovery was higher for *Quercus cerris.*
- Recent shifts in iWUE may point to potential future changes in the target species' composition.

GRAPHICAL ABSTRACT



Can climate warming and human disturbance affect potential future changes in tree species composition?

Changes in long-term climatic drivers sensitivity favoured the trend reversal between Fagus and Quercus growth.

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ABSTRACT

In highly climate-change-sensitive regions, such as the Mediterranean, increasing knowledge of climate-driven growth dynamics is required for habitat conservation and forecasting species adaptability under future climate change. In this study, we test a high spectrum of climatic signals, not only monthly and seasonal but also on a multi-year scale and include the single tree analysis to answer this issue, focusing on a low-elevation thermophilic old-growth beech forest surrounding the Bracciano Lake in Central Italy. Through a dendroecological and isotope analysis, we evaluate both short- and long-term sensitivity of *F. sylvatica* and the coexisting better-drought-adapted species *Q. cerris* to climatic and hydrological variability in terms of growth reduction and δ^{13C} responses. After the 1990s, beech trees showed a climate-driven decrease in growth compared to oak, especially after 2003 (−20 % of basal area increment), with a significant growth trend reversal between the species. For *F. sylvatica*, the significant correlations with precipitation decreased, whereas for *Q. cerris*, they increased, with a higher number of trees positively influenced. However, the temperature highlighted more clearly the contrasting climate–growth correlation pattern between the two species. In *F. sylvatica* after the ‘90s, the negative effect of temperatures has significantly intensified, as shown by past summer values up to four years previously, involving about half of the trees. Surprisingly, the water-level fluctuations showed a highly significant influence on tree-ring growth in both species. Nevertheless, it reduced after the ‘90s. Finally, *Q. cerris* trees showed a significantly higher ability to recover their growth levels after extreme droughts (+55 %). The growth trend reversal and the shift in iWUE of the last years may point to potential changes in the future species

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composition, raising the need for climate-adaptive silviculture (e.g., selective thinning) to reduce growth decline, enhance resilience and favour the natural regeneration of the target species for habitat conservation.

1. Introduction

Plants' survival within their distribution range is mainly driven by climatic and environmental factors (e.g., stress and disturbances), limiting the ecophysiological processes over time and, thus, affecting specific functional adaptations (Grime and Pierce, 2012). Differences in the tree species' sensitivity to climate features between elevation and latitudinal gradients across its distribution range are relevant and significant in driving tree growth (King et al., 2013). Trees at the low-elevation edge of their species distribution are expected to respond to increased temperatures and drought and long-term precipitation decrease with a reduction in growth, resilience capacity and increased mortality (Jump et al., 2010). Understanding the main climatic factors driving plants' survival along a latitude and altitude gradient is one of the most current challenges for ecologists to predict vegetation response to future changes in climatic scenarios (Körner, 2012; Bricca et al., 2022).

Fagus sylvatica L. (European beech) is a tree species widely distributed in Europe, with great historical economic importance for timber production, recently acquiring a naturalistic value related to biodiversity conservation in the old-growth beech forests (Gessler et al., 2007; Leuschner, 2020). It is a highly drought-sensitive species and has often been used as a target species for investigating the current and future climate change impact on forest ecosystems (e.g., Kramer et al., 2010). The growth of *F. sylvatica* is particularly limited by summer drought at low elevations more than at high-altitude sites, especially in southern Europe (Di Filippo et al., 2007; Hartl-Meier et al., 2014). However, significant positive correlations with summer precipitation were also recently found in stands growing at low elevations in central Europe and from the optimal growing conditions at the northern limits, particularly within the core of the species distribution range, suggesting a drought limitation on radial growth as in sites at the southern margin (Hacket-Pain et al., 2016; Kasper et al., 2022).

For the habitat selection at the distribution range edge, marginal populations tend to occupy locations where the interaction among local features (e.g., favourable geomorphological, soil and hydric conditions) improves the regional climate for the species' survival, creating more favourable site-specific growing conditions (Hampe and Jump, 2011; Cavin and Jump, 2017; Vilà-Cabrera and Jump, 2019). This selective behaviour is more likely pronounced at low-elevation sites to contrast warmer and more arid climates and the potential climatic factors limiting growth, such as summer drought (Hacket-Pain et al., 2016). However, the increase in temperature and summer drought not compensated by higher precipitation in southern Europe over the past half-century (Giorgi, 2002), reduced performance in many of these southern populations (Fyllas and Troumbis, 2009). That said, the general picture of climate warming's impact on beech forest growth has recently become more complex, with contrasting evidence both in northern and southern European beech forests (Tegel et al., 2014; Hacket-Pain and Friend, 2017; Martinez del Castillo et al., 2022; Kulla et al., 2023). There is, therefore, a pressing need to improve our understanding of *F. sylvatica* growth dynamics and responses to recent climate change impacts (e.g., increasing temperatures and summer drought stress, long-term precipitation reduction), particularly at the southern distribution margin, where beech forests are less studied compared to central and northern Europe (Hacket-Pain and Friend, 2017). An increase in drought intensification and recent climate warming could alter the competitive hierarchy between beech and other more drought-tolerant tree species, shifting the species composition in the natural forest vegetation, as already found in central European mixed forests (Cavin et al., 2013; Zimmermann et al., 2015). Moreover, declining-growth trees have a higher mortality risk (Gillner et al., 2013), affecting biodiversity and priority habitats conservation, forest-based economic activities, and forest carbon cycling (Kasper et al., 2021).

Dendrochronology provides an appropriate scientific method for investigating the forests' responses to climate variations, identifying the key climatic parameters controlling a tree species' growth and adaptability to climate change (Mazza and Sarris, 2021). Moreover, it is a powerful technique for detecting the local interactions between site characteristics and climatic conditions (Cook et al., 2001; Tardif et al., 2003), especially when coupled with stable isotope analyses (McCarroll et al., 2017) and in restricted niches such as marginal populations where the site-specific favourable growing conditions allow tree survival. Indeed, carbon stable isotope analysis of tree rings provides a powerful method to assess physiological processes in trees retrospectively, and it can be considered an integrated indicator of tree vitality over time (Cherubini et al., 2021).

The study site is in a low-elevation thermophilic beech forest in central Italy within the Regional Natural Park of Bracciano-Martignano. The presence of beech is strictly related to favourable soil and microclimatic growing conditions. Deep and fertile soils and high atmospheric humidity due to the Bracciano Lake mitigate the effects of summer drought. However, in recent years, Bracciano Lake experienced a significant water-level decline after intensive water withdrawals, which, together with the recent rise in temperatures and drought conditions, increased its water loss, raising concerns about the ecological impacts on the surrounding forest ecosystem's vulnerability (Taviani and Henriksen, 2015; Mazza et al., 2020). Based on this background information, the local favourable microclimatic conditions are threatened by the recent increase in climate warming and water withdrawals for human activities, affecting the species' survival and the potential to thrive under a warmer climate. It would be particularly relevant for the surrounding thermophilic old-growth beech forest, altering the competitive hierarchy between *F. sylvatica* and the coexisting better-drought-adapted species *Q. cerris*. In this context, we hypothesise that *F. sylvatica* trees, being close to their low-elevation distribution margins, under the current climate change, would become more sensitive to the main climatic factor limiting tree growth, especially to the summer climatic conditions. It would be particularly evident in the past few decades and compared to *Quercus cerris*. Moreover, we hypothesise a significant influence of the lake on tree growth, also related to its recent water level (WL) decrease. Under these hypotheses, we aimed to evaluate i) the impact of drought on the two tree species in terms of growth reduction and δ^{13}C responses and ii) their sensitivity to both short- and long-term climatic and hydrological signals driving tree growth dynamics and trends. Furthermore, we aimed to identify within these beech stands what percentage of trees between the two coexisting species studied is the most vulnerable to future drought intensification.

2. Materials and methods

2.1. Study site and climate characterization

The study site is a Special Area of Conservation – SAC (“Faggete di Monte Raschio e Oriolo”, IT6010034) within the Regional Natural Park of Bracciano-Martignano in central Italy (42.10 N – 12.10 E) at an elevation of about 450 m asl. It is considered a secondary old-growth forest, with stands actively managed in the past but left to natural evolution (Frelich and Reich, 2003). The thermophilic beech forest represents the ecosystem with the highest naturalistic value, classified as priority habitat (9210 – Apennine beech forests with *Taxus baccata* and *Ilex aquifolium*, EU Habitats Directive). The beech forest portion of

Monte Raschio is the 33° natural UNESCO heritage “Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe”.

The study site is about 3.5 km from the Bracciano Lake on the highest part of its northern headland (Fig. 1). The hydrogeologic basin covers an area of 150 km^2, which contains the lake area (57 km^2). The Bracciano Lake, holding a water volume of 4.85 km^3, is relatively deep, with a maximum depth of about 165 m and a mean of about 81 m asl (Taviani and Henriksen, 2015).

The dominant layer of the beech stands consists of *F. sylvatica* trees, with isolated or grouped *Q. cerris* and, secondly, *Castanea sativa* Mill., increasing in the transition areas. Within the understory tree layer, several species are mainly individually widespread such as *Fraxinus ornus* L., *Acer pseudoplatanus* L., *Acer campestre* L., *Ilex aquifolium* L., *Sorbus torminalis* and *domestica* L., *Prunus avium* L., and some trees of *Ulmus glabra* Huds. The shrubby and herbaceous layer is poorly developed due to the dense canopy cover. It consists mainly of *I. aquifolium* L., *Crataegus monogyna* Jacq., *Ruscus aculeatus* L., and a lower presence of *Cornus sanguinea* L., *Corylus avellana* L., and *Sambucus nigra* L., besides the natural regeneration of *F. sylvatica*.

The soils belong mainly to the type of Andosol, typically found in volcanic areas, and usually contain high proportions of glass and amorphous colloidal materials, resulting in very fertile soils. They are characterised by a sandy loam texture and are very porous with good drainage.

The climate data were recorded at the Bassano Romano meteorological station (Piano Mola - 457 m asl) and integrated with the climatic dataset closest to forest stands from the regional hydrological service to cover the period 1951–2021. Standardised Precipitation-Evapotranspiration Index (SPEI) was calculated through Potential Evapotranspiration (PET) according to the Thornthwaite equation as implemented in the R package SPEI (Vicente-Serrano et al., 2010) using mean temperature values from the nearby Bassano Romano meteorological station data. The use of SPEI is relevant to the quantification of the effects of droughts on tree growth because of its ability to capture the main impact of increased temperature on water demand (Vicente-Serrano et al., 2010). Monthly water-level records (WL, cm) of Bracciano Lake (from 1921 to 2021) were provided by the Regional Natural Park. The climate is the typical Mediterranean with a mean annual rainfall of 1067 mm concentrated mainly in autumn (35 %) and winter (32 %), and a dry summer in which July and August are the driest months with 25.6 and 34.3 mm of rainfall, respectively (Fig. 1). The mean annual temperature is 14.9 °C. The study site falls under the Mediterranean biome, category Temperature Deciduous Forest, and specifically Warm temperate moist forest. The bioclimate is Mediterranean Pluviseasonal oceanic, the thermotype is Upper mesomediterranean and the ombrotype is sub-humid lower (Pesaresi et al., 2017).

2.2. Tree sampling and dendrochronological analysis

Dominant healthy and straight trees with a symmetrical crown, without any visible injuries to the crown and stem or any signs of past tree cutting in their neighbourhood, were selected. Two cores per tree were extracted with a 5-mm diameter increment borer at breast height on the cross-sides of the trunk from 40 trees of *F. sylvatica* and 32 of *Q. cerris*. The increment cores were mounted on wooden supports, air-dried, and then smoothed with the slide microtome WSL-Core-

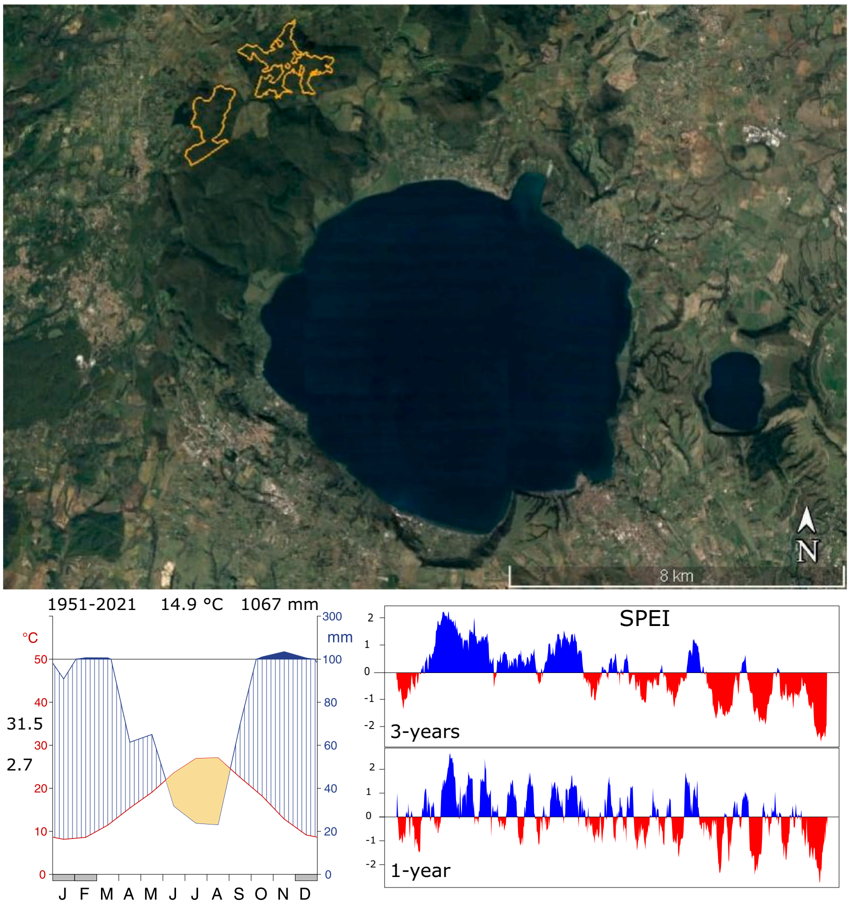

Fig. 1. Location of the beech forest study site and climatic characterization of the study area (Walter & Lieth climatic diagram and Standardised Precipitation-Evapotranspiration Index - SPEI). Average annual temperature and the total annual rainfall (top). Mean maximum temperature of the warmest month and mean minimum temperature of the coldest month (beside the left y-axis). The dotted area in the Walter & Lieth climatic diagram indicates seasonal water deficit.

microtome (Gärtner and Nievergelt, 2010).

Annual tree-ring widths (TRW) were measured from bark to pith with a 0.01-mm precision by a computer-linked measuring table (LINTAB™ 6, Rinntech, Heidelberg, Germany) under a stereo microscope (Leica S9i, magnification range: 6.1× – 55×) and using the software package TSAP-Win™ scientific version 4.6× (Time Series Analysis and Presentation, TSAP, Frank Rinn, Heidelberg, Germany).

Each tree-ring series was statistically verified for cross-dating and measurement errors using the Gleichläufgkeit ("glk") function and Spearman's rho correlations of the package Dendrochronology Program Library in R ("dplR") (Bunn, 2010; R Core Team, 2020). The tree-ring series that cross-dated poorly with the master chronology were corrected for measurement errors when possible or discarded.

In removing the effect of the "age trend" from our tree-ring width (TRW) series (the age-dependent trend due to the geometrical constraint of adding a volume of wood to a stem of increasing radius), TRWs were converted into basal-area increments (BAIs) to retain both low- and high-frequency climatic signals in tree-ring chronologies (Mazza and Sarris, 2021). The BAI method was employed because it provides a better proxy for the three-dimensional mass increment than ring width. It avoids the effect of reduction in ring widths due to the diameter increase of trees (i.e., it is free of age trend) without eliminating the patterns of increase or decrease in ring width due to other causes (Biondi and Qaedan, 2008; Linares and Tíscar, 2011; Dorman et al., 2015). BAI, in cm^2, was derived using the following equation implemented in the R package dplR (Bunn, 2008): $BAIt = \pi\,(wt^2 + 2wtR(t\text{-}1))$ where wt is the annual ring width and R(t-1) is the stem radius at the beginning of the annual increment. A raw BAI chronology was built for each site as the average by year of the individual-tree BAI series.

2.3. Stable C isotope analysis

For each species, the same trees used for dendrochronological analyses were prepared for isotopic measurement: tree rings were annually divided with a razor, pulverized with a pulverizing mill (ZM 1000, Retsch, Germany) and were weighed in tin capsules.

Carbon isotopic analyses were performed at the laboratory of the University of Campania using an IRMS system (Isotopic Ratio Mass Spectrometry - Delta V Advantage, Thermo Scientific), connected in continuous flow with an EA (Elemental Analyzer, Flash 1112 series, Thermo Scientific), where the combustion of the woody samples occurs. Carbon isotopic ratios are expressed in delta notion, according to the formula (Farquhar et al., 1989):

$$\delta^{13}C_{plant} = \delta^{13}C_{atm} - a\text{–}(b - a)\cdot c_i/c_a \tag{1}$$

where *a* is the fractionation factor due to CO_2 diffusion through stomata (4,4 ‰) and *b* is the fractionation factor due to Rubisco enzyme during photosynthesis (27 ‰), c_i is the is the partial pressure of CO_2 in leaf intracellular space and c_a is the partial pressure of CO_2 in the atmosphere. After measurements, the $\delta^{13}C$ row data were calibrated using international isotopic standards (IAEA-CH3 cellulose, IAEA CH6 sucrose and IAEA-C3 cellulose). Finally, the $\delta^{13}C$ series were corrected for the fossil fuel combustion effect (Francey et al., 1999).

2.4. Climate–growth relationships

Our analysis was focused on a stabilised growth period starting from 1953/1954 to reduce the influence of site-specific characteristics on tree growth variability. Additionally, from the second half of the twentieth century, climatic data were more reliable, and the number of tree-ring series was more representative. Pearson's correlations were used after testing for normal distribution with the Kolmogorov-Smirnov and Shapiro-Wilk tests, including precipitation, temperature, SPEI, lake WL, and relative air humidity recorded by the Bassano Romano meteorological station for the period 2004–2021 (more statistical details on the Pearson's correlation analysis are included in *Appendix A Supplementary Material*).

Fourteen monthly climatic variables sequenced from October of the year before growth (t − 1, uppercase acronyms) to November of the year of growth (t, lowercase acronyms) were used. This temporal window includes the previous autumn as the climatic condition preconditioning tree-ring growth in the next growing season (e.g., water reserve from autumn-winter precipitation inputs stored in the soil) and the current autumn until November, because the cambial activity continues during autumn given the favourable climatic conditions. For seasonal variables, twelve and nine different seasons from the same temporal window for two specified season lengths in one-month steps (three and six months, respectively) were computed.

Considering that one of the most common signals identified in the literature as a key feature for the distribution-wide climate–growth relationships for *F. sylvatica* was the previous summer temperature, monthly and seasonal (three months from May to September in one-month steps) past summer temperatures averaged up to four years before the year of tree ring formation were additionally tested. Similarly, climate–growth correlations included the possible past effects of the hydroclimatic conditions on tree growth at a yearly scale, calculated as the sum (for precipitation) or average (for temperature, SPEI and WL) of the *i*-esimo previous year: $t + t_{-i}$, where *t* is the value of the current year and *i* ranges from one to four. Because a series of dry years could seriously affect tree growth and survival, this approach would help identify any possible effects of previous years' precipitation, temperature, SPEI and WL on tree growth (Ogle et al., 2015; Dorman et al., 2015; Peltier et al., 2017). Starting from 2004, relative air humidity values recorded by the Bassano Romano meteorological station was also tested.

To improve the reliability of the correlation analysis and test how the hydroclimatic factors (the independent variables) influenced tree-ring growth, including the relative humidity and $\delta^{13}C$ (the dependent or response variables), partial least squares regression (PLSR) was performed using the R package "plsdepot". PLSR was tested using raw basal area increments (BAI), and two components were always retained. Model strength was assessed by the sum of the R^2 of the two significant components and the proportion of variance in the dependent variable that can be predicted by the model (goodness of prediction, Q^2). For more information on the partial least squares regression analysis, see *Appendix A Supplementary Material.*

Then, a downscaling approach from stand to single-tree level was used, testing the best climatic predictors for every single tree to find the percentage of trees sharing the main climatic drivers. This method improves the reliability of growth responses to climate at the stand or population level (Mazza et al., 2018).

Finally, after defining years of extreme drought as those with annual SPEI below the tenth and fifth percentile (Knapp et al., 2015), raw BAIs during these critical years were compared with those of the years before and after to quantitatively analyse drought-related growth dynamics. Any potential influence of different growing conditions at the stand level was removed, standardising each raw BAI chronology by dividing it by its mean, and resistance (Rt: the inverse of growth reduction during the episode), resilience (Rs: the capacity to reach pre-episode growth levels) and recovery (Rc: the growth increase relative to the minimum growth during the episode) – indices linked to components of growth stability – avoiding the overlap of consecutive drought years were calculated as follows (from Lloret et al., 2011; Mazza et al., 2021):

$$\text{–Resistance (Rt)} : Rt = \left(D_0 - D_{pre}\right)/D_{pre} \times 100$$

$$\text{–Resilience (Rs)} : Rs = \left(D_{post} - D_{pre}\right)/D_{pre} \times 100$$

$$\text{–Recovery (Rc)} : Rc = \left(D_{post} - D_0\right)/D_0 \times 100$$

where D_0 is the raw basal-area increment corresponding to the year of drought, D_{pre} and D_{post} are the averages of raw basal-area increments from one to four years before and after drought, respectively.

All the data analysis was performed in the R software environment (R Core Team, 2020. http://cran.r-project.org/).

3. Results

3.1. Growth patterns and trends

The length of tree-ring chronologies spans from 60 to 119 years, with a mean BAI of 49.0 cm^2 (SD = 22.6) for *F. sylvatica* and 51.6 cm^2 (SD = 20.6) for *Q. cerris* (Table 1). The Gleichläufgkeit (GLK–Schweingruber, 1989) values were 0.67 for *F. sylvatica* and 0.70 for *Q. cerris*, indicating a high percentage of common signs of year-to-year growth change. The strong common growth signal was also confirmed by the mean inter-series correlation (rbar.bt) and the expressed population signal. The good coherence in synchronisation patterns of all tree-ring series points to similar factors affecting the tree growth dynamics of the two species.

Starting from the early 1950s, thus excluding the establishment growing phase of the first decades, tree growth was higher for beech than oak trees until 1990, with a major and a minor peak around the early ‘60s (+31.4 %, $p < 0.001$) and the ‘80s (+14.4 %, $p < 0.01$), respectively (Fig. 2a). The mean oak chronology of BAIs was lower but showed a significant upward trend ($p < 0.01$). After 1990, a growth trend reversal of the two coexisting species was observed, with higher growth rates for oak (+17.1 % with $p < 0.01$ after 1990 and + 32.2 % with $p < 0.001$ after 2003) and characterised by a significant downward trend for beech trees ($p < 0.05$) (Fig. 2b).

Compared to the previous high-growth rate periods, the decreasing growth after the ‘90s for beech trees was significant after 2003 (about −20 % with $p < 0.01$). Indeed, the growth recovery was less than that observed after 1990 (Fig. 2b). In contrast, for oak trees, the growth rate after 1990 remained significantly higher over time (about +31.5 % with $p < 0.01$), although the growth recovery after 2003 was slower than that observed after 1990 (Fig. 2b). Another difference in growth pattern reversal between species after the ‘90s was the change in growth variability over time: it decreased for beech, especially after 2003, and increased for oak (Fig. 2b).

The carbon isotope analysis, carried out on the tree rings and performed for the period between 1966 and 2016, showed an average value of $\delta^{13}C$ of −26.80 ± 0.65 ‰ for *F. sylvatica* and − 26.91 ± 0.43 ‰ for *Q. cerris*, without significant difference. For both species, the chronologies of $\delta^{13}C$ showed a slightly increasing trend (toward fewer negative values) and, starting from 2016, an abrupt and steep decrease (toward more negative values). For *F. sylvatica*, after 2003, there was a divergence between the raw BAI and $\delta^{13}C$ curves, which showed an increasing trend ($p < 0.01$), whereas for *Q. cerris*, the two curves are much more in agreement (Fig. 3). Indeed, only for *Q. cerris*, the mean raw BAIs curve was significantly correlated with $\delta^{13}C$ (rho = 0.61, $p < 0.001$).

Table 1
Main dendrochronological statistics of the two species. D.B.H. classes range of the dominant/co-dominant trees cored, mean basal area increment (M.BAI) ± standard deviation (SD), mean sensitivity (MS), first-order serial autocorrelation (AC1), mean interseries correlation (rbar.bt) and the expressed population signal (EPS), computed on the whole length of the raw BAI chronologies.

		F. sylvatica	*Q. cerris*
Time span		1903–2021	1917–2021
N° years	(max ÷ min)	119 ÷ 60	105 ÷ 60
	(mean ± SD)	91 ± 14	83 ± 10
N° cores/N° trees		59/40	51/32
D.B.H. range (cm)		70.7 ÷ 109.5	71.0 ÷ 114.6
M.BAI ± SD (cm^2)		49.0 ± 22.6	51.6 ± 20.6
MS		0.272	0.238
AC1		0.64	0.60
rbar.bt		0.42	0.45
EPS		0.93	0.93

3.2. The influence of hydroclimatic factors on tree-ring growth dynamics

The pattern of growth responses to climatic and hydrological factors showed a significant change after the ‘90s, in line with the growth dynamics and trend reversal of the two species, most significant when increasing the time scale from monthly to seasonal and yearly.

For precipitation, the pattern of monthly–seasonal correlations with tree-ring growth of *F. sylvatica* over time was sufficiently stationary. Conversely, the significant correlations with rainfall accumulated in the years preceding the tree-ring formation in the reference period 1953–1990 considerably decreased in the past few decades (1991–2021). For *Q. cerris*, all the correlations with tree-ring growth increased, especially at the seasonal and yearly time scale (Fig. 4 – P). At the single tree level, after the ‘90s, *F. sylvatica* reduced the percentage of trees significantly correlated with monthly and especially yearly time scale variables. In contrast, *Q. cerris* increased the number of trees positively influenced by precipitation, especially on the longer time scale as six-month seasons and yearly (Fig. 5). In detail, June precipitation was the monthly climatic variable most significantly influencing tree growth in both species over the two periods. At the monthly and seasonal scale, *F. sylvatica* lost the positive influence of previous year's autumn precipitations, and *Q. cerris* increased the positive effect of those falls in the late spring-summer of the current year of growth (Fig. 4 – P).

As precipitation, SPEI showed a contrasting correlation pattern between species and temporal periods. In *F. sylvatica* after the ‘90s, there was an increase in monthly and yearly significant correlations with growth. At the seasonal scale, the negative influence of summer drought increased (Fig. 4 – SPEI). For *Q. cerris*, the negative impact of the recent increase in drought conditions on tree growth compared to the period before the ‘90s was more significant than for *F. sylvatica*, mainly because *Q. cerris* growth was not strongly sensitive to previous drought conditions (Fig. 4 – SPEI). At the single tree level, the monthly drought impact involved a high percentage of trees for both species, whereas it decreased at the seasonal scale for *F. sylvatica* and at the yearly scale for *Q. cerris* trees (Fig. 5).

The temperature effect emphasises even more significantly the contrasting climate–growth correlations pattern between the two species. In *F. sylvatica* after the ‘90s, the negative effect of spring and summer temperatures has significantly intensified when increasing the time scale of the variables tested up to also early-autumn temperatures and five consecutive years prior to the ring formation (Fig. 4 – T). For *Q. cerris*, the recent increase in temperature negatively affected tree growth only as a short-term effect at monthly and seasonal (three months) scales (June, April–May–June, and May–June–July). On the contrary, the cumulative effect of the longer seasonal periods (six months) and several consecutive previous years was not correlated with tree-ring growth reduction. Moreover, the increase in winter temperatures produced positive correlations with tree-ring growth still as short-term variables: January, December–January–February, and January–February–March (Fig. 4 – T). At the single tree level, after the ‘90s, the negative effect of increased temperatures affected mainly *F. sylvatica*, with a significant increase in the percentage of trees negatively correlated with all time-scale variables, especially six-month seasons, and yearly temperatures (half of the trees experienced the cumulated increase in mean yearly values – Fig. 5). This pattern was confirmed by the significant increase in tree growth sensitivity of *F. sylvatica* to past summer temperatures after the ‘90s, with about 50 % of the trees significantly correlated with monthly and seasonal variables (*Fig. S1_ Appendix A Supplementary Material*). *Q. cerris* trees started to suffer the temperature increase only at the monthly and seasonal three-month scales (about 43 %), and about 31 % of trees showed positive correlations with winter months' temperatures that were absent previously.

The WL fluctuations, surprisingly, showed a strong influence on tree-ring growth in both species. Significant correlations were found at each

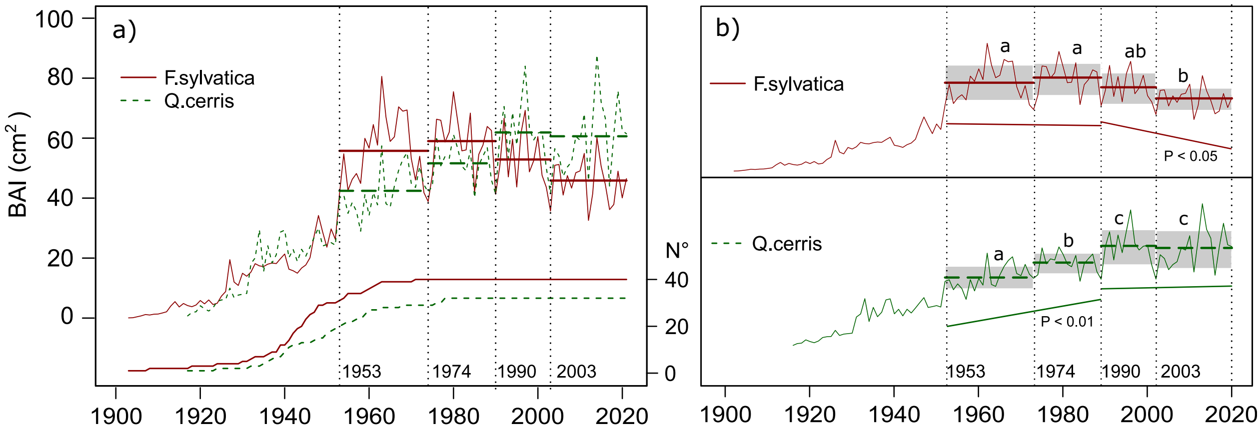

Fig. 2. (a) Mean raw basal area increments (BAIs) with average growth rates and number of cores (N°) for the two species. Horizontal continuous and dashed lines refer to *F. sylvatica* and *Q. cerris*, respectively. (b) Differences among the average growth rates of each species indicated by different letters and linear trends with significance levels. The shaded areas show the growth variability over time expressed as standard deviation. The vertical dashed lines indicate the periods of comparison of growth rates.

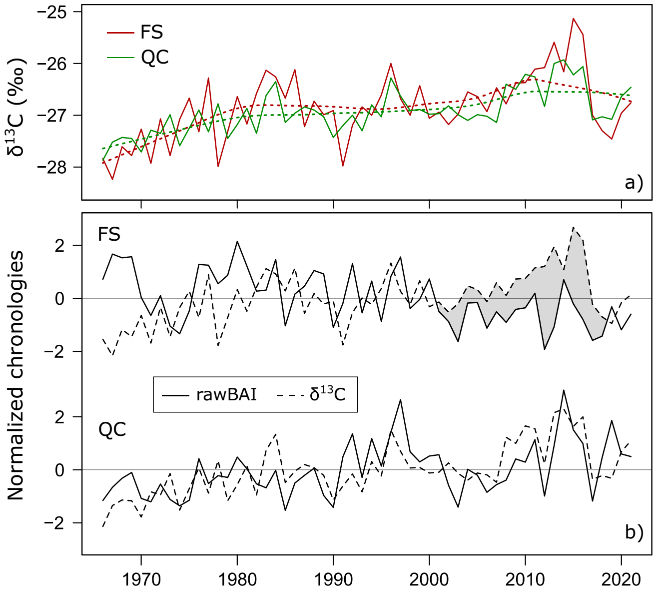

Fig. 3. (a) δ13C mean chronologies with linear trends. (b) Normalised raw basal area increments (rawBAI) and δ13C mean chronologies.

timescale and for most of the variables included in the analysis (Fig. 4 – WL). The main differences between the two species were the higher correlation coefficients in *F. sylvatica* and the delayed effect on *Q. cerris* at the monthly-seasonal scale in both temporal periods. In the past few decades (1991–2021), this delayed effect also appeared on *F. sylvatica* tree-ring growth, much prolonged at the seasonal scale and excluding the previous autumn and winter months when the water lake recharge occurs. At the yearly scale, the influence of past WL fluctuations disappeared after the third preceding year for *F. sylvatica* and the second one for *Q. cerris* (Fig. 4 – WL). At the single tree level, after the '90s, *F. sylvatica* considerably reduced the percentage of trees (about −45.5) correlated with the lake WL for all the variables involved in the analysis. On the contrary, *Q. cerris* showed a slight increase mainly on the shorter time scale as in monthly and three-month seasons (Fig. 5).

Finally, the relative air humidity in the 2004–2021 period was correlated with tree-ring growth in the summer months, more for *Q. cerris* than *F. sylvatica*, especially at seasonal and yearly scales (Fig. 6a). Regarding its relationship with the other climatic variables, the relative air humidity was positively correlated with precipitation in winter, spring, and summer months, without significant differences over time. Conversely, the negative correlations with temperature in the past decade (2012–2021), compared to the previous period (2004–2012), significantly increased mainly in the summer-early autumn period. Similarly, lake WL fluctuations showed a pronounced increase in positive correlation coefficients in summer-autumn months, especially on the longer time scale as in six-month seasons and yearly (Fig. 6b).

PLSR and VIP analysis highlighted the recent contrasting pattern in climate–growth relationships between the two species (see Appendix A Supplementary Materials for detailed information).

3.3. Impact of drought on growth dynamics and recovery

Effects of drought on growth patterns were significantly higher for *F. sylvatica* than *Q. cerris* trees. The selected drought years, using as the threshold the tenth percentile, were 1971, 1985, **2001**, **2003**, **2007**, 2012 and **2017** (bold years are below the fifth). During the critical drought years, resistance (Rt) indices revealed a quite similar growth reduction between species. In contrast, resilience (Rs) indices showed lower growth levels for *F. sylvatica* after the critical droughts compared to the previous ones (one and for years before). *Q. cerris* appeared more resilient, although the positive values are very low (Fig. 7). The recovery (Rc) indices revealed a significantly higher ability of *Q. cerris* trees to recover their growth levels, especially after the reduction experienced during the critical droughts below the fifth percentile. Including all the single trees per species, *Q. cerris* showed a significantly higher resilience when experiencing droughts below the tenth percentile ($P < 0.01$) and higher post-drought growth recovery after droughts below the fifth percentile ($P < 0.01$). Moreover, *Q. cerris*, in addition to showing the most significant growth improvement, had the highest percentage of trees able to recover their growth after drought. Indeed, at the single-tree level, oaks exhibited the highest tree percentage with positive indices both for resilience and post-drought growth recovery (Fig. 7).

4. Discussion

4.1. Climate influence on the main species (F. sylvatica)

The survival of tree marginal populations is strictly related to the favourable interaction between local/site specific features and regional climate, driving the habitat selection (Cavin and Jump, 2017). The recent coupled increase in climate warming and human impact can negatively affect these favourable growing conditions, making marginal tree populations sensitive to climate change. Consequently, old-growth forests in marginal sites and their resilience to the climatic extremes

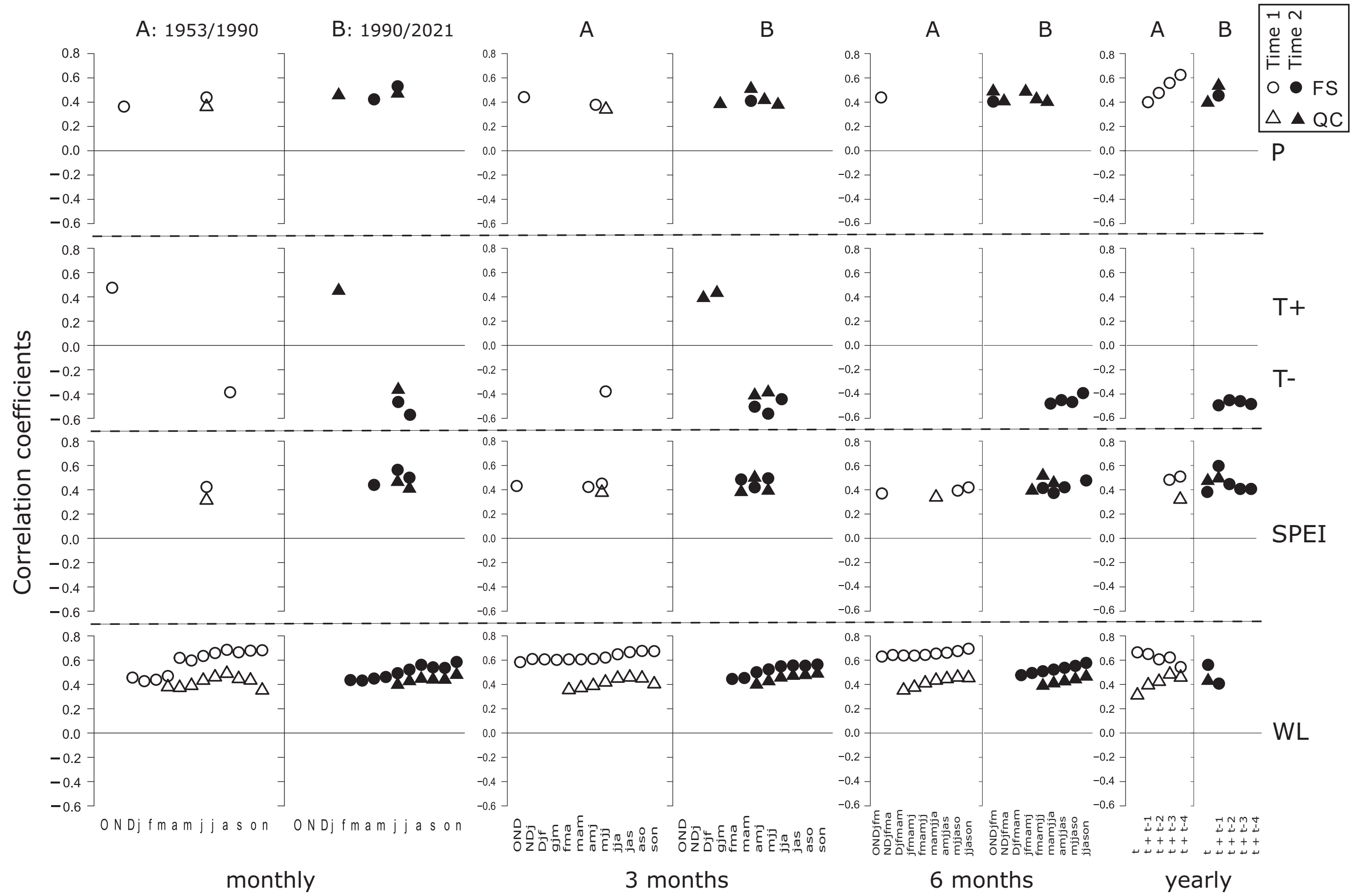

Fig. 4. Pearson's correlation coefficients between raw BAI chronologies and the climatic variables at monthly, seasonal and annual time scale (P: precipitation – SPEI: standardised precipitation evapotranspiration index – T: mean temperature – WL: lake water level). Empty and filled symbols indicate the two temporal periods: 1953–1990 and 1990–2021. Lowercase and uppercase letters on the x-axis refer to the current year of growth and the year before, respectively. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

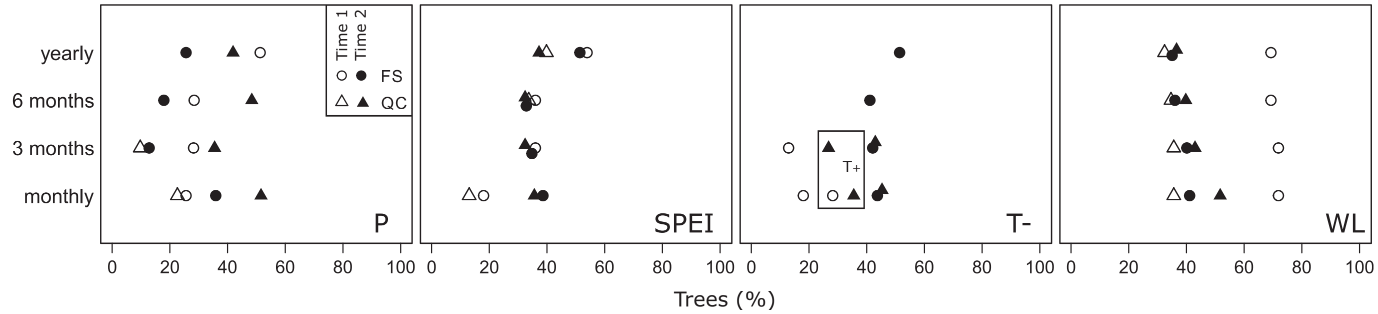

Fig. 5. Percentage of trees showing significant correlations with the four categories of precipitation (P), mean temperature (T), SPEI, and lake water level (WL) predictors (monthly, three- and six-month seasons, yearly). Empty and filled symbols indicate the two temporal periods: 1953–1990 and 1990–2021. For temperature, the main box shows the percentage of trees negatively correlated, whereas the small box inside shows the positive coefficients.

are relevant ‘sentinels’ of climate change. In southern Europe, the highly drought-sensitive behaviour of *F. sylvatica*, which is negatively affected by summer drought, is now well established, especially at low-elevation sites (Di Filippo et al., 2007; Hartl-Meier et al., 2014). In line with this general pattern, we found a significant negative effect on the growth and ecophysiology of beech with the recent increase in temperatures, intensified in the past few decades, not only in summer months but also in late spring and early autumn, and when increasing the time scale up to five consecutive years before the ring formation. The lagged correlation between tree growth and previous summer temperatures can be related to carbohydrate depletion during unfavourable (warm) years, leading to a growth reduction in the following year. However, older trees have overall larger stores of carbon (Genet et al., 2010; Sala et al., 2012), implying that carbohydrate depletion during unfavourable conditions should have a lower effect on growth the following year in older (and larger) trees (the carryover mechanism), as in the case of old-growth forests. We could not exclude the effect of climate-driven masting events (Drobyshev et al., 2010) caused by warm previous summer temperatures, resulting in a strong decline in growth and narrow rings in the years of ring formation. Indeed, fructification can make up a third to half of the trees' net primary production in full mast years, significantly reducing leaf and stem production (Müller-Haubold et al.,

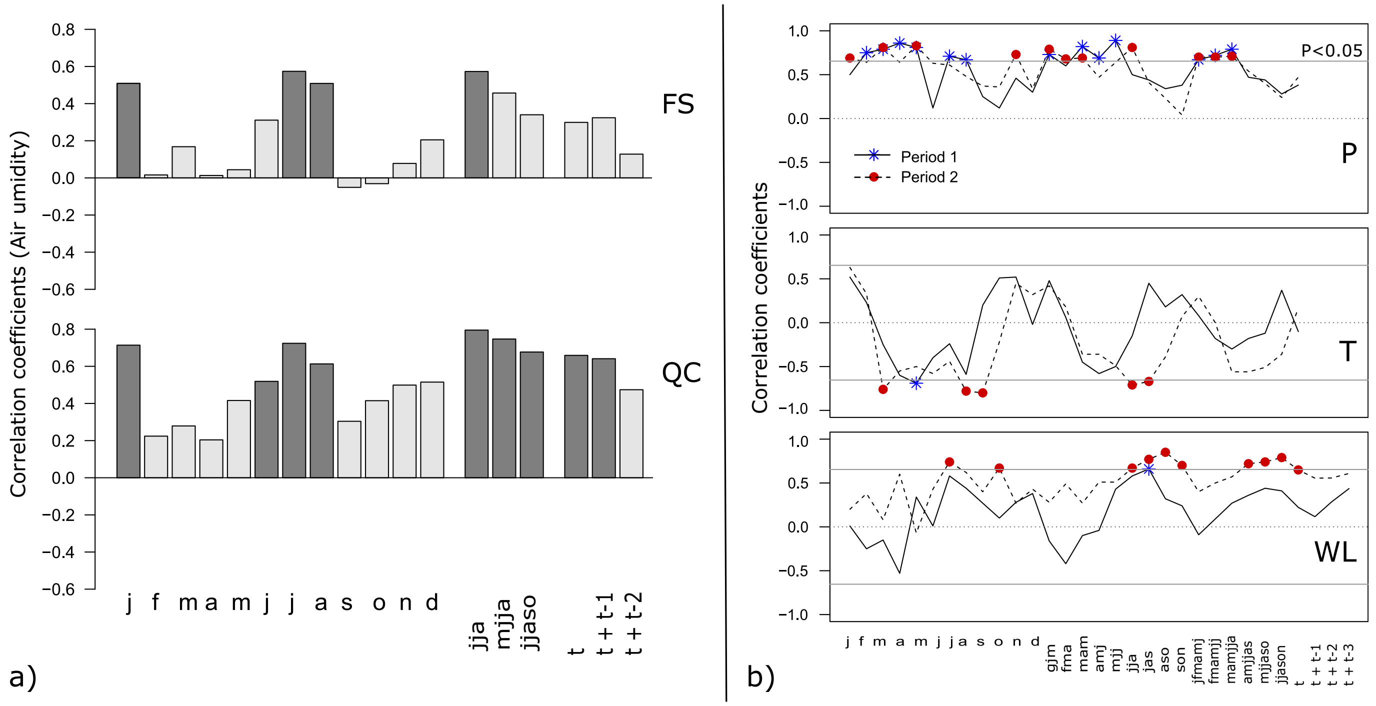

Fig. 6. Spearman's correlation coefficients between: (a) raw BAI chronologies and relative air humidity. *: P < 0.05; **: P < 0.01; ***: P < 0.001 and (b) the relative air humidity and precipitation, temperature, and lake WL in two recent reference periods (2004–2012 vs. 2012–2021). FS: *Fagus sylvatica*, QC: *Quercus cerris*.

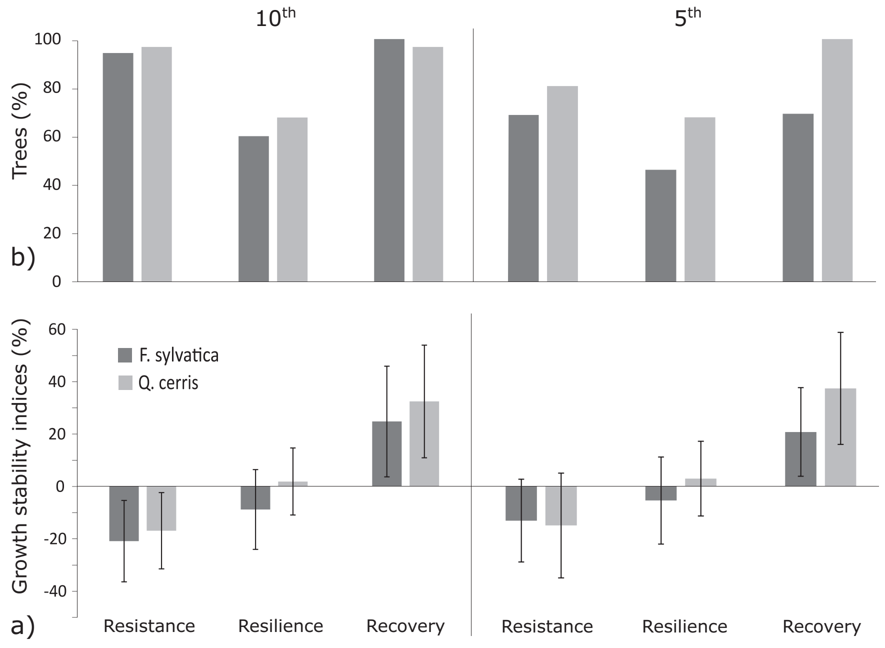

Fig. 7. (a) Resistance (Rt), resilience (Rs), and recovery (Rc) indices linked to components of growth stability (% ± SE) calculated using raw BAI averaging from one to four years before and after drought and the drought episodes under tenth and fifth percentile thresholds. (b) Percentage of trees showing the corresponding growth stability indices.

2013). Moreover, the effect of masting on growth increases with tree age because older trees increase their investment in reproduction relative to stem growth (Genet et al., 2010; Hacket-Pain et al., 2015). However, the intensification of the long-term effect of temperature on tree growth decline in the past few decades, as found in our study site, would suggest an interaction among climatic conditions, seed production (mast events) and growth patterns.

Current summer precipitation represents another key climatic signal influencing *F. sylvatica* tree growth, especially at the most xeric sites (Hacket-Pain et al., 2016; Cavin and Jump, 2017). However, in northern Europe, Harvey et al. (2019) reported a strong positive relationship between growth and current June precipitation, indicating that moisture availability in the growing season influences predominantly annual growth increment of *F. sylvatica* throughout its distribution range (Hacket-Pain et al., 2016; Cavin and Jump, 2017; Babst et al., 2019). We found significant correlations with late spring-early summer (mainly

June) and previous autumn precipitation, suggesting that monthly and seasonal precipitation in the summer period is not the main climatic driver or limiting factor for tree growth, as assumed for most xeric sites. Indeed, the study site has a mean annual rainfall of 1067 mm, concentrated mainly in autumn and winter, which works as soil water recharge. For this reason, we most likely found highly significant correlations with rainfall accumulated in the years preceding the tree-ring formation. This pattern suggests a relationship between *F. sylvatica* trees and long periods of water supply to utilise the deeper water content pools stored due to the previous rainy years. The few summer precipitations around 100 mm are much lower than a reference threshold reported by some authors for mature beech stands on loamy soils (about 190 mm – Zimmermann et al., 2015), driving trees to utilise the water content stored in deeper soil layers. The significant correlations with the previous precipitation accumulated over consecutive years can suggest that climatic conditions in preceding years are a determining factor in the ability of trees to overcome the effects of drought or intra- and inter-specific competition on growth (Ogle et al., 2015; Peltier et al., 2017; Mazza et al., 2018, 2021).

The highly significant influence of lake WL on tree growth still confirmed the importance of water resources (e.g., groundwater, soil moisture pools) for *F. sylvatica* trees at the low-elevation study site, where the favourable soil and microclimatic growing conditions for the presence of Bracciano Lake improve the regional climate for the species survival. According to a groundwater/surface water model developed by Taviani and Henriksen (2015) to test the vulnerability of Bracciano Lake to climatic and water-use stresses, when the WL drops, the groundwater inflow to the lake increases. It can reduce, for example, the groundwater availability for surrounding tree vegetation (e.g., riparian vegetation; see Mazza et al., 2020). It may explain the reduction of significant correlations between tree-rings growth and WL in 1990–2021, when the mean annual WL dropped by about 54 % (also due to the intensive water withdrawals for human needs), and the influence of past yearly WL fluctuations disappeared. This pattern was also evident in the percentage of trees significantly correlated with lake WL fluctuations, reduced by about 1.8 times compared to the period before 1990. However, the WL fluctuations produced much more significant correlations with tree growth than the climatic variables, as confirmed by the PLSR analysis in the past twenty years. This somewhat unexpected result leaves its interpretation open and needs further investigation. We can hypothesise the presence of temporary shallow aquifers that supply the lake and influence its water level, explaining an indirect relationship between tree growth and water level fluctuations (personal communication). After the ‘90s, the availability of this water input decreased, most likely due to changes in climate conditions (e.g., reduction in precipitation, increase in dry periods) and a higher groundwater inflow to the lake because of the WL lowering, also in the short term, resulting in a reduction in significant correlations.

4.2. Climate-driven growth trend reversal between *F. sylvatica* and *Q. cerris*

After 1990, there was a relevant growth dynamic change between the two coexisting species, with a significant downward trend for *F. sylvatica* trees and an increasing growth rate for *Q. cerris*. For *F. sylvatica*, a continuous growth decline of dominant beech trees by 10 % to >50 % has been recognised from 2010 onwards in many Central European beech forest regions in the core of the distribution range, often starting in the 1980s or 70s (Leuschner, 2020 and references therein). A widespread decreasing trend has been documented since the 1980s in even-aged stands in north-eastern France (−18 %, Bontemps and Esper, 2011), in the Spanish Pyrenees at low altitudes (−49 %, Jump et al., 2006) and in the Central Apennines in Italy between the 1970s and 2000s (−25 %, Piovesan et al., 2005). In Slovakia, *F. sylvatica* growth increased between the 1960s and 90s, and then decreased (Bosela et al., 2016). In western Romania, the BAI decline during the past 10–20 years was most prominent in the xeric stands, but also occurred in the mesic ones (Kasper et al., 2022).

In our site, the BAIs trend reversal of the two species after the ‘90s, with a significant growth decline of *F. sylvatica*, was in line with the relevant change found for the relationships between growth and hydroclimatic factors. This pattern was more significant when increasing the time scale of hydroclimatic factors from monthly to seasonal and yearly. *Q. cerris* increased the correlations with precipitation accumulated over seasonal (three and six months) and yearly periods, up to two consecutive years, suggesting that trees utilised more significantly the deeper water content pools stored due to the previous rainy periods. The percentage of trees significantly correlated with the shortest timescale precipitation signals (e.g., monthly) increased by about three times, and about 48 % and 42 % of trees started to utilise the water resources stored due to six-months seasonal and yearly precipitation, respectively. Conversely, *F. sylvatica* increased the percentage of trees using monthly precipitation input and halved those correlated to longer timescale precipitation signals. This behaviour can be explained through a root-system stratification between the two species. According to literature findings, when *Fagus* and *Quercus* are growing in mixed stands on deep soil, the soil layers are occupied differently by both species: the *Fagus* shallow rooting system is mainly concentrated in the upper soil layers, whereas *Quercus* trees also explore the deepest ones (Packham et al., 2012; Bert et al., 2022; Marín et al., 2023. In *F. sylvatica* adult trees, about two thirds of total fine root biomass is contained typically in the uppermost 30 cm of the soil profile, whereas under 1 m depth, it is usually <5 % (Meier et al., 2018; Kirfel et al., 2019). However, despite the limited ability of the *F. sylvatica* root system to explore deeper and moister soil layers, a shift in the depth of maximum root water absorption to deeper horizons was found in response to topsoil drying (Brinkmann et al., 2019). The *Quercus* root system exploring deeper soil layers (especially of 2–5 diameter class) may guarantee a more stable water supply during drought than the nearby *F. sylvatica* trees (Leuschner et al., 2001). Moreover, mature trees of this *Quercus* species can develop long horizontal first-order roots (Di Iorio et al., 2007), which can also take advantage of water and nutrient uptake throughout the growing season from the uppermost soil layers. In a mixed oak-beech forest, a shallower distribution of *Quercus* fine roots in the topsoil compared to the coexisting *Fagus* was reported, with the maximum density in the uppermost organic horizon (Büttner and Leuschner, 1994). This, in turn, can be an added advantage during dry years and when there is not enough rainfall to permit a deeper water infiltration (Breda et al., 2006; Dorman et al., 2015).

During dry years or summer droughts, *Q. cerris* can also take advantage of relative air humidity, as shown by the higher significant correlations of this parameter compared to *F. sylvatica*. In summer months, the increased vapour pressure deficit (VPD) in conjunction with summer warming could, thus, most likely negatively affect mainly *F. sylvatica* cambial growth (Lendzion and Leuschner, 2008; Leuschner, 2020).

Another of the most distinctive patterns driving the contrasting BAI trends was the influence of temperature, with a negative effect much more significant for *F. sylvatica*. It was hypothesised that, after the 1980s, respiration could release a higher proportion of fixed carbon, reducing the amount of wood formed each year, also for the effect of temperature on VPD through stomata mechanisms (Timofeeva et al., 2017). In Spain, *Quercus pyrenaica* Willd showed a higher efficiency in nutrients and water utilisation compared to *F. sylvatica*, as expected for a xerophytic oak adapted to higher temperatures and longer summer droughts characteristic of Mediterranean conditions (Marín et al., 2023). In a natural beech–oak forest in western Romania, the increase in mean summer temperature was related to the *F. sylvatica* negative growth trend, particularly over a high specific threshold (Kasper et al., 2022). The beech foliage is relatively sensitive to heat, especially coupling its effect with drought (Leuschner, 2020). Rising summer temperatures may negatively influence the cambial water status through a higher evaporative demand, increasing water loss via transpiration. However, reductions in BAI of *F. sylvatica* and the *Quercus* species may not only relate to heat stress and drought but also to a consequence of irregular mast-fruiting. Indeed, high temperatures and insolation in dry summers most likely determine the mast-fruiting one or two summers after the drought (Vacchiano et al., 2017). Regarding the positive effect of winter-early spring temperature on *Q. cerris* tree-ring growth, the increase in winter-early spring temperatures may have anticipated the growing vegetative period and reduced the constraints of low temperatures, enhancing tree growth (Mazza et al., 2021).

4.3. Impact of drought on growth dynamics and recovery

The significant role of current late spring-early summer climatic conditions on *F. sylvatica* tree growth, as found for precipitation, also resulted in correlations with SPEI, confirming the strong impact of growing season drought at low-elevation sites (Piovesan et al., 2008).

After the '90s, the negative effect of long-term drought conditions on *F. sylvatica* increased, especially at the yearly scale for up to four preceding years. Recent studies on the sensitivity of *F. sylvatica* trees to drought events in European sites have documented an increasing relationship in recent decades (Latte et al., 2015). Piovesan et al. (2008) reported that summer drought was significantly related to BAI occurring one and two years later, and this delayed response has become more significant in recent times. As for temperature, these significant correlations could depend on an interaction with floral and masting processes and the resulting allocation of photosynthates to either vegetative or reproductive parts.

For *Q. cerris*, the negative influence of drought conditions increased, especially in the late spring-early summer period and when considering their prolonged effect up to two years before the year of ring formation. Several researchers on deciduous *Quercus* species widespread across the Mediterranean regions reported late spring-early summer drought as a significant driving factor for radial growth decline (Di Filippo et al., 2007; Bose et al., 2021; Mazza et al., 2021).

Considering the drought-related growth dynamics, most trees of both species expressed significant growth reductions during drought years, showing negative resistance indices. Conversely, *Q. cerris* trees appeared more resilient, although with very low positive values, because the growth levels after the critical droughts were slightly higher compared to the previous ones up to four years before. In northern mixed stands with other *Quercus* species, drought intensity was more correlated with BAI decline of *F. sylvatica* than *Quercus* species, and *F. sylvatica* showed the lowest resistance and resilience for the studied drought episodes (Vanhellemont et al., 2019). In our site, the main contrasting pattern in growth-dynamics responses to drought between the two species was the growth increase relative to the minimum growth during the drought episode. Indeed, the recovery (Rc) indices revealed a significantly higher ability of *Q. cerris* to recover their growth levels, especially in relation to the critical droughts below the fifth percentile (about 1.8 times more than *F. sylvatica*, $p < 0.01$). This mean behaviour at the stand level was confirmed by the single tree analysis, which showed the highest percentage of trees able to recover their growth after a drought year for *Q. cerris* (100 % and 69 % of trees with a positive post-drought growth recovery index for *Q. cerris* and *F. sylvatica*, respectively).

However, according to Kasper et al. (2022), when comparing different species, the Rc index may be a poor indicator of drought resistance, because small radial growth rates occurring during a drought due to low resistance generally lead to higher Rc scores than in more resistant species, which have to compensate for a lower growth reduction. For assessing the longer-term drought impact on growth, resilience (Rs) may be a more informative measure. In our case, both species showed similar negative resistance values, so the compensation of growth reduction during a drought can be considered comparable. These findings on drought-related growth dynamics suggest a generally significant impact of drought on tree growth reduction in both species and a higher sensitivity to drought stress for *F. sylvatica* trees in this low-elevation site.

Earlier dendrochronological and physiological observations on Central European mixed stands with oak species reported higher growth resistance (lower growth depression) and higher resilience than *F. sylvatica* (Kasper et al., 2022 and references therein). Carbon isotope data seem to confirm this hypothesis with the observed different trends in carbon-derived intrinsic water-use efficiency (iWUE) found in the two species (Battipaglia et al., 2009). iWUE reflects the balance between assimilation rate and stomatal conductance and thus is an indicator of the internal regulation of carbon uptake and water losses (Saurer et al., 2004; Battipaglia et al., 2014). Indeed, *F. sylvatica* in recent years showed a decrease in discrimination with a consequent increase in the iWUE. Nevertheless, an increase in iWUE alone is not directly translated into higher BAI, indicating that other factors, including high temperature, recurrent drought, nutrient limitation and/or plant acclimation, may preclude tree growth (Rezaie et al., 2018) and indicate climate stress (Niccoli et al., 2023). A comparable increase in iWUE, which did not avoid a decrease in forest growth, has been reported from other southern European beech forests because of climate change (Piovesan et al., 2005; Peñuelas et al., 2008). This suggests serious consequences for tree populations where current increases in temperature are not matched by increases in precipitations (Battipaglia et al., 2009).

In contrast, the positive correlation between iWUE and BAI of *Q. cerris* and the low statistically significant climate-$\delta^{13}C$ correlations indicate a better water use strategy of this species and a lower sensitivity to climate factors (Altieri et al., 2015). Further investigation of the oxygen–carbon composition of tree rings would help us to better understand the ecophysiological pattern driving tree growth of both species (Battipaglia et al., 2009) and to exploit the sources of water uptaken by trees along their lifespan (Battipaglia et al., 2020).

5. Conclusions

Our findings suggest that the increase in climate warming sensitivity in climatically marginal sites can negatively affect the adaptation capacity of the target species, driving a potential composition shift. The thermophilic beech forest studied, growing at a low elevation in Central Italy, was significantly affected by a decline of the favourable site-specific microclimatic conditions, weakening the future survival capacity of *F. sylvatica* and consequently compromising the conservation of this valuable ecosystem. The growth trend reversal of the two coexisting species and the shift in iWUE of the past few years may point to potential future changes in the species composition of these forests, suggesting a loss of competitive superiority of *F. sylvatica* under the current climate warming (about −20 % of BAI after 2003) for the better drought-adapted species *Q. cerris*, whose trees showed a significantly higher ability to recover their growth levels after extreme droughts (+55 %).

The results of this study can add new information for improving our understanding of the tolerance limits of a widespread European tree species such as *F. sylvatica* in terms of climatic and edaphic aridity. However, coordinated research efforts are needed to quantify the critical climatic thresholds for maintaining growth and vitality at the dry limit of the species distribution range, including molecular studies to introduce more drought-tolerant genotypes and proveniences. These research efforts should be coupled with climate-adaptive tree-oriented silvicultural strategies based on selective thinning to reduce growth decline and the related higher mortality risk, enhance resilience at the stand level and favour the natural regeneration of *F. sylvatica*, promoting the coexistence of both species under climate change scenarios for habitat conservation.

CRediT authorship contribution statement

Gianluigi MAZZA: conceptualization and methodology, data collection and analyses, writing the original draft, supervision.

Maria Cristina MONTEVERDI: helping in samples preparation for the isotopic analysis.

Simona ALTIERI: running laboratory isotopic analysis.

Giovanna BATTIPAGLIA: helping, writing and review the isotopic analysis.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Gianluigi Mazza reports financial support was provided by Regional Natural Park of Bracciano-Martignano (Lazio region, Italy).

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.2023.168250.

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