

Integrating annual radial growth analyses and carbon isotope discrimination to forecast early warning of beech forest dieback across the Italian Peninsula

Running head: Forecasting European beech mortality risk

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ABSTRACT

Tree mortality and forest dieback episodes are increasing due to drought and heat stress. However, a comprehensive understanding of the mechanisms enabling trees to cope with droughts remains lacking. Here, we employed a multi-proxy method utilizing tree-ring width, basal area increment (BAI) trends, and $\delta^{13}\text{C}$ -derived intrinsic water-use-efficiency (iWUE) to unravel beech resilience against drought stress. We selected four sites spanning the latitudinal gradient and beech distribution in northern (Trentino-TRE), central (Lazio-LAZ), southern (Campania-CAM) and southernmost Italy (Calabria-CAL) with different climate conditions and soil water availability.

First-order autocorrelation (AR1) analysis was performed to detect early warning signals for potential tree dieback risks during extreme drought events. Results revealed a negative correlation between vapour pressure deficit (VPD) and BAI, especially at southern latitudes. GAMM analysis showed a negative trend in BAI across most sites, stronger at the TRE site following the 2003 drought event. During this event, $\delta^{13}\text{C}$ and iWUE increased with rising VPD, indicative of conservative water-use (lower stomatal conductance) and contributing to the decline in BAI. Conversely, CAM exhibited a steady increase in BAI and iWUE , likely influenced by rising atmospheric CO_2 and water availability. LAZ site exhibited a decrease in $\delta^{13}\text{C}$, attributed to greater soil water holding capacity, enabling it to sustain higher transpiration rates. Conversely, southern sites presented higher iWUE , likely as high VPD initially reduces stomatal conductance but not the net assimilation rate, resulting in increased iWUE . Nevertheless, almost all sites exhibited a co-occurrence of increase in AR1 (except for CAM) and standard deviation, suggesting a reduction of resilience to future extreme events.

Overall, multi-proxy, retrospective quantifications of BAI, iWUE and resilience provide a robust and complementary tool for differentiating water-use strategies and predicting tree growth decline and dieback, as well as identifying those that have the potential to survive in warmer and drier future conditions.

1 INTRODUCTION

Forest ecosystems are facing significant challenges due to anthropogenic climate change (Allen et al., 2010; McDowell et al., 2020). The combination of reduced water availability and rising temperatures directly impacts the process of photosynthetic carbon assimilation, thereby reducing forest carbon sequestration (Keenan, 2015; Zuidema et al., 2018). This could potentially lead to negative feedback on carbon balance (Pan et al., 2011). Furthermore, hotter droughts have caused substantial alterations in forest structure and function, affecting tree growth performance and triggering episodes of dieback and tree mortality (Allen et al., 2015; Anderegg et al., 2016; Puchi et al., 2021). In addition, climatic models predict that the frequency, duration, and intensity of extreme droughts will increase in the future (IPCC 2021), so it is crucial to a better understanding of how forests are going to cope with these extreme climatic conditions (Brodribb et al., 2020).

Despite the importance of identifying suitable tree species and future management practices in response to climate change, our understanding of species-specific physiological responses and site- and species-specific vulnerabilities to drought-induced tree mortality during extreme droughts remains incomplete (Allen et al., 2015; Trugman et al., 2021; De Marco et al., 2022). This gap is especially critical for European beech (*Fagus sylvatica* L.), one of the most distributed, ecologically and economically significant tree species in Europe (Fang and Lechowicz 2006). This species comprises 17% of all broadleaf tree stands in Italy (Gasparini et al., 2022) and is one the most affected by extreme events occurring during the initial vegetative phase across the Italian peninsula (D'Andrea, et al., 2020; Martinez del Castillo et al., 2022; Tonelli et al., 2023).

Given the anticipated that climate change will exert a significant influence on both regional and local drought patterns in the Mediterranean region (Adams et al., 2017; Sangüesa-Barreda et al., 2019). In particular, mountain-Mediterranean beech forests would face increased vulnerability due to their location in the southernmost distribution of this species' range (Noce et al., 2016, 2017; Leuschner

2020; D’Andrea et al., 2021). Consequently, predicting resilience and adaptation across its distribution has become a prioritized goal.

Recent studies have shown that prolonged heat and drought events can have detrimental effects on both hydraulic function and carbon use in trees (McDowell et al., 2008; Anderegg et al., 2013). Understanding these physiological mechanisms is crucial for comprehending how trees respond to drought, as they directly influence water use regulation. For instance, isohydric species adopt a conservative behaviour by closing stomata to minimize water loss, thereby reducing photosynthetic activity, and increasing the risk of carbon starvation (Timofeeva et al., 2017). On the other hand, anisohydric species adopt an opportunistic behaviour, exhibiting higher transpiration rates even when soil moisture is low, leading to an elevated risk of hydraulic failure (McDowell et al., 2008; Petrucco et al., 2017).

Currently, there is contrasting information regarding how European beech forests respond to heat and drought events (Leuschner, 2020; D’Andrea et al., 2021). Most studies on young beech stands have suggested a conservative response during droughts (Leuschner, 2020; Walthert et al., 2021; Martinez del Castillo et al., 2022). However, in a few studies, adult trees have conversely displayed opportunistic behaviour (Leuschner, 2020). Therefore, it is crucial to exploit better the plasticity of this species in the water use strategies to determine the trajectories of species distribution and its resilience to a warming and drier climate (Gessler et al., 2020; Walthert et al., 2021).

Long-term changes in intrinsic water use efficiency (δ WUE), i.e. the cost of fixing carbon per unit of water loss (Seibt et al., 2008; Gagen et al., 2022), can be assessed by measuring carbon isotope composition in tree rings ($\delta^{13}\text{C}$). Tree-ring $\delta^{13}\text{C}$ is equivalent to the ratio between photosynthesis (A) and stomatal conductance (g_s) and this can vary, since both affect the ratio between CO_2 partial pressure in leaf intercellular space and in the atmosphere (Farquhar et al., 1982; Battipaglia and Cherubini, 2022). Variations in δ WUE, within and across tree species, have revealed a continuous ecophysiological gradient of plant water-use strategies ranging from “profligate/opportunistic” (low

102 δ WUE) to those considered “conservative” (high δ WUE) (Moreno-Gutiérrez et al., 2012). For
 103 instance, studies in tree rings have shown that the increase of δ WUE did not enhance tree growth
 104 (Peñuelas et al., 2011), however, others showed the opposite effect or both (Peñuelas et al., 2008;
 105 Tognetti et al., 2014; Walker et al., 2021). These indicators of hydraulic strategies and carbon
 106 discrimination provide valuable insights into the long-term impacts of climate change on forest health
 107 and the risk of tree mortality (Gessler et al., 2018; Cherubini et al., 2021; Puchi et al., 2021).

108 On the other hand, recent studies have provided evidence that one of the primary mortality risk
 109 indicators in forests is growth reduction also occurring many decades before visible symptoms of
 110 decline, such as leaf discolouration, increased defoliation, and branch dieback (Camarero et al., 2015;
 111 Cailleret et al., 2016; 2019; DeSoto et al., 2020). Similarly, another proxy indicator of loss of
 112 resilience and thus increasing tree mortality risk is the autocorrelation, better called ‘early warning
 113 signal’ (EWS), which has been proposed to detect a critical transition in long-term time series after a
 114 perturbation, causing a critical slowing down of the capacity of recovery (Dakos et al., 2012a; Gessler
 115 et al., 2020; Forzieri et al., 2021). EWS can be highlighted as increasing autocorrelation and variance
 116 in tree growth, indicating loss of resilience and stability (Dakos et al., 2012a; 2012b). These changes
 117 have been observed in conifers; however, angiosperms did not show changes in these indicators, and
 118 this could be due to their capacity to recover after a stress-induced growth decline (Camarero et al.,
 119 2015; Cailleret et al., 2019). These findings highlight the importance of early monitoring in
 120 understanding forest resilience and adaptation to climate change.

121 This study aimed to assess the forest vitality of beech in response to drought stress by examining
 122 historical and recent growth patterns across the Italian peninsula, with a particular emphasis on water
 123 use strategies (conservative vs. opportunistic) at long-time scales. Secondly, we tested early warning
 124 signals of potential tree dieback by analyzing autocorrelation and variability patterns, as indicators of
 125 stand resilience and stability to future extreme events.

We hypothesized that beech populations in the southernmost distribution exhibit conservative behaviour as an acclimation strategy. This behaviour is characterized by δWUE being more responsive to VPD than those in the northern regions, reflecting a reduction in stomatal conductance to maintain a minimum midday water potential, and also a decline in intercellular CO_2 concentration, but a more slowly decrease in photosynthetic rate. Although a drought-driven decline in photosynthetic rate may also occur, non-stomatal limitation was expected in populations with more opportunistic behaviour. Additionally, we expected to find varying degrees of growth reduction as an early warning signal of tree mortality risk across different sites, with the strongest signals in response to severe drought events.

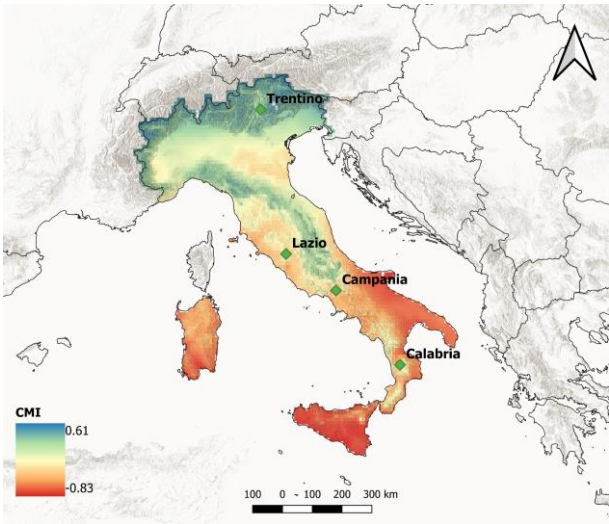
2 MATERIALS AND METHODS

2.1 Study sites and climate

Analyses were conducted at four sites along a ~900 km latitudinal transect in pure European beech forests across the Italian Peninsula (Figure 1, Table 1). The sites were Trentino-Alto Adige (hereafter abbreviated as ‘TRE’), Lazio (hereafter abbreviated as ‘LAZ’), Campania (hereafter abbreviated as ‘CAM’) and Calabria (hereafter abbreviated as ‘CAL’). All the stands analyzed had not been managed since the last 20-30 years.

The selection of the sites allowed the comparison of moisture availability across the Italian Peninsula (Figure 1), using the Climate Moisture Index (CMI) calculation method explained in section 2.6. These sites differ along the latitudinal transect regarding both climatic conditions and soil types. From north to south, the mean annual temperature ranges from 9 to 14.1 °C, with the mean annual precipitation varying from 1003 to 825 mm, based on the E-OBS dataset (as explained in section 2.4; Figure S1)

150 The soil types from north to south are Andisols, Luvisols, and Inceptisols. Additionally, by examining
151 soil texture data, we inferred variations in soil water holding capacity (SWHC) among these sites
152 (Table S1, Hengl and Nauman, 2018). Specifically, we inferred that the SWHC in TRE is relatively
153 low, whereas LAZ exhibited a high SWHC. CAM also showed a high SWHC, while CAL presented
154 a moderate SWHC (Kutílek and Nielsen, 1994).



155
156 **Figure 1** a) Map displaying the Climate Moisture Index ($CMI = \text{Precipitation} / \text{Potential}$
157 $\text{EvapoTranspiration}$) across the Italian Peninsula, indicating humid and dry climate zones through
158 positive (blue) and negative (red) CMI values, respectively. The index was calculated for the
159 growing season (May-October) from 1965 to 2014. Green dots indicate the location of the four
160 study sites where dendrochronological samples were extracted.

161

162 **Table 1.** Geographical and mean annual climate characteristics for the four sites.

Site	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)	Mean minimum annual temperature (°C)	Mean annual temperature (°C)	Mean maximum annual temperature (°C)	Annual precipitation (mm)	Reference
TRE	46°12'	11°16'	1276	3.8	9.0	13.9	929	TRW data Versace et al., 2020

LAZ	42°24'	12°12'	1000	8.9	14.3	19.5	829	Battipaglia et al., unpublished
CAM	41°24'	14°20'	1140	6.3	9.8	13.1	825	Battipaglia et al., unpublished
CAL	39°19'	16°23'	1601	5.8	11	16	1003	Battipaglia et al., unpublished

163

164 2.2 Field sampling and processing dendrochronological data

165 During the period 2014-2018, a total of 174 beech trees were sampled at 1.3 m from the ground using
166 a 5 mm increment borer (Table S2). In the laboratory, wood cores were air/dried and polished with
167 sandpaper of successively increasing grains to visualize the ring boundaries. Ring widths were
168 measured to a precision of 0.01 mm using the TSAP measuring device (Rinntech). Tree-ring (TRW)
169 series were then visually cross-dated using standard dendrochronological methods (Stokes and
170 Smiley, 1968) and checked for dating accuracy and measurement errors with the COFECHA program
171 (Holmes, 1983).

172 Later, tree growth measurements were converted to basal area increment based (BAI) based on the
173 distance between the outermost measured ring (pith) and the last ring of the tree (i.e., the ring next to
174 the bark), using the following formula:

$$175 \quad \text{BAI} = \pi (R_t^2 - R_{t-1}^2), \quad (1)$$

176 where R_t the tree's radius at the end of the annual increment, and R_{t-1} is the tree's radius at the
177 beginning of the annual increment. This method assumes a circular cross-section, and the mean BAI
178 of defined periods can be compared over time, as it is not affected by biological trends (Biondi and
179 Qeadan, 2008a; 2008b) and it is more tightly related to stem biomass compared to TRW. We worked
180 with mean non-standardized BAI values to preserve the long-term cumulative effects of climate on
181 tree growth (Tognetti et al., 2014). All analyses were restricted to the period covered by the youngest

trees (at LAZ), i.e. from 1965 until 2014 (Table S2). All computations were performed using the R-package ‘dplR’ (Bunn, 2008; Bunn et al., 2021; R Core Team, 2022).

2.3 Water-use efficiency from carbon isotope discrimination

To compare long-term changes in $iWUE$ among beech trees across the Italian Peninsula, we measured $^{13}C/^{12}C$ isotope ratios in the TRW. Ten samples per each stand presenting the best cross-dating (GLK > 0.70) with the corresponding average chronology, were selected for stable isotope analyses (Battipaglia et al., 2017) and they were annually dissected using a razor blade under a binocular microscope for the period 1965-2014.

Wood samples were milled to a fine powder (ZM 1000; Retsch), weighed 0.05-0.06 mg of wood for carbon isotope analyses and encapsulated in tin capsules.

The isotope composition was measured at the IRMS laboratory of the University of Campania “Luigi Vanvitelli” by using mass spectrometry with continuous flow isotope ratio (Delta V plus Thermo electron Corporation). The standard deviation for repeated analysis of an internal standard (commercial cellulose) was better than 0.1‰ for carbon. The $\delta^{13}C$ series were corrected for the fossil fuel combustion effect for anthropogenic changes in the atmospheric $\delta^{13}C$ composition ($\delta^{13}C_{atm}$) (Francey et al., 1999; McCarroll and Loader, 2004).

Isotopic discrimination between the carbon of atmospheric CO_2 and wood carbon to determine $iWUE$ can be calculated starting from the $\delta^{13}C$ of the plant material ($\delta^{13}C_{tree}$), which is related to atmospheric $\delta^{13}C$ ($\delta^{13}C_{atm}$) and the ratio c_i/c_a , according to Farquhar and Richards (1984) and Farquhar et al. (1982):

$$\delta^{13}C_{tree} = \delta^{13}C_{atm} - a - [(b - a) c_i] / c_a, \quad (2)$$

where a is the fractionation factor due to $^{13}\text{CO}_2$ diffusion through stomata (4.4‰), and b is the fractionation factor due to Rubisco enzyme during the process of carboxylation (27‰) (McCarroll and Loader, 2004). Therefore, we can calculate c_i by using the formula:

$$c_i = c_a(\delta^{13}\text{C}_{\text{atm}} - \delta^{13}\text{C}_{\text{tree}} - a) / (b - a) . \quad (3)$$

Finally, the $i\text{WUE}$ can be calculated as follows:

$$i\text{WUE} = (c_a b - \delta^{13}\text{C}_{\text{atm}} + \delta^{13}\text{C}_{\text{tree}}) / 1.6 (b - a) . \quad (4)$$

However, the $i\text{WUE}$ should not be considered equivalent to instantaneous WUE at leaf level, which is the ratio of assimilation to stomatal conductance and considers the atmospheric water demand (Pacheco et al., 2020; Seibt et al., 2008). Thus, the equation used is the “simple” form of isotopic discrimination that does not include effects due to mesophyll conductance and photorespiration, which were unavailable for the study species.

We used $\delta^{13}\text{C}_{\text{atm}}$ values from Belmecheri and Lavergne (2020). We obtained the atmospheric concentration of CO_2 from the Mauna Loa station data (<http://www.esrl.noaa.gov/>).

2.4 E-OBS daily climate data, CMI and SPEI calculation

Daily climate data for precipitation (P), minimum (T_{\min}), mean (T_{mean}), and maximum (T_{\max}) temperature, as well as relative humidity (RH), were extracted from the E-OBS dataset on a regular 0.1-degree grid (Table 1). The data were obtained as netCDF files from (http://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php). Using the RH and temperature data, the vapour pressure deficit (VPD) in hPa was calculated based on the Tetens formula (Tetens 1930).

225 The Climate Moisture Index (CMI, Willmott and Feddema, 1992) represents the relationship between
226 plant water demand and available precipitation. The CMI indicator ranges from -1 to $+1$, with wet
227 climates showing positive CMI and dry climates negative CMI. CMI was calculated as follows:

$$228 \quad \text{CMI} = P/PET \quad (5)$$

229 Where P is the precipitation, and PET is the potential evapotranspiration. Specifically, $\text{CMI} = (P/PET)$
230 -1 when $P < PET$ and $\text{CMI} = 1 - (PET/P)$ when $P > PET$, to recast the limit to $-1 < \text{CMI} < 1$.

231 PET can be calculated through the Hargreaves equation (Hargreaves, 1985), modified by Allen
232 (1993):

$$233 \quad PET = 0.0029 R_{\text{solar_rad}} (T_{\text{mean}} + 20) TR^{0.4} \quad (6)$$

234 Where $R_{\text{solar_rad}}$ is the extraterrestrial solar radiation, T_{mean} in Celsius degree and TR is the temperature
235 range ($T_{\text{max}} - T_{\text{min}}$).

236 CMI was calculated for the growing season (May-October) using the E-OBS v. 27.0
237 (https://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php#datafiles) daily products (T_{min} ,
238 T_{max} , precipitation, and global solar radiation) at 0.1 deg spatial resolution and averaged over the
239 period 1965-2014. E-OBS global solar radiation at the surface was converted to extra-terrestrial solar
240 radiation with the ‘envirem’ R-package (Title and Bemmels, 2018).

241 Additionally, to quantify drought severity, we calculated the Standardized Precipitation-
242 Evapotranspiration Index (SPEI), based on a statistical transformation of the climatic water balance,
243 i.e. precipitation *minus* potential evapotranspiration ($P - PET$) (Vicente-Serrano et al., 2010). The
244 multiscalar drought index was calculated at different time scales (from 1 to 24 months, Figure S2) for
245 the period 1965-2014 (constrained to the youngest site LAZ) in R using the ‘SPEI’ package (Beguería
246 et al., 2014; Beguería and Vicente-Serrano, 2017).

247 Later, to assess the relationships between climate and BAI and stable isotope for the period 1965–
248 2014, we calculated Pearson’s correlations between monthly P , T_{mean} , VPD, and SPEI (1-3-6-9-12-

18 and 24 months) series from previous $(t-1)$ and current year (t) , using monthly response function in the ‘DendroTools’ R-package (Jevšenak and Levanič, 2018).

2.5 Growth trends and climate response

We used Generalized Additive Mixed Models (GAMM) to study the long-term annual BAI and their responses to changing climatic conditions, particularly concerning water balance within the growing season (May-October) using SPEI indexes at the four study sites. We tested SPEI drought index at 1,3,6,9,12,18, and 24 months as the potential influence of drought on BAI. GAMM is a flexible semiparametric method that allows the simultaneous modelling of linear and nonlinear relationships between the response variable as a function of some explanatory variables (Wood, 2006) that allows the treatment of autocorrelation and repeated measures (Wood, 2006). The variables included in the model were the following:

$$BAI_i = s[\text{year}_i * (\text{Site})] + s(\text{age}_i) + s(\text{SPEI}_i) + Z_i B_i + \epsilon \quad (5)$$

Where the BAI_i of a tree $_i$ were modelled as a function of calendar year, individual tree age and SPEI per site. In addition, given that BAI represents multiple measurements performed in each tree, tree identity ($Z_i B_i$) is regarded as a random effect (Z_i and B_i indicate matrix variables and related coefficients). Thin plate regression splines (s) were used to represent all the smooth terms, with a degree of smoothing determined by internal cross-validation (Wood, 2006). We ranked all the potential models that could be generated using different explanatory variables and different levels of smoothing according to the Akaike Information Criterion (AIC). Finally, we chose the model with the lowest AIC (Burnham and Anderson, 2002). The time scale that best explained the variability in BAI was the 18-month SPEI (for the growing season May-October). The GAMMs were performed and fitted using the function ‘*gamm*’ in the ‘*mgcv*’ R-package (Wood, 2006).

2.6 Early warning signals of forest dieback

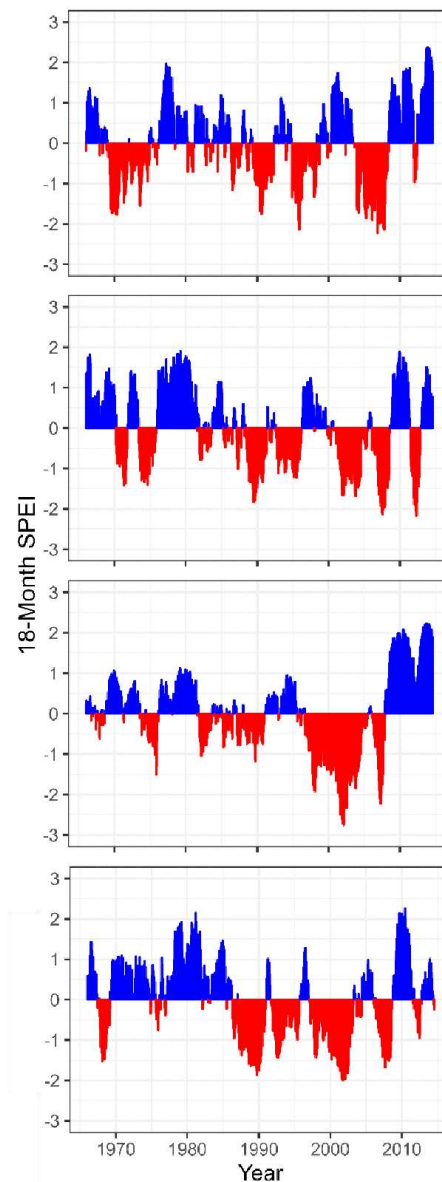
For assessing stand resilience for each site and each time series of BAI, we computed the autocorrelation at lag-1 (AC) and the standard deviation (SD) over the period 1965 to 2014 using a 15-year moving window (30% of the entire time series). These metrics are widely recognized indicators of changes in time series and proximity to critical transitions to new states (Dakos et al., 2012a; Camarero et al., 2015; Forzieri et al., 2022). The trend of AC and SD metrics over the considered temporal window was computed by means of the non-parametric Mann-Kendall Tau statistics. For each site, the significance of a positive (or negative) AC and SD trend was tested with a one-sided t-test. We employed the R-package ‘early warnings’ (Dakos et al., 2012b) to compute the selected metrics. All statistical analyses were conducted using the R-statistical software (R Development Core Team, 2022)

3 RESULTS

Climate trends and drought variability

Annual precipitation (P) has increased significantly at TRE and CAM sites ($p < 0.01$, Figure S2a), while LAZ showed a reduction in P trend during the period from 1965 to 2014 ($p < 0.05$, Figure S2a), and CAL did not present any trend in P pattern. Notably, T_{\min} increased significantly in TRE, LAZ, and CAM ($p < 0.001$, Figure S2b), whereas in the southern site (CAL), T_{\min} presented a pronounced decrease ($p < 0.01$, Figure S2b). Simultaneously, both T_{mean} and T_{max} exhibited a substantial and significant increase across all sites ($p < 0.01$, Figure S2c and S2d). Interestingly, only at the northernmost site (TRE), VPD increased drastically and significantly during the 2000s ($p < 0.001$, Figure S2e), while at the southernmost site (CAL) VPD showed the opposite pattern (Figure S2e, $p < 0.001$).

297 As for the P trend, the SPEI index showed an increase in water availability in recent years across
 298 sites, although not significant, except for LAZ, which showed a negative trend ($p < 0.05$, Figure 2,
 299 Figure S3). Notably, the SPEI-derived drought index showed the widespread impact of the 2003
 300 drought across all sites, more evident at CAM (Figure 2, Figure S3).



301
 302 **Figure 2** Standardized 18-Month SPEI at the four study sites (TRE, LAZ, CAM, and CAL) for the
 303 1965–2014 period. Negative (red) and positive (blue) values indicate drier and wetter conditions,
 304 respectively.

305

Long-term growth trends of *Fagus sylvatica* across the Italian Peninsula

Mean TRW, the highest and the lowest growth rates were observed in LAZ and CAM sites, respectively with statistically significant differences. Conversely, TRE and CAL showed similar growth rates values ($p < 0.05$, Table S3). The age distribution of tree populations exhibited notable differences across the four sites, with LAZ featuring the youngest trees and CAM the oldest trees ($p < 0.05$, Table S3).

BAI exhibited a significant decline, particularly pronounced in the relatively northern sites (TRE and LAZ), following the drought of 2003 (Figure 3b). In contrast, CAM presented a steady increase in BAI, while in CAL, BAI decreased after 2010 (Figure 3b).

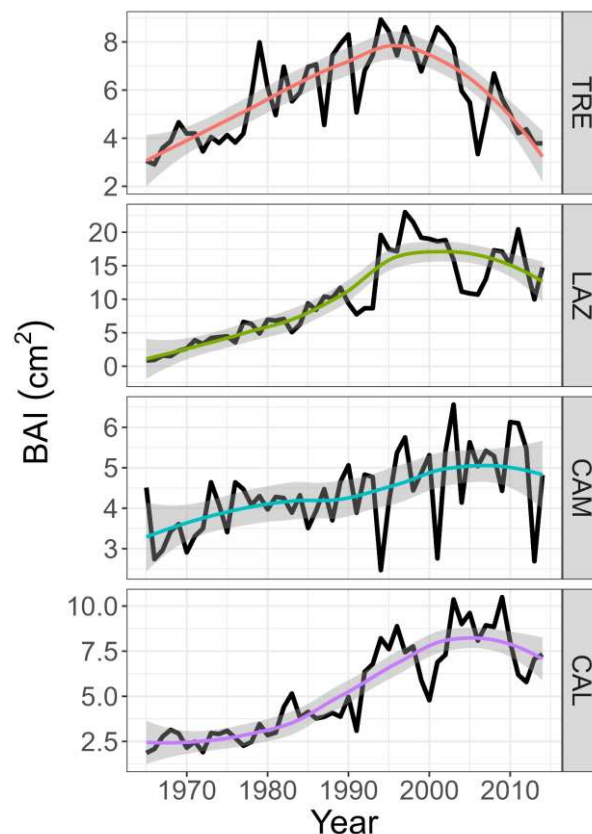


Figure 3 Long-term growth of basal area increment (BAI) of the four sites along a latitudinal gradient (north to south) for the period 1965–2014. Colour lines for each site indicate the linear model, shaded areas represent 95 % confidence intervals.

320

321 **Growth response to climate variables**

322 Basal area increment exhibited significant relationships with climatic variables in all study sites
323 (Figure 4). Overall, BAI was positively correlated with monthly P and T_{mean} and, notably, strongly
324 negative correlations with VPD were evident from May to September. This negative VPD correlation
325 intensified toward the southern sites (Figure 4).

326 At TRE, BAI was positively correlated with monthly P from May to July, with a stronger effect when
327 considering P values in the previous year. Additionally, BAI correlated positively with May T_{mean} of
328 the current year, instead of showing weak negative correlations with VPD and SPEI (Figure 4).

329 LAZ showed a strong positive correlation between BAI and T_{mean} from March to November (previous
330 and current year). Conversely, strong negative correlations with VPD from May to September and
331 weak negative correlations with P and SPEI were found in August (Figure 4).

332 AT CAM, a positive response of BAI to P of July of the previous years, and a strong positive
333 correlation with T_{mean} during May to July, were observed, while a strong negative response to VPD
334 from March to September (more evident in the current year) was found.

335 At CAL, BAI showed strong positive correlations with October P and with T_{mean} from March to
336 August. In contrast, BAI displayed a strong negative correlation with VPD from March to September
337 (current and previous year). Similarly, negative scattered correlations with SPEI were observed
338 during summer at the southern sites (CAM and CAL, Figure 4).

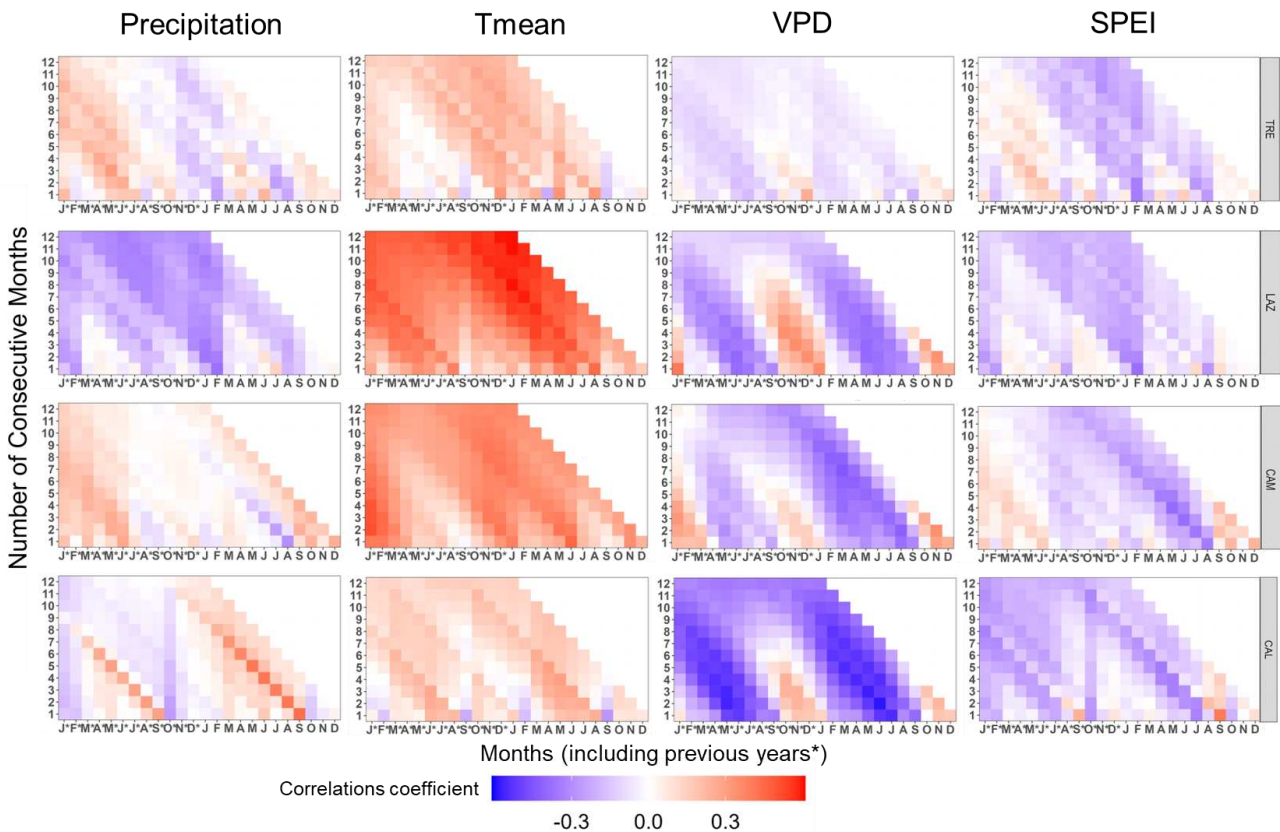
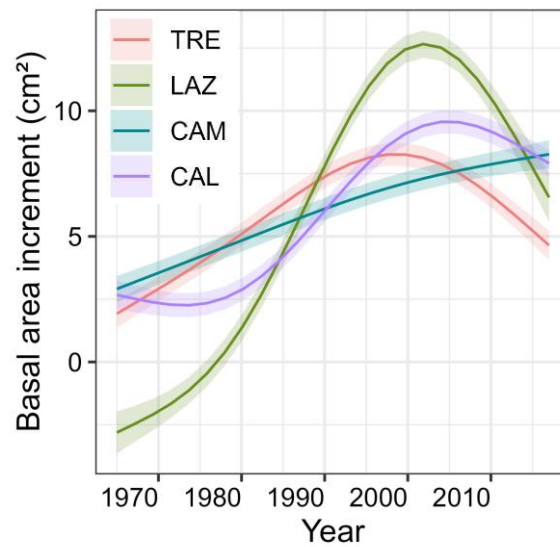


Figure 4. Pearson's running correlations between BAI with monthly precipitation, mean temperature, VPD, and SPEI1 for the current and the previous year (*) over the period 1965-2014 at each site. The y-axis represents the time window in months. Colours (see the key) represent correlation coefficients that are significant at the level of $r = 0.279$ ($p < 0.05$).

Growth trends of beech

The GAMMs revealed different BAI trends of beech among the four sites (Figure 5, Table S4). GAMM showed a monotonic increasing growth trend among the sites; however, they started to diverge in the mid-1990s. Notably, the northernmost site (TRE) started to decline earlier than the other sites (Figure 5). Secondly, LAZ exhibited the highest increase, followed by a drastic decline during the 2000s – a similar pattern was also observed in CAL. In contrast, the oldest site CAM trees demonstrated a steady increase in BAI over the observed period (Figure 5).



352

353 **Figure 5** Growth trends of basal area increment trends of beech for the four sites. Trends were based
354 on the best-fitted generalized additive mixed models (GAMM) for the period 1965-2014.

355

356 Long-term carbon isotope chronologies and water use strategies

357 At the southernmost site (CAL), trees presented the highest increase of $\delta^{13}\text{C}$ values that translate in
358 an increase of iWUE (Table 3, Figure 6). On the contrary, CAM (oldest site) showed the lowest value
359 of iWUE (Table 3, Figure 6). LAZ and TRE on average presented similar $\delta^{13}\text{C}$ and iWUE (Table 3).

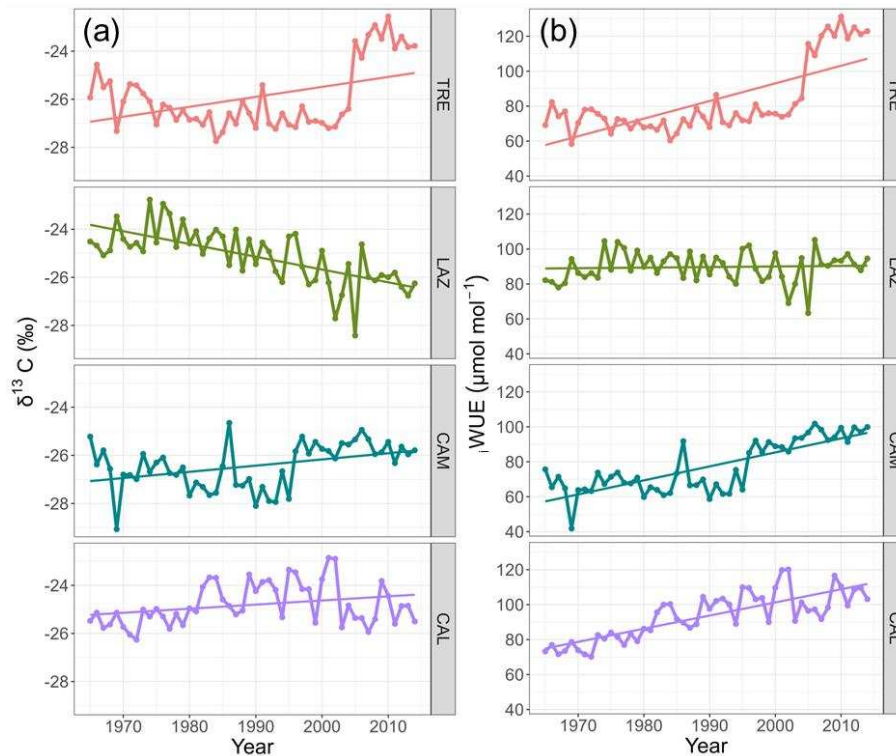
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361 **Table 3.** Statistics of mean $\delta^{13}\text{C}$ and iWUE of the tree-ring width series of beech per site for the period
362 1965–2014. Data are mean values \pm SE.

Site	$\delta^{13}\text{C}$ (‰)	iWUE ($\mu\text{mol mol}^{-1}$)
TRE	-25.9 ± 1.4	82.4 ± 20.4
LAZ	-25.1 ± 1.1	89.6 ± 8.7
CAM	-26.4 ± 0.9	76.9 ± 14.8
CAL	-24.8 ± 0.9	93.4 ± 13.5

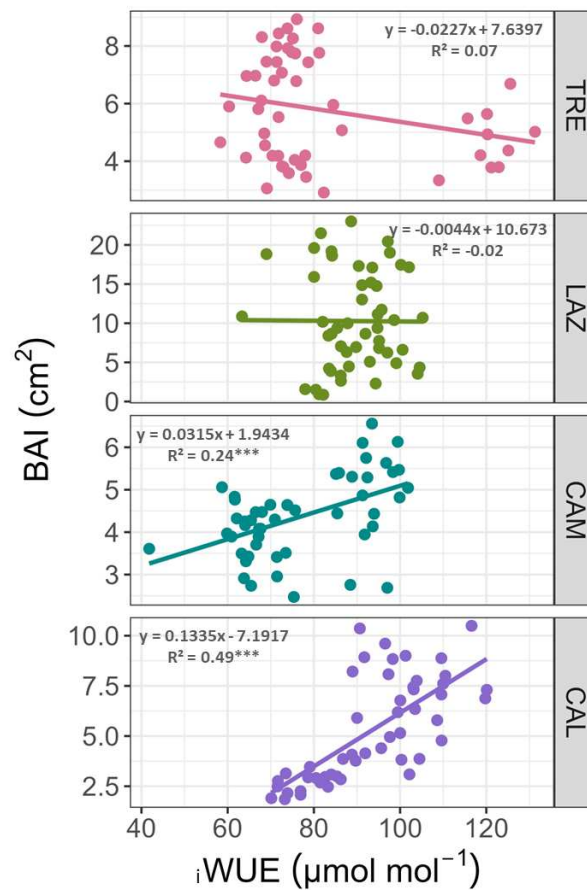
363

364 For most sites, $\delta^{13}\text{C}$ showed a positive and significant trend over time ($p < 0.05$, Figure 6), except for
 365 LAZ, which showed an opposite pattern during the period 1965–2014 ($p < 0.001$, Figure 5). In the
 366 northernmost site (TRE), the $\delta^{13}\text{C}$ and $i\text{WUE}$, started to increase sharply after the drought of 2003.
 367 Similarly, the southern sites CAM and CAL presented a steady increase in $i\text{WUE}$ ($p < 0.001$, Figure
 368 5). On the contrary, LAZ did not present any significant trend ($p = 0.701$).



369
 370
 371 **Figure 6** Trends of: a) $\delta^{13}\text{C}$ (‰), and b) $i\text{WUE}$, and fitted linear trends for the period 1965–2014 in
 372 four stands across a latitudinal gradient in Italy.

373
 374 In the southern sites, CAM and CAL, we observed significant positive relationships between $i\text{WUE}$
 375 and BAI ($p < 0.001$, Figure 7). On the contrary, at the northern site (TRE), we observed the opposite
 376 trend pattern; however, this trend was not significant ($p > 0.05$). AT LAZ, no relationship was found
 377 between $i\text{WUE}$ and BAI (Figure 7).



378

379 **Figure 7** Relationship between annual BAI and $iWUE$ in beech across the Italian Peninsula for the
 380 period 1965-2014. Linear regressions and the equations are indicated for each site. Significance
 381 values are encoded by *** $p < 0.001$.

382

383 $\delta^{13}C$, $iWUE$, and climate relationship

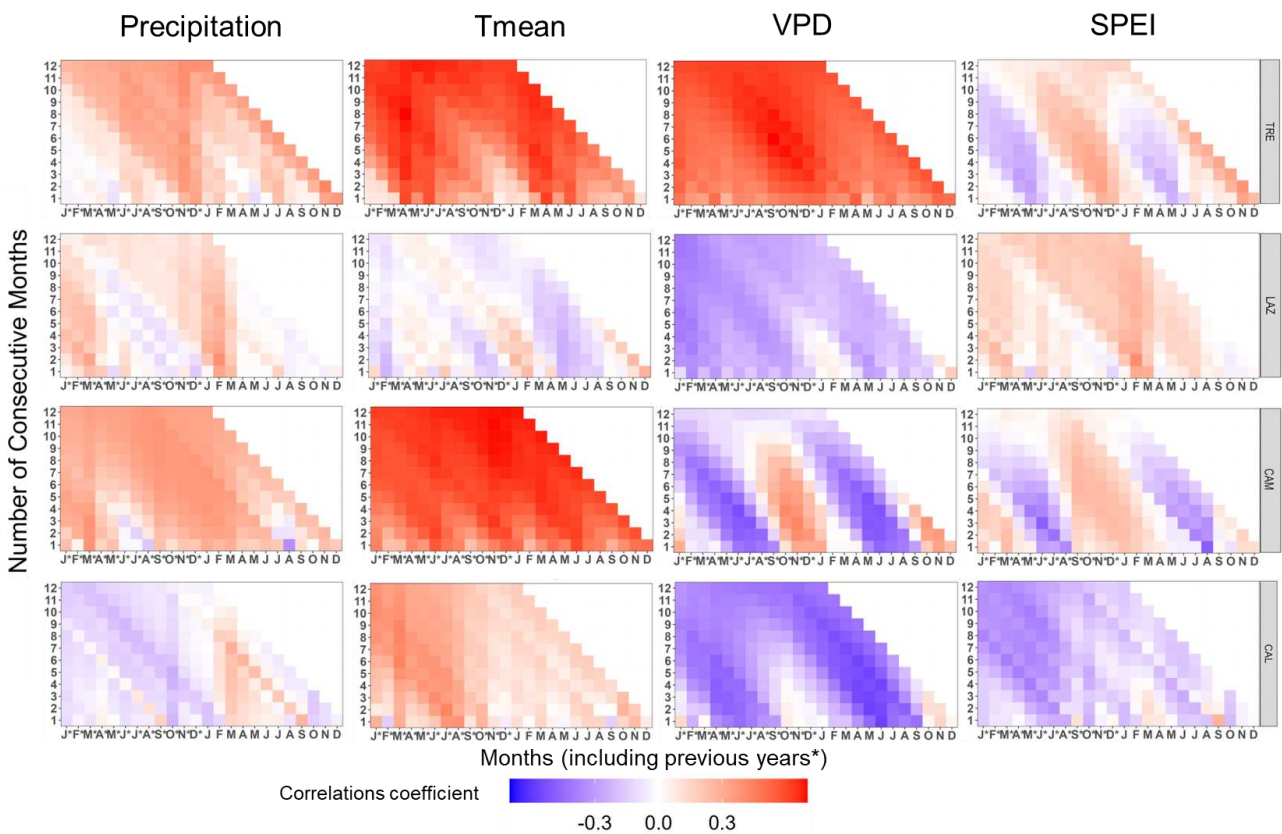
384 Carbon isotope composition ($\delta^{13}C$) and $iWUE$ showed a similar relationship with climate variables.
 385 However, $iWUE$ presented stronger correlation with climate than $\delta^{13}C$ (Figure 8, Figure S4). An
 386 exception was observed at LAZ, where $\delta^{13}C$ showed a negative and significant correlation with T_{mean}
 387 compared to $iWUE$ (Figure 8, Figure S4).

388 At the northernmost site, $iWUE$ showed significant and positive correlations with T_{mean} and VPD of
 389 the previous and current year, while negative and scattered correlations with P and SPEI of April and
 390 May were observed (Figure 8).

391 At LAZ, $iWUE$ was negatively and significantly correlated with VPD from March to November of
 392 the current and previous year.

393 At CAM, $iWUE$ exhibited a positive and significant correlation with P from March to May (previous
 394 and current year), while T_{mean} of the current and previous year was positively and significantly
 395 correlated with $iWUE$. On the contrary, $iWUE$ correlated strongly and negatively with VPD from
 396 May to August (current and previous year) and with SPEI in August (Figure 8).

397 At the southernmost site, $iWUE$ correlated positively with P from March to September (current year),
 398 and strongly and positively with T_{mean} from March to August of the previous year. At CAL, VPD and
 399 SPEI exhibited strong and negative correlations with $iWUE$ from May to June (current and previous
 400 year, Figure 8).



401

402 **Figure 8** Pearson's running correlations between $iWUE$ with monthly precipitation, mean
 403 temperature, VPD, and SPEI1 for the current and the previous year (*), over the period 1965-2014 at

each site. The *y-axis* represents the time window in months. Colours (see the key) represent correlation coefficients that are significant at the level of $r = 0.279$ ($p < 0.05$)

Early warning signals of declining forest resilience

The statistical analysis of the BAI time series performed to detect EWS on beech forests revealed contrasting results among the sites (Figure 9a and 9b). In TRE and LAZ, BAI showed a rise in AR(1) among trees, which started to increase after the 2003 drought in TRE, while in LAZ already during the 1990s (Figure 9a). In contrast, CAM showed a significant steady decrease in AR(1). No significant autocorrelation trend was found at CAL. Nevertheless, the standard deviation (SD) started to rise by the end of the 1980s (Figure 9b). A significant increase in SD of the BAI signal was observed across all the sites.

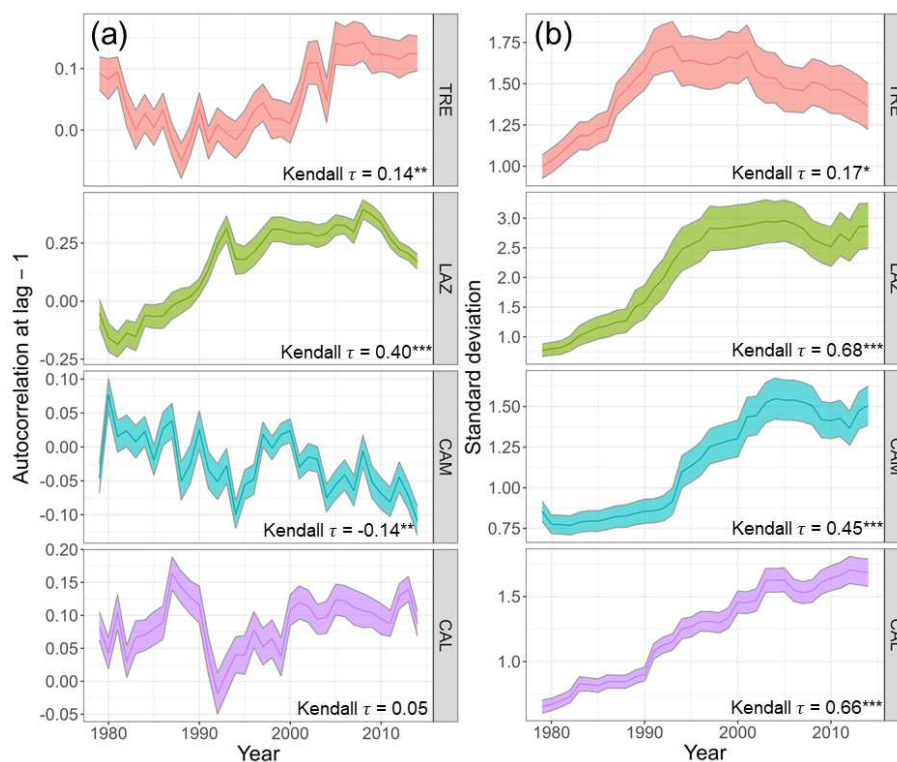


Figure 9 Early warning signals: a) AR(1), first-order autocorrelation, b) SD, obtained using a 15-year moving window for basal area increment (BAI) of *Fagus sylvatica* for four study sites for the period 1965-2014. The statistics of BAI were calculated using the residuals of the time series after

removing the low-frequency signal (Gaussian filter) using 15-year-long windows (e.g. 1979 corresponds to the interval 1965-2014). The Kendall τ statistics indicate the strength of trends along the time series for each variable and site. For each site, the bold line represents the mean of the statistics among trees, and the shaded area is the standard error. (* $p < 0.05$, ** $p < 0.001$, *** $p < 0.001$).

4 DISCUSSION

Long-term growth patterns and climate variability impact on beech across Italy

Our analysis revealed diverse long-term growth responses of European beech across the Italian Peninsula, closely associated with local climate and site conditions. The northern sites (TRE and LAZ) showed a decrease in BAI trends after the severe drought event in 2003, while the southernmost site (CAL) exhibited a growth decline after 2010. In contrast, CAM displayed a steady increase in growth over the 50 years analysed, likely due to increased precipitation in the last decades.

Our findings confirmed that European beech in the northern sites might be more susceptible to die-off, even without visible decline symptoms (such as branch dieback or decolouration of leaves). Trees exhibited greater growth sensitivity to VPD during summer, and this effect became more pronounced at the southernmost site. VPD can be used to estimate atmospheric water status and is one of the most important environmental factors influencing plant growth (Zabri and Burrage, 1997). Elevated VPD, associated with dry conditions, impacts stomatal conductance and the balance between carbon assimilation and water loss (McDowell et al., 2008; Zhang et al., 2015). This indicates that drought, driven by enhanced evapotranspiration, will play a critical role throughout the beech forest's latitudinal range in Italy.

Recent global-scale research by Yuan et al. (2019) highlighted the increase of VPD as a major atmospheric driver affecting forest productivity by imposing water stress on photosynthesis. Water-use strategies, particularly conservative/opportunistic responses within and across species, have been closely linked to soil moisture availability (Moreno-Gutiérrez et al., 2012; Martínez-Vilalta et al., 2014). Higher VPD and temperature accelerate soil moisture depletion causing a significant reduction in carbon uptake (Sulman et al., 2016), elevating the risk of drought-induced dieback through hydraulic failure and/or carbon starvation (Anderegg et al., 2016; Adams et al., 2017; Grossiord et al., 2020).

Our results demonstrate a significant increase in VPD after the 2003 drought event in TRE, however we found a weak negative correlation between VPD and BAI. We can hypothesise this might be attributed to a lower soil water holding capacity (SWHC) at this site, potentially increasing vulnerability to growth decline, as observed in our GAMM model. Conversely, LAZ exhibited higher SWHC, likely contributing to higher transpiration rates and growth compared to other sites. CAM and CAL sites presented moderate SWHC and a declining VPD trend, indicating less stress than the TRE site. The GAMM model integrated responses to the SPEI index and individual age of each tree, thus, we speculate that hydraulic strategies under drought significantly impact long-term growth rates, reflecting site-specific and ontogenic plasticity responses of the species. These findings may suggest that young beech trees initially benefit from favourable climate conditions and higher transpiration rates; however, this advantage depends on soil water availability and makes them susceptible to rapid declines in growth during extreme drought events, as already observed in Switzerland (Vanoni et al., 2016).

Our study, to our knowledge, is the first to show evidence of the negative impact of VPD on basal area increment in beech forests across the Italian peninsula. This correlation was evident in all sites but was even stronger at southern latitudes. In contrast, previous studies in mature beech stands did not find a significant climate correlation, attributed to the species' mast-seeding behaviour and

sensitivity to late frosts at the beginning of the growing season (Piovesan and Adams, 2001; Castagneri et al., 2014; D'Andrea et al., 2021; Tonelli et al., 2023). Other studies have identified lagged climate correlation with masting (Vacchiano et al., 2017). Additionally, Zimmermann et al. (2015), in central Germany, found that beech growth was highly sensitive to summer temperatures and extreme drought events after the 1980s.

Drought sensitivity and water-use strategies effect on growth

European beech has commonly been classified as an opportunistic species, capable of maintaining higher transpiration rates even in relatively dry soil conditions (Leuschner, 2020; and references therein); however, this strategy increases the risk of cavitation (McDowell et al., 2008; Martinez-Vilalta et al., 2014).

Our findings indicated that temperature and VPD emerged as primary drivers of $\delta^{13}\text{C}$ in TRE, while VPD played a dominant role in the southern sites. However, in LAZ, $\delta^{13}\text{C}$ did not exhibit a clear correlation with climate variables. This complex relationship highlights the interaction between VPD, stomatal conductance, and photosynthesis, as high VPD initially reduces stomatal conductance but not net CO_2 assimilation rate, resulting in increased $\delta^{13}\text{C}$. Nevertheless, severe VPD-induced stomatal conductance restrictions, combined with declining soil moisture and other non-stomatal limitations, ultimately reduce photosynthetic rate and may lead to declining $\delta^{13}\text{C}$ as VPD continues to rise (Flexas et al., 2012). Thus, the overall relationship between $\delta^{13}\text{C}$ and VPD is likely hyperbolic (Zhang et al., 2019), and the sensitivity of photosynthesis to VPD will likely be weaker than the sensitivity of conductance to VPD.

Our study highlights contrasting water use strategies of beech across the Italian peninsula. We observed an increase of $\delta^{13}\text{C}$ and $\delta^{13}\text{C}$ values in TRE, CAM, and CAL, indicating a conservative water use strategy when water availability is low. In contrast, LAZ exhibited a decrease of $\delta^{13}\text{C}$,

491 suggesting an opportunistic response with stable δ WUE regardless of the moisture condition. While
 492 at LAZ, changes in photosynthetic rate and stomatal conductance appeared to occur in the same
 493 direction with similar magnitude, at TRE, CAM, and CAL, stomatal conductance appeared to
 494 decrease proportionally more than photosynthetic rate, or the latter remaining stable or increasing
 495 with declining stomatal conductance. Thus, our findings confirm that water use strategies employed
 496 by beech are mostly site-specific and influenced by microclimatic conditions and soil water
 497 availability (McCarroll and Loader, 2004), consistent with our hypothesis and consistent with prior
 498 research (Peñuelas et al., 2008).

499 Interestingly, our results indicate that higher mean δ WUE did not result in an increase in the basal
 500 area increment on beech (Nock et al., 2011; Peñuelas et al., 2011; Mazza et al., 2024); instead, we
 501 observed contrasting responses consistent with previous studies (Peñuelas et al., 2008; Tognetti et al.,
 502 2014). Notably, the northern site displayed a drastic increase in δ WUE after the 2003 drought event,
 503 coinciding with elevated VPD and temperature that may have led to stomatal closure (g_s) and reduced
 504 photosynthesis (A), suggesting that the growth decline in this site was might triggered by intensified
 505 evapotranspiration and the lower SWHC as observed in other sites by others (e.g. Peñuelas et al.,
 506 2011; Li et al., 2023). At LAZ, there was no relationship between δ WUE and growth, which can be
 507 explained by higher SWHC allowing higher transpiration rates and metabolic respiration, resulting in
 508 greater losses of photosynthetic assimilates, especially at higher temperatures (Nock et al., 2011;
 509 Mazza et al., 2024). Interestingly, in the southern sites, the increase of δ WUE enhanced growth. This
 510 discrepancy may be attributed to the adaptation of beech trees in the southernmost distribution to
 511 water stress and high VPD (Anderegg et al., 2019; Battipaglia and Cherubini, 2022), suggesting that
 512 high δ WUE is an adaptative trait (Medrano et al., 2009). Consequently, we can infer that the observed
 513 “conservative strategy” - characterized by low stomatal conductance and constant CO_2 assimilation
 514 rate that enhanced growth – at CAM might be explained by a positive CO_2 fertilization effect or long-
 515 term acclimation to elevated CO_2 (Walker et al., 2021). Similar findings were reported in mature
 516 European beech stands in Spain, where an increased sensitivity to drought was observed across the

southern range-edge distribution (Peñuelas et al., 2008). Recently, Qi et al. (2023) in China revealed varying water use strategies among larch trees. Mature trees presented a more ‘conservative strategy’ (low g_s , constant assimilation rate (A)), whereas young trees maintained constant g_s and high A , indicating an opportunistic behaviour. Notably mature trees displayed a greater sensitivity to atmospheric CO_2 concentrations than their young counterparts.

It should be pointed out that a major influence of photosynthetic rate on intercellular CO_2 concentration and $\delta^{13}C$, and the minor contribution of the regulation of stomatal conductance to $\delta^{13}C$ and $\delta^{13}C$ were observed in other studies on the same species (Tognetti et al., 2014). These findings suggest unclear patterns of potential increased drought-related tree decline signs in mountain beech forests along the Italian latitudinal transect. Differences between leaf-level physiology and tree-ring level processes may arise, reflecting potential variations in the (re)translocation patterns of non-structural carbohydrates to organs (Martínez-Vilalta et al., 2016; Merganičová et al., 2019). Such complexities make tree-ring analysis a challenging tool for decipher tree responses to fluctuating seasonal conditions in the short term.

Early Warning Signals of mortality

Our second hypothesis, linking the degree of growth reduction and tree growth instability to drought severity, was only partially confirmed by our findings. We observed an increase in the autocorrelation of the BAI signal across almost all sites, indicating heightened intrinsic biological memory of the trees and signaling a loss of ecological system resilience (Lloret et al., 2011; Seidel et al., 2022; Smith et al., 2022). Such increases have been linked to instabilities preceding external disturbances in various biological systems (e.g., Dakos et al., 2012a; Boulton et al., 2022; Forzieri et al., 2022), potentially leading to a transition to a new system state (Majumder et al., 2019; Buxton et al., 2021). Recent studies investigating ecosystem productivity’s autocorrelation have identified reduced resilience in diverse forest types due to increased water limitations and climate variability (Forzieri

et al., 2022; Fernandez-Martinez et al., 2023). Notably, after a severe drought, declining trees exhibited increases in BAI autocorrelation and variability before mortality (Camarero et al., 2015).

In line with our expectations, the northern site showed a significant increase in AR and a decline in BAI after the 2003 drought event. Conversely, CAM showed a decrease in AR, suggesting a greater resilience to changing climate conditions, despite experiencing the severe drought period of 2003. This higher resilience at CAM might be linked to the legacy of past conditions with less water availability variability compared to the TRE site, as supported by the SPEI multiscalar index. TRE experienced several prolonged dry periods (i.e. $SPEI < -1.5$), before the 2000s. Additionally, the presence of relatively mature trees at CAM site might contribute to the population's apparent stability (see Colangelo et al., 2021). Our data also revealed increase BAI series SD across all stands. While this variability encompasses both tree physiological signals and climate-driven vegetation dynamics (Bochow and Boers, 2023), the co-occurrence rise in AR, decline in BAI, and increase in SD in TRE, LAZ and CAL sites, may indicate a loss of system stability (Dakos et al., 2012a). This indicates potential challenges for trees to mitigate the impact of extreme events in the future.

Several studies have demonstrated that long-term rises in instability and reduced growth predispose European beech to elevated mortality risks under future climate-induced stress conditions (Gillner et al., 2013; DeSoto et al., 2020; Cabon et al., 2023). This emphasizes the need for continuous monitoring and proactive management of beech forests, particularly in regions where climate change is projected to increase the frequency and severity of droughts. Ongoing monitoring enables early detection of tree mortality risks, facilitating timely interventions to protect and sustain these vital ecosystems with wide ecological amplitude.

566 5 CONCLUSIONS

567 In conclusion, in this study our goal was to advance the early prediction of mortality risk in healthy
568 beech stands without, apparently, visible declining symptoms across the Italian Peninsula. This is
569 especially pertinent considering the recent growth decline observed in this species (Piovesan et al.,
570 2008; Martinez del Castillo et al., 2022; Dorado-Liñan et al., 2022), although the available evidence
571 is not yet conclusive (Tognetti et al., 2014).

572 These findings highlight the importance of considering the plasticity and site-specific δ WUE
573 responses to varying environmental conditions and the impact of VPD on stomatal conductance when
574 predicting the future of beech forests in the context of climate change. It is important to note that not
575 all beech populations considered in this study exhibited an increase in δ WUE in response to rising
576 VPD. This variability reflects differing sensitivities to changes in environmental drivers and the
577 plasticity of conservative to opportunistic water-use strategies.

578 Furthermore, our analysis of EWS reveals the loss of resilience after an extreme event, as notably
579 observed at the TRE site. In the context of climate change projection, the increase in the frequency
580 and severity of droughts, the ability to detect earlier tipping points of critical slow down in declining
581 systems and the potential for recovery to the current state or an alternative state remains uncertain
582 (Cabon et al., 2023).

583 Nonetheless, this research raises further questions, such as how to generalize the relationships
584 between increased δ WUE and conservative behaviour, thus explaining contradictory results obtained
585 in tree ring studies on beech populations and assess temporal changes in this functional trait. Further
586 research considering young and old trees and their physiological mechanisms (Leuschner, 2020; Qi
587 et al., 2023), micro-site conditions (Puchi et al., 2021), and genetics will also elucidate intraspecific
588 variations in drought response (Alderotti et al., 2023). This knowledge is essential for developing
589 effective conservation and also future forest management strategies to ensure the long-term health,
590 vitality, and resilience of these crucial ecological and socio-economical ecosystems.

591

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