A single-tree approach to determine climate-growth patterns of European beech and their seasonality in the species southern distribution area

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ABSTRACT

Dry and warm climate conditions in southern Europe represent clear limits for European beech (*Fagus sylvatica*) growth near the species southern distribution limit, but it is unclear how aridification and changes in seasonal precipitation regimes will affect these forests at the individual level. We explored climate-growth relationships and the seasonality of peak climate signals in European beech using daily climate data and a large collection of tree-ring width series from southern and southeastern Europe through Generalised Linear Mixed Models (GLMMs). In most cases we found a positive and significant influence of precipitation on tree growth, and a significant negative effect of maximum temperature. Predictions from the GLMMs revealed a positive impact of precipitation during an 88 day window from spring to early summer (mid-April to mid-July), for an average tree across our network. This critical growing time window ranged from 75 days in warmer and drier conditions, and extended up to 100 days in areas with mild temperatures and moderate summer precipitation. Maximum temperatures negatively affected trees for an average of 27 day window in summer (June-July). This period was reduced to <10 days in locations with wetter and colder summers, rising up to 45 days in sites with drier and warmer summers. The positive effect of precipitation on growth was stronger and commenced earlier in larger trees. Similarly, the negative effects of maximum temperatures were more pronounced for larger trees. The use of daily climate data and a tree-centred approach allowed for capturing critical temporal dynamics in climate-growth relationships that are often overlooked by conventional methods. These insights significantly enhance our understanding of climatic factors influencing individual beech growth at the edge of its distribution range and their seasonal variations.

1. Introduction

The European beech (*Fagus sylvatica* L.) is a prominent deciduous tree that thrives across a wide range of forests throughout Europe (Houston Durrant et al., 2016). Preferring humid environments and moist but well-drained soils, it often outcompetes other tree species in favourable conditions (Houston Durrant et al., 2016). The current distribution of the tree species reflects a recolonisation since the end of the last ice age about 12,000 years ago, when beech was restricted to small remnants in the glacial refugia of southern Europe (e.g., Brus, 2010). The species post-glacial expansion coincided with the early development of agriculture and the establishment of permanent human settlements. Historically, it has been a crucial resource for both humans and animals, providing food (leaves and seeds), firewood and timber for buildings and various objects. With over 250 known uses for its wood, European beech is one of the most important and versatile industrial wood species in Europe (e.g., Houston Durrant et al., 2016; Pramreiter and Grabner, 2023).

Although European beech is typically regarded as a Central European tree species inhabiting temperate forests, it also grows outside the core area of its distribution (Bolte et al., 2007), including Mediterranean regions, Alpine and other mountain areas and continental zones. In these areas the species exhibits a plastic behaviour and response to climate limitations with adaptable growth patterns (Cavin and Jump, 2016; Martínez del Castillo et al., 2016; Klesse et al., 2024; Schurman et al., 2024), but is restricted to temperate microclimates in warmer and drier locations (Calderaro et al., 2020; Leuschner, 2020; Serra-Maluquer et al., 2019; Rozas et al., 2015; Tegel et al., 2014).

With the current pace of global warming (e.g. Esper et al., 2024; Serrano-Notivoli et al., 2023) and the projected increase of drought occurrence (IPCC, 2023), uncertainties about how European beech forest dynamics will be altered are increasing. Although the tree species demonstrates a relatively high capacity to cope with current climate change (Hacket-Pain and Friend, 2017), it also suffers significantly in southern areas, where the effects of climate change are more pronounced (e.g., Adamič et al., 2023; Buonincontri et al., 2023; Skrk et al., 2023; Levanič et al., 2023). Numerous recent studies have found that European beech is vulnerable to future climate change (Chakraborty et al., 2021; Diers et al., 2022; Leuschner, 2020), particularly at the geographical edge of its distribution range (Klesse et al., 2024; Martínez del Castillo et al., 2022; Petit-Cailleux et al., 2021). Low elevation, dry and southern areas are expected to be especially affected (Buonincontri

et al., 2023; Leifsson et al., 2024; Martínez del Castillo et al., 2022; Roibu et al., 2022; Škrk Dolar et al., 2023; Stjepanović et al., 2018). Previous research (Martinez del Castillo et al., 2022; Klesse et al., 2024) used an extensive tree-ring database of European beech growth across its entire geographic and climatic range and showed a decline in growth in the last decades. Furthermore, the studies forecast growth reductions of European beech over its current natural range, aggravated under warmer climate change scenarios. The projections show productivity decreases in many locations, with the greatest declines in the southern and eastern limit of the species' distribution range, i.e. areas where an increase in drought and temperature is very likely (Moss et al., 2010; Ukkola et al., 2020). On the other hand, the predictions of Prislan et al. (2019), and Bosela et al. (2023) present a more optimistic outlook for the future growth of the species. However, their projections are limited to humid or mountainous European beech forests, where future precipitation predictions are more stable. Moreover, other extreme events such as late spring frosts before drought periods can also have a significant effect on xylem ring formation (D'Andrea et al., 2020).

European beech trees are often reported to be sensitive to drought conditions, especially during spring and/or summer (Calderaro et al., 2020; Serra-Maluquer et al., 2019; Cavin and Jump, 2016; Rozas et al., 2015; van der Maaten, 2012), and often positively affected by warm temperatures in cold areas, such as at high elevation (Di Filippo et al., 2007; Dulamsuren et al., 2017; Klesse et al., 2024). These general climate constrains are modulated across altitudinal and environmental gradients (Cailleret and Davi, 2011; Leifsson et al., 2024; Martínez del Castillo et al., 2019) and also affected by site characteristics and tree features, such as forest composition, individual tree competition, tree size or age, soil characteristics, forest management history, or disturbances, among others (Goisser et al., 2016; Martínez del Castillo et al., 2024; Schurman et al., 2024; Weber et al., 2013; Zimmermann et al., 2015).

Despite previous studies, we still lack a comprehensive understanding of how different climatic factors influence the growth dynamics of European beech in the species southern-eastern distribution range, and if these differ among individual trees within forests. The widely used classical dendroecological approach, which relies on monthly resolved climate data and their correlation with the mean site chronologies, has some inherent limitations. One of these is the variability in research objectives across different studies, which significantly influences both site and tree selection. Consequently, the age/size structure, sample size and structural characteristics of sample sites differ significantly,

complicating direct comparison of results obtained across different regions. By calculating the correlation coefficients between tree growth and climatic variables, often based on data aggregated at monthly and seasonal scales, it is possible to identify the main climatic drivers at a specific site or in specific areas (Speer, 2010). Additionally, while using monthly or seasonal climate data is useful for certain purposes, it likely masks specific short-term climate effects that are crucial for a deeper understanding of climate effects in edge areas subjected to climate change. Lastly, a focus on individual growth responses to climate is needed given high tree-to-tree variability in the responses to climate (Carrer, 2011; Rozas, 2015).

Therefore, in this study, we focus on marginal, rear-edge European beech populations located in southern Europe, using a dense and updated tree-ring network. Furthermore, we leverage recently developed daily climate data available for the area and exploit updated open-source software to calculate daily climatic responses. The aim of this study is to describe detailed climatic growth relationships at the individual tree level, using 3807 individual tree-ring series of European beech in 185 study sites across the south and south-eastern distribution range. We seek to understand the seasonality of these climatic influences, how they vary across the sites and trees, and whether these variations are related to known climatic and environmental gradients and related to tree features. Ultimately, our goal is to gain a comprehensive and detailed understanding of how climate variability affects the growth dynamics of European beech in a part at risk of its distribution range.
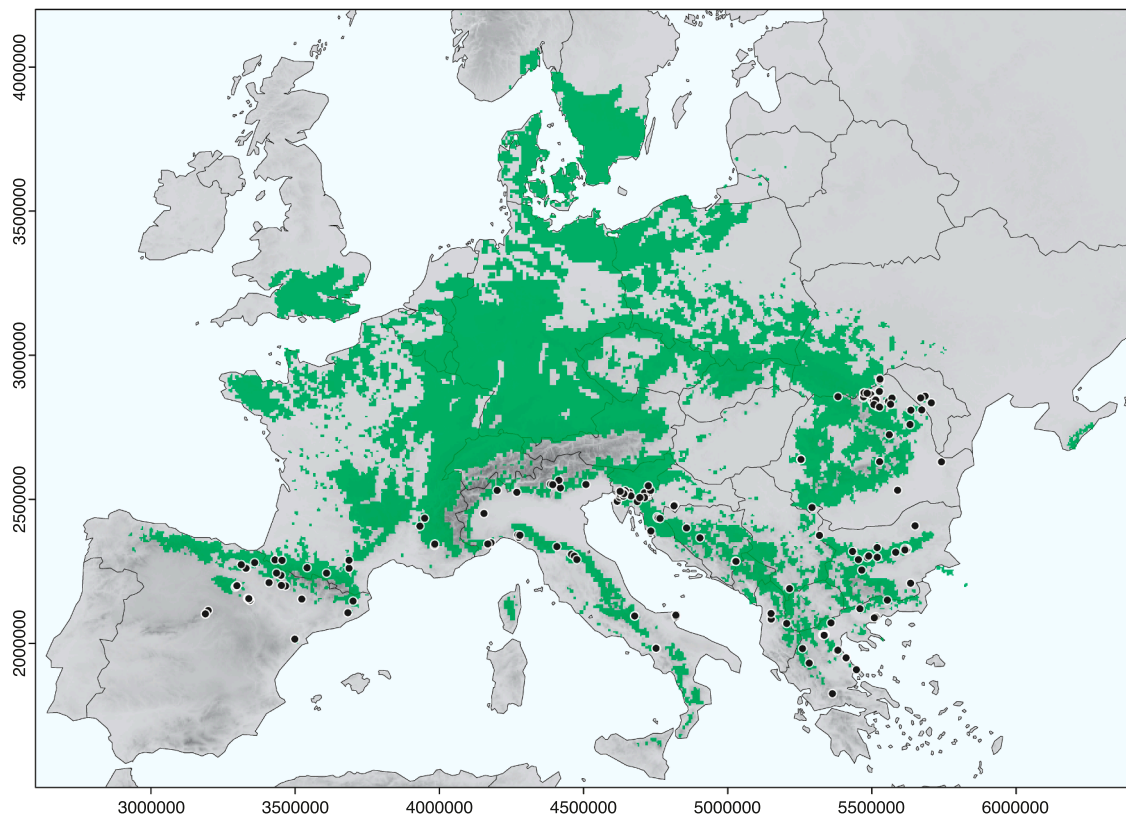
2. Material and methods

2.1. Tree-ring network

The dataset comes from a previously compiled ring-width data of the European Beech (*F. sylvatica*) Tree-Ring Network (EBTRN; as used in Hacket-Pain et al. 2018; Martinez del Castillo et al. 2022; Leifsson et al., 2024; Klesse et al., 2024). From it, we used tree-ring width (TRW) measurements from 185 study sites and a total of 3807 trees covering southern distribution limits of the species distribution range across Europe (Fig. 1; Supplementary Table S1). All sites included only dominant or co-dominant trees, sampled between 1989 and 2022. Sampling locations were originally selected as part of studies focused on climate–growth relationships, each designed to address different dendroclimatological research questions while aiming to minimize the influence of competition and other disturbances. The compiled network covers a large climatic gradient, with a mean annual temperature ranging from 5.8 to 13.6ºC, and precipitation varying between 405 and 1789 mm. TRW measurements were obtained using standard dendrochronological methods (Cook and Kairiukstis, 1990). These included tree coring or stem disc collection, drying, and preparation of the wood surface, followed by ring-width measurements on the wood cross section under the microscope and using the specialized tree-ring measuring stages (e.g., LinTab) or from high-resolution images using specialized software (e.g., CooRecorder). Cross-dating was applied to ensure that each individual tree-ring was assigned the exact year of its formation. To allow for a more objective comparison among different sites, trees and periods, age-related trends and the effect of other non-climatic factors were reduced by applying detrending methods. We used a negative exponential function followed by a cubic smoothing spline with a 50 % cutoff frequency and a 30-year response period which was applied to each individual series (Bunn, 2008). Next, the first-order autoregression for each previously obtained detrended series was calculated and removed to obtain residual series (de Luis et al., 2013). Finally, when more than one sample per tree was available, the residual series for each individual tree was calculated using a bi-weight robust estimation of the mean of the tree-ring index (TRWi).

To study the effects of individual tree characteristics on the obtained climate-growth patterns, we followed the individual-tree approach
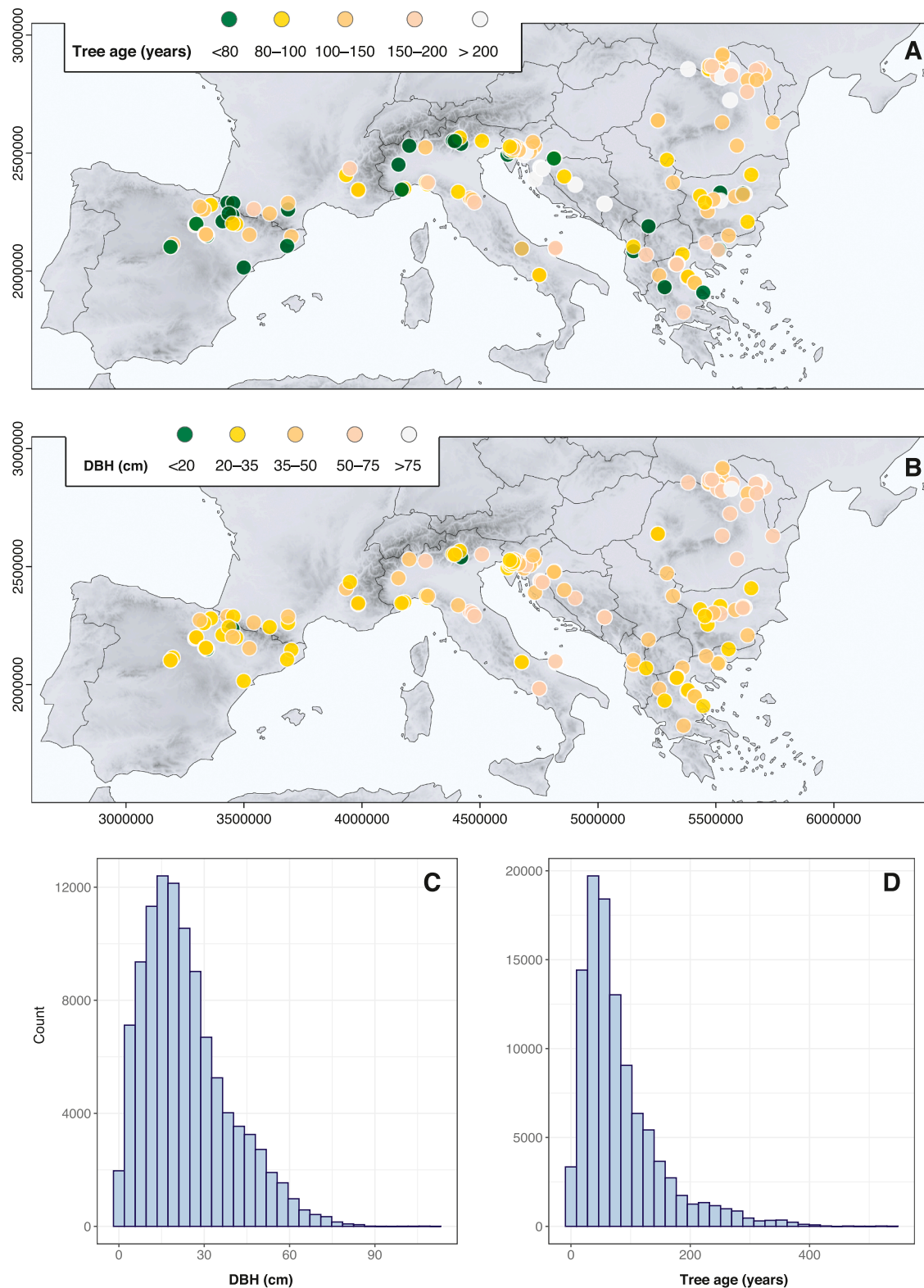

Fig. 1. Location of the 185 study sites (black dots) located across the southern and south-eastern distribution limits of the native distribution range of European beech (green shade) (Source: EUFORGEN map65; see Supplementary Table S1).

suggested by (cf. Carrer, 2011; Rozas, 2015; Sass-Klaassen et al., 2016). This method has been applied in previous studies describing the growth response of European beech to climate in its distribution range (Martínez del Castillo et al., 2022; Škrk Dolar et al., 2023).

2.2. Tree diameter and cambial age

The average DBH of all analysed trees at the beginning of the 30-years subperiods was 23.6 cm, ranging from values below 20 to higher than 75 cm (Fig. 2B). The cambial age of the trees at the beginning of the analysed subperiods varied from 30 to 540 years, with an average of 82
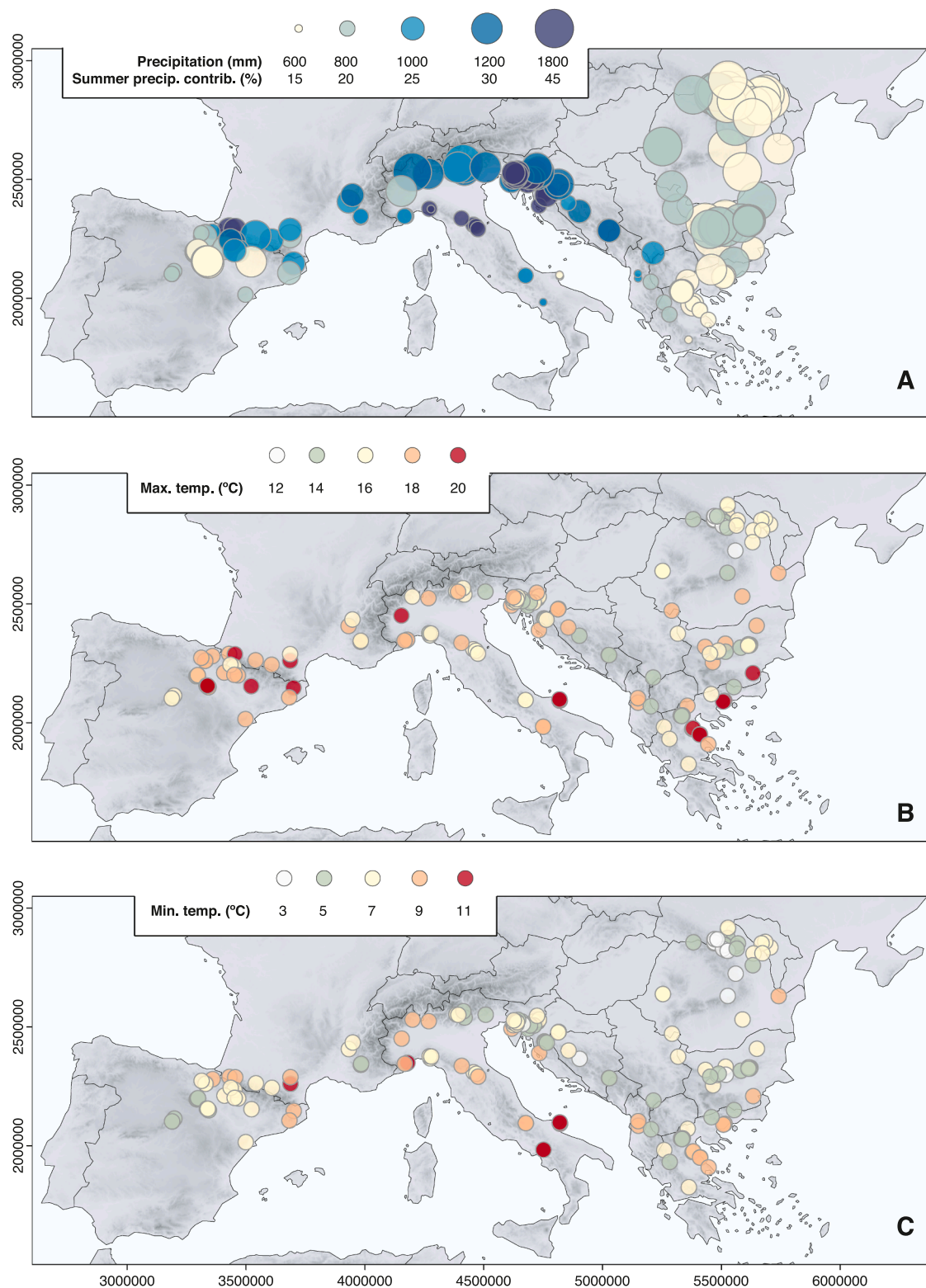

Fig. 2. Geographical variation of (A) cambial age and B) average diameter at the breast height - DBH structure of the sampled tree population across the 185 study sites. Histograms illustrate the frequency of DBH (C) and tree age (D) for the total number of tree/period combinations in all size/age groups.

years (Fig. 2A). The age/size structure of the analysed trees at the beginning of the 30-year analysed period strongly varied among the study sites with a mean DBH lower than 5 to higher than 50 cm, and mean cambial ages ranging from <10 to >300 years. The spatial distribution showed lower values of DBH in Spain, southern France, northern Italy and Greece, and larger values at the northeast of the analysed area, i.e. in Romania and Moldavia (Fig. 2A). The mean tree age was similar among sampling sites, but a smooth longitudinal gradient from younger to older trees was noticed from west to east.

Fig. 3. (A) Mean annual precipitation (colours) and percentage of summer precipitation contribution to the annual total (size of the circles); (B) Mean annual maximum temperatures and (C) mean annual minimum temperatures for the 185 study sites in the 1950–2022 period.

2.3. Climate characteristics across the southern distribution limit

Although site selection was restricted to the species rear edge, the European beech sites analysed exhibited a range of variable climatic conditions, both in terms of extent and seasonality.

Mean annual precipitation across study sites varied from <500 mm at some sites in Greece and Spain to above 1500 mm at some sites in Slovenia, Italy and Croatia (Fig. 3A). The seasonality of precipitation also showed strong variations between study sites, including Italy, Spain and southern areas of Greece where summer precipitation represented <15 % of the annual total, to other sites, especially those located in Romania, where summer was the main precipitation season representing more than the 40 % of the annual amounts.

Mean annual maximum temperatures also varied between the study sites with a spatial pattern strongly related to elevation and latitude, ranging from areas with temperatures above 18 ºC in the Spain, southern Italy and Greece to others with values below 12 ºC, especially in Romania (Fig. 3B). Variations in mean annual minimum temperatures exhibited similar patterns, highlighting the effect of continentality with sites where annual means were below 2 ºC at northeast of the sampling area and over 9 ºC in southern Italy (Fig. 3C).

2.4. Assessment of climate-growth relationships

We used daily climate data available for the whole area of interest from the E-OBS gridded dataset v22e at 0.1 × 0.1º spatial resolution (Cornes et al., 2018). For each sampled site, daily precipitation (PCP), maximum temperature (TMAX) and minimum temperature (TMIN) temperature data series from 1950 to 2022 were extracted from the overlapping grid cell.

To evaluate the statistical relationships between climate and individual tree growth series, we used the open-source software dendroTools R package to calculate daily climatic responses (Jevšenak, 2019; Jevšenak and Levanič, 2018). The daily climate data were aggregated considering all possible periods with a minimum length of 30 days and a maximum of 180 days. We considered only periods within a usual growing season, starting at the day of the year (DOY) 90, and ending on the DOY 275. To account for potential biases resulting from trends in climate data, each climate series was detrended before the calculation of the correlation coefficient (Ols et al., 2023). To do so, we used linear detrending, which involves fitting a linear regression model to represent the long-term trend across the climate series and subsequently subtracting this trend component from the original observations.

Climate–growth correlations were calculated individually for each tree residual series to assess the variability within each study site (Carrer, 2011; Rozas, 2015). In addition, since the length of the series and the period which they cover may differ between trees and sites, we calculated correlations for all trees using 30-year moving windows, shifted by one year at a time, starting from 1950–1979 and ending with 1993–2022. For each subset period, we also extracted the long-term seasonal and annual climate means, and estimated the diameter at the breast height (DBH) of the tree under calculation at the beginning of the analysed 30-year period through the R package *dplR* (version 1.7.2).

These explanatory variables were later used in the modelling part (see Section 2.5). Thus, considering 3807 trees in the 1950–2022 period, a total of 105,461 *dendroTools* runs were completed for each climate variable (PCP, TMAX and TMIN). For each run and for all three climate variables (PCP, TMAX, and TMIN) independently, we extracted the maximum (MAXcor) and the minimum (MINcor) correlation coefficient and the associated aggregated time period, i.e. the first (MAXcor_DOYstart and MINcor_DOYstart) and the last DOY (MAXcor_DOYend and MINcor_DOYend).

2.5. Modelling climate-growth relationships and associated seasons

We used Generalized Linear Mixed Model (GLMM) with quasi-binomial distributions of the response variables to model the variations among different sites, trees, and periods of the dependent variables considered, including the extracted maximum (MAX_COR) and minimum (MIN_COR) correlation values and the associated time periods, i.e. onset (MAX_START and MIN_START) and end (MAX_END and MIN_END). We modelled the positive (MAX_COR) and negative (MIN_COR) correlations to account also for potentially existing positive and negative effects of temperatures on European beech growth during different periods of the year. All dependent variables were rescaled to approximate a quasi-binomial distribution before model computation. Finally, the resulting predictions were restored to the original distribution of the dependent variables. The dependent variables were modelled for PCP, TMAX and TMIN, and the workflow followed three steps:

1) **Full models**: For each tree and 30-year subperiod of analysis, the independent variables included in the GLMM as fixed factors were: the DBH, the difference in altitude between the sampling site and the elevation of the grid cell of the climatic dataset, the corresponding mean seasonal values of PCP, TMAX and TMIN, and the interactions among mean annual values as well as their interaction with DBH. To ensure that the predictors were on the same scale, all independent variables were first standardized to have a mean of 0 and standard deviation of 1. The individual tree identity code was included as a random variable in the models to account for potential particularities of individual trees, as done in previous research (Klesse et al., 2024; Leiffson et al., 2024; Royo-Navascues et al., 2021 and 2022). The models were formulated as follows:

$$
\begin{aligned}
logit(P(VAR = 1)) = {} & \beta_0 + \beta_1(DBH) + \beta_2(PCP_{WIN}) + \beta_3(PCP_{SPR}) \\
& + \beta_4(PCP_{SUM}) + \beta_5(PCP_{AUT}) + \beta_6(TMAX_{WIN}) \\
& + \beta_7(TMAX_{SPR}) + \beta_8(TMAX_{SUM}) \\
& + \beta_9(TMAX_{AUT}) + \beta_{10}(TMIN_{WIN}) \\
& + \beta_{11}(TMIN_{SPR}) + \beta_{12}(TMIN_{SUM}) \\
& + \beta_{13}(TMIN_{AUT}) + \beta_{14}(PCP_{ANN} \cdot TMAX_{ANN}) \\
& + \beta_{15}(PCP_{ANN} \cdot TMIN_{ANN}) \\
& + \beta_{16}(TMAX_{ANN} \cdot TMIN_{ANN}) \\
& + \beta_{17}(DBH \cdot TMAX_{ANN}) + \beta_{18}(DBH \cdot TMIN_{ANN}) \\
& + \beta_{19}(DBH \cdot PCP_{ANN}) + \beta_{20}(ALT_{DIF}) + b_{TREE\_CODE} \\
& + \varepsilon
\end{aligned}
$$

where:

$logit(P(VAR = 1))$ is the logit link function to model the (quasi)binary response,

β_0 is the fixed intersection (intercept) of the model,

β_i represents the coefficients of the fixed effects of predictor variables,

$b_{TREE\_CODE} \sim \mathcal{N}(0, \sigma^2)$ is the aleatory effect associated to each individual tree,

ε is the error term of the model.

2) **Reduced models**: The model outputs were evaluated by comparing the full models, that included all independent variables, with reduced models where non-significant explanatory variables were omitted. The Akaike information criterion (AIC) scores (Akaike, 1987) were used for this purpose.

3) **Climate-growth responses**: Lastly, to illustrate differences in climate-growth responses and their seasonality across the southern distribution range, the reduced models were applied to the mean climate conditions observed across the study sites in the most recent 30-year period (1993–2022). These predictions were made for a

theoretical tree with a DBH of 23.6 cm, representing the average DBH of all the analysed combinations of trees and periods.

All statistical analyses were performed in R language. Detrending and chronology building were performed using the *dplR* package (Bunn, 2018), climate correlations were obtained by using the *daily_response()* function from the dendroTools R package (Jevšenak, 2020; Jevšenak and Levanič, 2018), and the GLMMs were calculated with the R package *lme4* (Bates et al., 2014).

3. Results

3.1. Variability of climate-growth relationships across sites, trees and periods
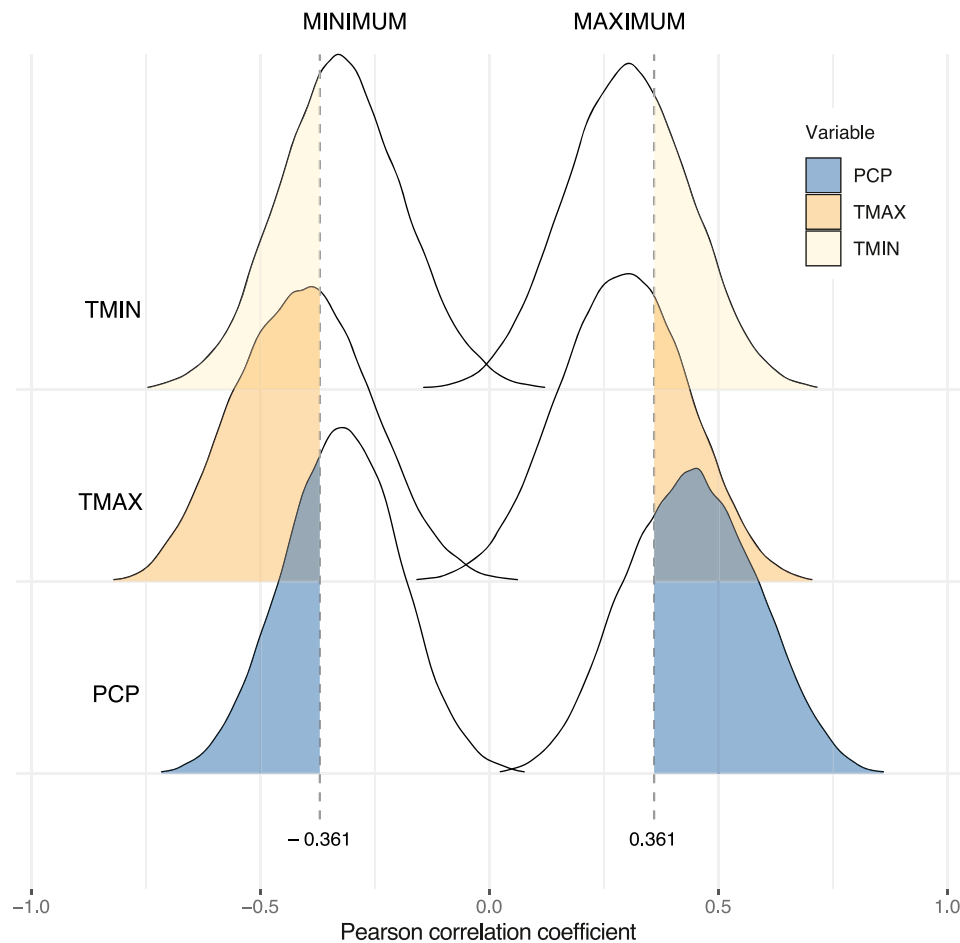
In addition to the high variability of tree characteristics and climate conditions across the study sites, we also found a remarkable variability in the climate-growth correlation values obtained. Overall, results showed that in most of the analysed combinations, precipitation is a primary driver of growth with a positive and statistically significant effect on tree growth. Similarly, a generalized significant negative effect of maximum temperatures on tree growth was detected across the studied distribution range. Negative effects of precipitation or positive effects of maximum temperatures were also observed for some tree/period combinations, though these effects were generally not significant. Similarly, non-significant effects of minimum temperatures were found for most combinations (Fig. 4).

The variability in the correlation values reflects important differences in the climatic influences observed between sites, as well as notable internal variability within each site, arising from differences in individual tree characteristics and the climate conditions during the analysed periods. Thus, positive effects of precipitation and negative effects of maximum temperatures were found together in 50.5 % of combinations and, when detected, such effects occurred for all trees and periods when detected. Similarly, the influence of the other climatic variables exhibited substantial variability both between and within sites. Consequently, the critical time periods (start and end of maximum correlations) greatly varied between and within sites (Fig. 7).

The observed within-site variability indicates the existence of an inherent instability in the climate-growth relationships, influenced by both the changing conditions during the analysed periods and differences in tree age and size characteristics.

The positive influence of precipitation prevailed across all the study sites (Fig. 5A). However, the central study area, encompassing Italy, Croatia and Bosnia-Herzegovina exhibited a lower frequency of significant correlations. In contrast, the negative influence of precipitation (Fig. 5B) showed the opposite behaviour, with significant negative correlations concentrated almost exclusively in these central areas. A similar pattern emerged for temperature. Notably, the spatial distribution of the negative influence of maximum temperature on growth (Fig. 5D) aligned with of positive influence of precipitation, indicating a combined positive precipitation and negative maximum temperature influence at the same sites.

A complete description of the number of trees and periods analysed

Fig. 4. Kernel densities of the minimum (left) and maximum (right) correlation values from the total 105,461 available combinations. Climate variables: PCP, daily precipitation; TMAX, maximum temperature; TMIN, minimum temperature. Correlation values higher than 0.361 or lower than −0.361 were significant at $p < 0.05$ ($n = 30$).
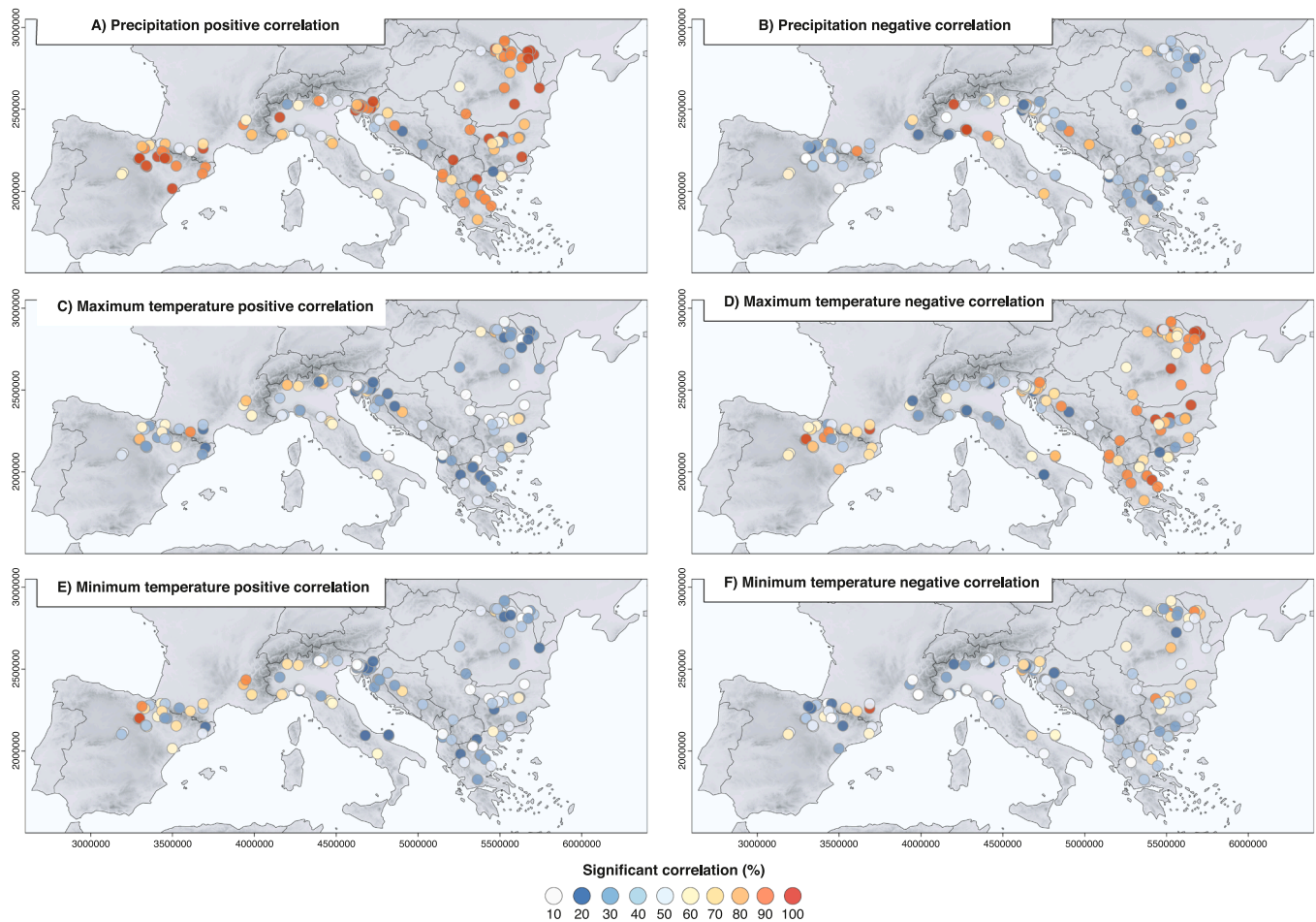
Fig. 5. Percentage of significant positive and negative correlation values considering all combinations (tree/period) at each study site.

at each study site, along with the mean, standard deviation, maximum and minimum correlation values, and the critical dates corresponding to these correlations, is provided in Supplementary Tables S2 to S19.

3.4. Main climatic gradients and individual tree factors explaining variations in climate-growth relationships

The intensity of the influence of each of the six climatic variables (positive and negative effects of precipitation, maximum and minimum temperatures) and their seasonality (starting, end and the length of the influences) were modelled using the GLMM approach. According to the AIC scores, the simplified model proved to be the most accurate to predict the correlation values of influences of each of the six variables and their seasonality (Supplementary Table S20). Complete details of model parameters can be found in Supplementary Tables S21–S38, while the accuracy, assessed by comparing observed and predicted values, is illustrated in Fig. 6.

The selected models reveal that previously observed variability in the intensity (correlations) and the seasonality (start and end of the period of influence) of the climate-growth relationships can be effectively explained by tree DBH and by the spatial and temporal variations of the climate conditions across the study sites (independent variables). Additionally, the application of these models enables the generation of comparable and unbiased predictions of the importance and seasonality of the climatic influences to be obtained.

In agreement with the previously described results, the predictions of the models for an average reference tree with a DBH of 23.6 cm growing in the period 1993–2022 showed that the positive effects of precipitation from April to July and the negative effects of maximum temperatures

from June to August are the predominant climatic influences affecting the growth of European beech throughout the study area. However, despite these general common influences, spatial variability in both correlation values and seasonality was less pronounced in the central study area, in Italy, Croatia and Bosnia-Herzegovina.

The DBH of trees played a significant role on both the intensity and seasonality of the climatic signals (Supplementary tables S21 to S38). Thus, the positive effect of precipitation was found to be stronger (i.e. higher correlation value) and to commence earlier in the year (i.e. earlier period of influence) for larger trees (i.e. higher DBH). Similarly, the negative effects of maximum temperatures are greater (i.e. more pronounced negative effects) in larger trees, although in this case the seasonality of this influence remained consistent regardless of tree size.

3.4.1. Precipitation

We found that the predicted correlations between precipitation and tree growth exceeded 0.6 across nearly the entire study area (Fig. 7A). However, this influence was more pronounced in the eastern part of the species' range, where the correlation values exceeded 0.75. On the other hand, lower correlation values overall were found in the southern distribution limits of Spain, Italy and Greece, mainly due to the drier conditions in these regions.

The onset day of the critical season with the strongest influence of the precipitation (Fig. 7C) occurred, on average, April 16 (DOY 106). The variations between the sites were mainly driven by precipitation and temperature gradients throughout the study area. In drier and warmer regions, precipitation from earlier dates played a critical role, whereas in more mesic areas, the importance of precipitation was delayed until late April.
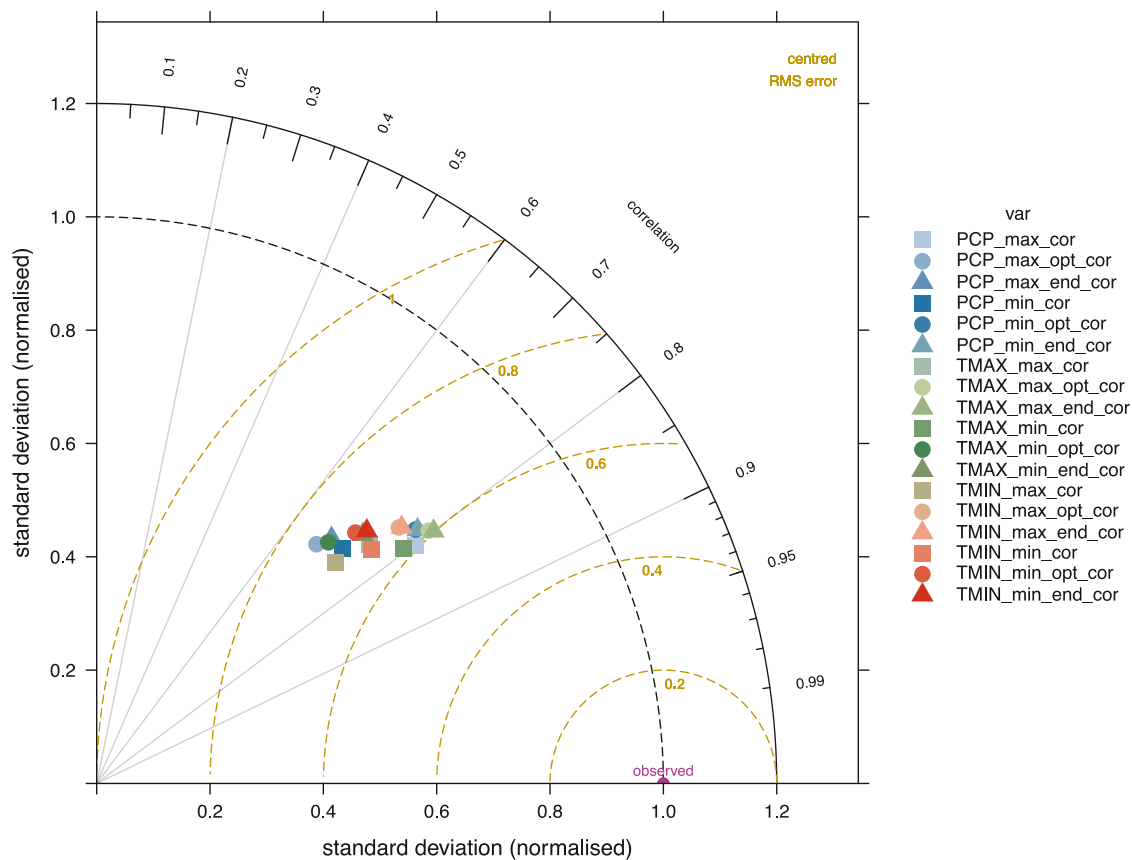
Fig. 6. Taylor diagram illustrating the performance of the selected models by comparing observed values with model estimates.

The end of the season with significant influence (Fig. 7D) extended, on average, to July 13 (DOY 194). However, in the most arid Spanish sites an earlier end date was observed, while later dates were predicted for the more mesic sites from Slovenia, Croatia and Serbia. Consequently, the duration of the precipitation influence averaged 88 days, ranging from <75 days in warmer and drier conditions to as many as 100 days in areas with mild temperatures and summer precipitation (Fig. 7B).

3.4.2. Maximum temperature

Although less significant and exhibiting a different signal and seasonality, the average maximum temperatures also had an important influence on European beech growth across the study area (Fig. 8A). The mean predicted correlation was −0.47, however, in regions with drier conditions in summer, e.g. in southern Spain, more extreme negative effects were predicted, close to −0.6. In contrast, in the western distribution area, with higher summer precipitation, the predicted correlations rarely reached −0.35.

The period in which the maximum temperatures had the greatest effect on tree growth lasted on average for 27 days. At some sites with wetter and colder conditions during the summer, this period was greatly reduced to <10 days, while at other sites with drier and warmer summer conditions it was extended to up to 45 days (Fig. 8B).

Summer and autumn precipitation emerged as key drivers of spatial patterns of the seasonal variations of this influence. For instance, the average start date was June 24 (DOY 175), but under warmer and wetter conditions it tended to occur earlier, around the first days of June (Fig. 8C). The negative influence of maximum temperatures extended on average until July 20 (DOY 201), although this date generally occurred earlier under more continental conditions and extended until mid-August at coastal regions (Fig. 8D).
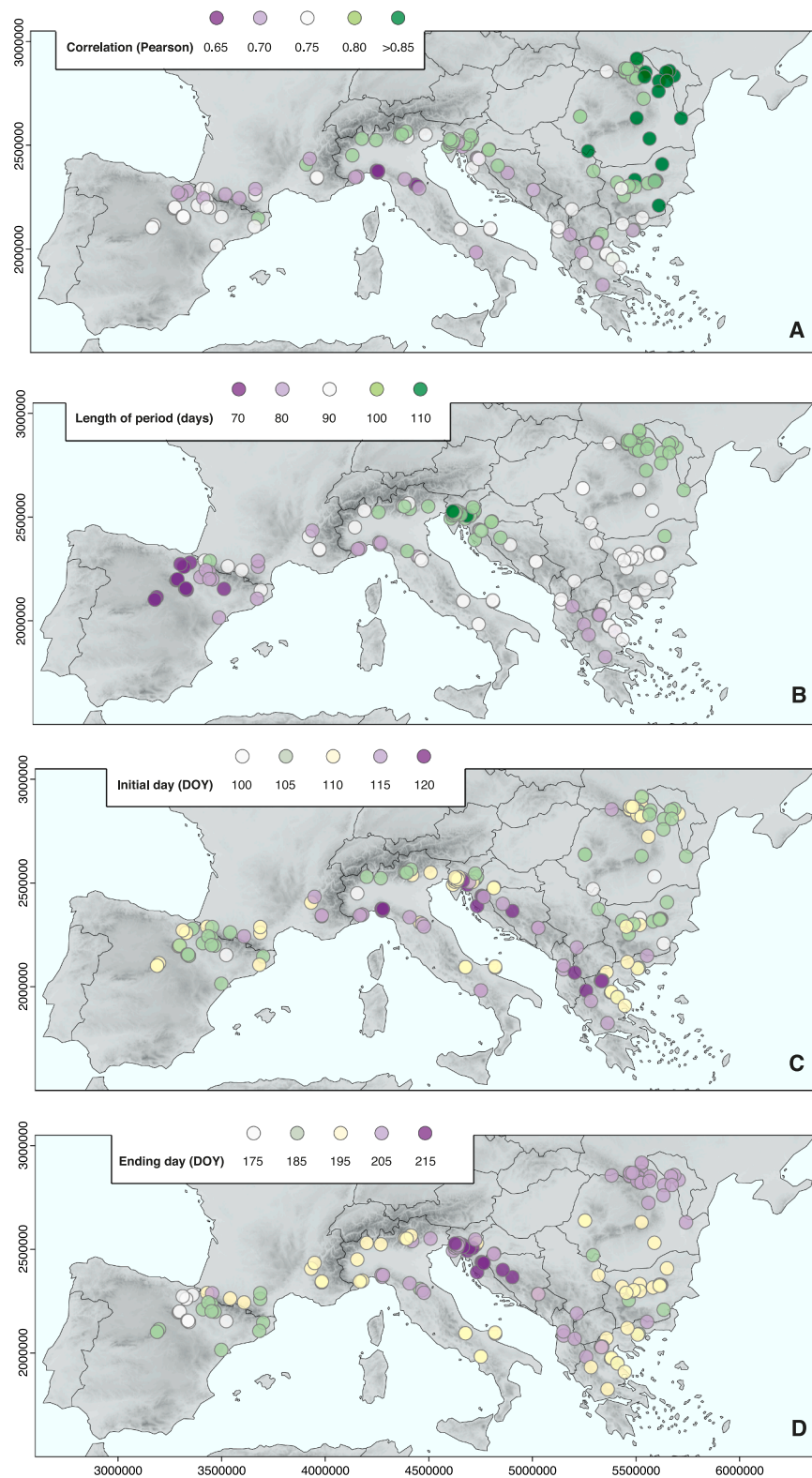
3.4.3. Other climatic variables

Overall, the other climate variables (PCP_MIN, TMAX_MAX, TMIN_MAX, TMIN_MIN) played a relatively minor role in the species growth, likely reflecting interactions with the previously discussed patterns (see graphical abstract). Thus, the negative effects of precipitation were most pronounced in autumn, with significant impacts predicted for certain sites in Italy, Greece and on the Adriatic coast - likely indicating confounding effects with autumn temperatures. The positive effects of maximum temperatures in spring were predicted for two sites in the Spanish Pyrenees, while some localized significant negative effects of minimum temperatures in early autumn were also observed, likely influenced by highly specific microclimatic conditions.

4. Discussion

Our study explored the climate-growth relationships of European beech across its southern distribution range, showing summer precipitation and temperature are key determinants of growth, but emphasizing the importance of tree size, age and local climatic conditions. Notably, we found that the positive effect of precipitation on tree growth was more pronounced in larger trees. The influence of precipitation also began earlier in the growing season for larger trees, and at warmer and drier sites. This suggests that bigger trees are likely to be more strongly affected by water limitation in the context of global warming, with strong effects of local climate.

We applied a tree-centred approach, which proved effective in capturing the growth responses of European beech to climate (Carrer, 2011; Rozas, 2015; Martínez del Castillo et al., 2022). Despite the significant variability in climate-growth relationships due to factors such as acclimatization and local influences, two climatic effects were consistently significant across the study sites; the positive influence of precipitation between mid-April and mid-July and the negative influence of
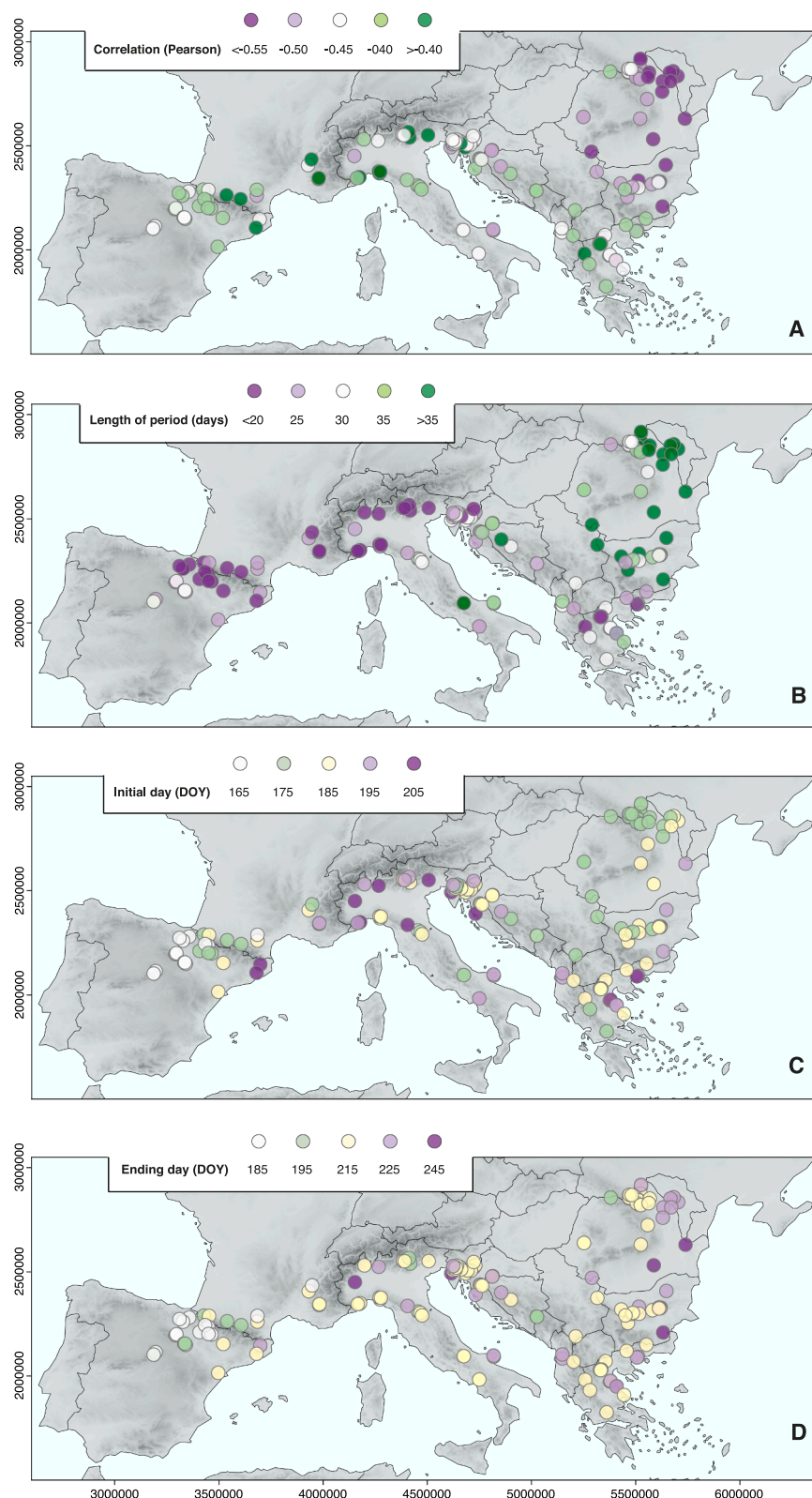
Fig. 7. Positive correlation (A) predicted between tree growth and precipitation calculated for a common theoretical tree for the common period 1993–2022 and predicted length (B) of the period between starting (C) and ending (D) day for which the positive correlation is predicted at each study site.

maximum temperatures, mainly from early June to late July. These results are broadly consistent with previous studies showing summer climate is the dominant factor determining interannual variability in beech growth (Calderaro et al., 2020; Hacket-Pain and Friend, 2017; Rozas et al., 2015; van der Maaten, 2012). However, we showed that the effects of climate on growth varied according to tree size. Larger trees

exhibited a stronger negative response to maximum temperatures, indicating higher sensitivity to summer drought in larger trees. Additionally, the critical window for precipitation started earlier in larger trees, and its overall duration was longer. These findings underscore the critical role of tree size in climate-growth relationships for conifers and broadleaves (e.g. de Luis et al., 2009; Mencuccini et al., 2005; Trouillier

Fig. 8. Negative correlation (colours) predicted between tree growth and maximum temperatures calculated for a common theoretical tree for the period 1993–2022 (A) and predicted length (duration) (B) of the period between starting (C) and ending (D) day for which the negative correlation is predicted at each study site.

et al., 2019), even at global scale (Anderson-Teixeira et al., 2021). For European beech, Mérian and Lebourgeois (2011) showed that tree size led to significant differences in the climate–growth relationships. Broadly consistent with our results, they showed that larger trees exhibited greater sensitivity to summer drought compared to smaller trees, with this difference becoming more pronounced under conditions of increasing climatic aridity. A more recent study by Leifsson et al. (2024), utilizing tree-ring data from across the entire distribution range of European beech showed that the species' drought sensitivity was highly variable and non-stationary. Our study, focusing on a more

targeted population, shows that the differences in concurrent high temperatures and low precipitation (drought alike) sensitivity are also related to tree size. Tree size emerges as a key feature and needs to be more frequently considered in future dendrochronological studies to ensure that sampling is appropriate and obtained results are reliable and representative. Non-stationary climatic growth relationships, as observed by Leifsson et al. (2024), may, therefore be partly attributed to the influence of tree size effects.

Our results indicate that the variability in drought sensitivity among European beech populations varies with existing climate gradients across its distribution range in southern Europe. We found stronger impacts of precipitation, that have a significant influence over growth for a long duration critical window, in populations growing under more favourable growing conditions. This finding is consistent with previous ecological studies, which have shown that tree species often exhibit significant spatial variability in their drought responses, influenced by factors such as local climate, soil properties, and topography (Anderegg et al., 2015; Gessler et al., 2020; Klisz et al., 2023; Klesse et al., 2024). For European beech, which is widely distributed across Europe, this variability is particularly pronounced at the southern margins of its distribution range, where trees are often subjected to more extreme climatic conditions, including higher temperatures and lower precipitation (Rukh et al., 2023). Similar findings have been reported for other tree species, further emphasizing the importance of understanding acclimatization processes in response to varying climatic conditions (de Luis et al., 2013). For example, studies on Scots pine (*Pinus sylvestris* L.) and pedunculate oak (*Quercus robur* L.) have shown that populations at the edge of their distribution ranges often develop adaptive strategies, such as altered phenology and increased water-use efficiency, to cope with increased drought stress (Carnicer et al., 2011; Matías et al., 2014; Camarero et al., 2021). Similarly, *Pinus nigra* J. F. Arnold from southern and northern distribution limits exhibited distinct spatial patterns of climate-growth relationships, resilience and vegetation indices (Izmir et al., 2024). These acclimatization processes may include both phenotypic plasticity and/or genetic adaptation in provenance that may allow trees to survive in environments that differ significantly from their historical climate regime (Valladares et al., 2014).

Recent research has also highlighted the role of local adaptation in shaping the drought responses of European beech populations. For instance, several studies have shown that populations from drier, southern regions of Europe tend to be more drought-tolerant compared to their northern counterparts, suggesting that they have developed specific adaptations to their local climatic conditions (Bolte et al., 2016; Hampe and Petit, 2005). Other environmental variables such as soil moisture and nutrient availability, nutrient status, and forest management practices also play critical roles in influencing drought sensitivity (Cartwright et al., 2020; Castagneri et al., 2022). For example, forests with well-managed undergrowth and sufficient soil organic matter may be better prepared to buffer against drought stress, thereby enhancing the resilience of European beech populations (Mainiero and Kazda, 2006; Pretzsch et al., 2022). However, as climate change progresses, the drought conditions will become more extreme in many regions, leading to potential shifts in species distributions (Dyderski et al., 2018), changes in forest composition, and potentially collapses in reproduction and large-scale die-off and mortality events (Allen et al., 2010; IPCC, 2023; Bogdziewicz et al., 2023). For European beech, this could mean a contraction of its range, particularly in southern Europe, where the species is already near the edge of its climatic tolerance (Martínez del Castillo et al., 2016).

Our study underscores the value of utilizing daily climate data to accurately capture the precise timing and intensity of climatic influences on the growth of individual trees, which can be obscured when using traditional monthly datasets. By employing the daily approach, we revealed the growth response to high frequency climate variability. The influence of the precipitation and maximum temperatures manifest at different times of the year and over varying time periods. For example,

precipitation impacts growth over an average of three months on average in spring and early summer, while maximum temperature effects are typically observed over a shorter period – averaging just one month in June-July. Additionally, geographical differences in these patterns exists across the study area. Several drought indices are multiscalar, but must be calculated for a common climate window (1 to n months) (Vicente-Serrano et al., 2010) therefore, they may not capture the actual period of climate influences. This approach is particularly relevant when studying species across a broad geographic range, where local studies may not be generalizable to the entire distribution (e.g. Bolte et al., 2007; Dittmar et al., 2003; Jump et al., 2006). However, these approaches can be time-consuming and computationally intensive. To address this challenge, we benefited from new features in the dendroTools R package, which enabled a reduction in the total number of seasonal combinations analyzed, reducing computation demand.

While our study advances the understanding of climate impacts on beech trees and forests at the southern distribution limits of the species, several limitations should be acknowledged. Firstly, our analysis focused on dominant and co-dominant trees, which may not represent the entire population, particularly understory trees that might exhibit distinct growth responses. Future studies should investigate whether the observed patterns are consistent among non-dominant trees, which are often underrepresented in traditional dendrochronological research. Moreover, other important factors such as competition, stand density, composition and disturbances were not considered in this study due to data unavailability. Incorporating these factors could offer a more holistic understanding of the forest dynamics affecting tree growth (Alexander et al., 2018; Dulamsuren et al., 2022; Schurman et al., 2024). Secondly, we did not account for the potential effects of the previous year's climate on tree growth, despite evidence suggesting that these effects can be significant (Rohner et al., 2016). This omission was primarily due to computational constraint associated with managing large climate datasets. Future research should aim to include these lagged climatic effects to further refine our understanding of tree growth dynamics.

However, the use of daily scale data and the aggregation of climatic influences across different time periods offer new possibilities for obtaining insightful results, there are inherent risks associated with this approach. Specifically, when performing multiple correlations of time series in moving windows, there is a potential risk of encountering spurious correlations that can lead to misleading interpretations (Torbenson et al., 2024), particularly in complex ecological systems where climatic signals are less pronounced and multiple factors interact over varying temporal scales. While the significant correlations obtained in this study generally align with well-known ecological responses of European beech, it is important to acknowledge this potential limitation. Lastly, a more robust connection between the described spatial and temporal variations in European beech climate-growth relations and the physiological processes involved needs to be confirmed through experimental studies in xylogenesis, tree phenology and ecophysiology.

5. Conclusions

We investigated the relationships between climate and tree growth of European beech in its southern distribution range. Employing a novel daily approach, we modelled the response of individual trees to climate at a daily scale, with a focus on the seasonality of these interactions. This approach allowed us to unveil the dominant temporal and spatial patterns of this species' response to climate at its limits. Results showed a clear and significant positive influence of precipitation and a negative effect of maximum temperatures. More specifically, we found that precipitation influence on annual growth commenced earlier in dry and warm areas than in more mesic conditions, where its influence is delayed until mid-spring. Finally, these effects varied depending on tree size, with larger trees exhibiting more pronounced responses.

Our study underscores the importance of tree size and local climatic

conditions in shaping the growth responses of European beech. The use of daily climate data and a tree-centred approach allowed us to capture critical temporal dynamics in climate-growth relationships that is often overlooked with traditional methods. These findings have significant implications for a better understanding of acclimation processes of trees that are crucial for forest management, particularly in the context of tree adaptation of trees and mitigating the impacts of climate change. Moving forward, integrating more comprehensive datasets, and expanding the scope of research to include other species and environmental factors will be essential for developing robust strategies to conserve and manage forest ecosystems in a changing climate.

CRediT authorship contribution statement

Roberto Serrano-Notivoli: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Jernej Jevšenak:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Edurne Martinez del Castillo:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Katarina Čufar:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nina Škrk-Dolar:** Writing – review & editing, Writing – original draft, Data curation. **Giovanna Battipaglia:** Writing – review & editing, Data curation. **Jesus Julio Camarero:** Writing – review & editing, Data curation. **Andrew Hacket Pain:** Writing – review & editing, Writing – original draft, Data curation. **Alistair Jump:** Writing – review & editing, Writing – original draft, Data curation. **Renzo Motta:** Writing – review & editing, Data curation. **Paola Nola:** Writing – review & editing, Data curation. **Momchil Panayotov:** Writing – review & editing, Data curation. **Ion Catalin Petritan:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Andrei Popa:** Writing – review & editing, Data curation. **Ionel Popa:** Writing – review & editing, Data curation. **Catalin-Constantin Roibu:** Writing – review & editing, Data curation. **Miroslav Svoboda:** Writing – review & editing, Data curation. **Christian Zang:** Writing – review & editing, Data curation. **Tzvetan Zlatanov:** Writing – review & editing, Data curation. **Angela Balzano:** Writing – review & editing, Data curation. **Franco Biondi:** Writing – review & editing, Data curation. **Vojtech Čada:** Writing – review & editing, Data curation. **Dimitar Petrov Dimitrov:** Writing – review & editing, Data curation. **Jožica Gričar:** Writing – review & editing, Data curation. **Pavel Janda:** Writing – review & editing, Data curation. **Srdjan Keren:** Writing – review & editing, Data curation. **François Lebourgeois:** Writing – review & editing, Data curation. **Guangqi Li:** Writing – review & editing, Data curation. **Luis Alberto Longares:** Writing – review & editing, Data curation. **Ivan Lukić:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maks Merela:** Writing – review & editing, Data curation. **Stjepan Mikac:** Writing – review & editing, Data curation. **Klemen Novak:** Writing – review & editing, Data curation. **Any Mary Petritan:** Writing – review & editing, Data curation. **Peter Prislan:** Writing – review & editing, Data curation. **Ana-Maria Roibu:** Writing – review & editing, Data curation. **Alvaro Rubio-Cuadrado:** Writing – review & editing, Data curation. **Miloš Rydval:** Writing – review & editing, Data curation. **Miguel Ángel Saz:** Writing – review & editing, Data curation. **Ernesto Tejedor:** Writing – review & editing, Data curation. **Willy Tegel:** Writing – review & editing, Data curation. **Roberto Tognetti:** Writing – review & editing, Data curation. **Elvin Toromani:** Writing – review & editing, Data curation. **Volodymyr Trotsiuk:** Writing – review & editing, Data curation. **Daniel Turcu:** Writing – review & editing, Data curation. **Martin de Luis:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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Data availability

Data is published in Zenodo: https://zenodo.org/records/14753469 and attached as supplementary material.

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