

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

3 **Running head:** Forecasting European beech mortality risk

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20 water use efficiency, carbon stable isotopes, autocorrelation.

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27 **ABSTRACT**

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

35 First-order autocorrelation (AR1) analysis was performed to detect early warning signals for potential
36 tree dieback risks during extreme drought events. Results revealed a negative correlation between
37 vapour pressure deficit (VPD) and BAI, especially at southern latitudes. GAMM analysis showed a
38 negative trend in BAI across most sites, stronger at the TRE site following the 2003 drought event.
39 During this event, $\delta^{13}\text{C}$ and iWUE increased with rising VPD, indicative of conservative water-use
40 (lower stomatal conductance) and contributing to the decline in BAI. Conversely, CAM exhibited a
41 steady increase in BAI and iWUE , likely influenced by rising atmospheric CO_2 and water availability.
42 LAZ site exhibited a decrease in $\delta^{13}\text{C}$, attributed to greater soil water holding capacity, enabling it to
43 sustain higher transpiration rates. Conversely, southern sites presented higher iWUE , likely as high
44 VPD initially reduces stomatal conductance but not the net assimilation rate, resulting in increased
45 iWUE . Nevertheless, almost all sites exhibited a co-occurrence of increase in AR1 (except for CAM)
46 and standard deviation, suggesting a reduction of resilience to future extreme events.
47 Overall, multi-proxy, retrospective quantifications of BAI, iWUE and resilience provide a robust and
48 complementary tool for differentiating water-use strategies and predicting tree growth decline and
49 dieback, as well as identifying those that have the potential to survive in warmer and drier future
50 conditions.

51

52

53 1 INTRODUCTION

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

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

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

77 2020; D'Andrea et al., 2021). Consequently, predicting resilience and adaptation across its
78 distribution has become a prioritized goal.

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

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

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

102 i WUE) to those considered “conservative” (high i WUE) (Moreno-Gutiérrez et al., 2012). For
103 instance, studies in tree rings have shown that the increase of i 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.

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

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136

137 **2 MATERIALS AND METHODS**

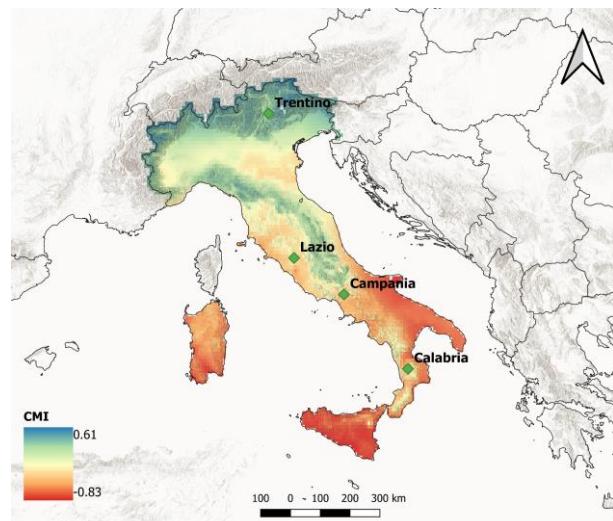
138 **2.1 Study sites and climate**

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

144 The selection of the sites allowed the comparison of moisture availability across the Italian Peninsula
145 (Figure 1), using the Climate Moisture Index (CMI) calculation method explained in section 2.6.
146 These sites differ along the latitudinal transect regarding both climatic conditions and soil types. From
147 north to south, the mean annual temperature ranges from 9 to 14.1 °C, with the mean annual
148 precipitation varying from 1003 to 825 mm, based on the E-OBS dataset (as explained in section 2.4;
149 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 = Precipitation / Potential
157 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
$$BAI = \pi (R_t^2 - R_{t-1}^2), \quad (1)$$

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

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

184

185 **2.3 Water-use efficiency from carbon isotope discrimination**

186 To compare long-term changes in i WUE among beech trees across the Italian Peninsula, we measured
187 $^{13}\text{C}/^{12}\text{C}$ isotope ratios in the TRW. Ten samples per each stand presenting the best cross-dating (GLK
188 > 0.70) with the corresponding average chronology, were selected for stable isotope analyses
189 (Battipaglia et al., 2017) and they were annually dissected using a razor blade under a binocular
190 microscope for the period 1965-2014.

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

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

199 Isotopic discrimination between the carbon of atmospheric CO_2 and wood carbon to determine i WUE
200 can be calculated starting from the $\delta^{13}\text{C}$ of the plant material ($\delta^{13}\text{C}_{\text{tree}}$), which is related to atmospheric
201 $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{atm}}$) and the ratio c_i/c_a , according to Farquhar and Richards (1984) and Farquhar et al.
202 (1982):

$$203 \delta^{13}\text{C}_{\text{tree}} = \delta^{13}\text{C}_{\text{atm}} - a - [(b - a) c_i] / c_a, \quad (2)$$

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

207
$$c_i = c_a(\delta^{13}\text{C}_{\text{atm}} - \delta^{13}\text{C}_{\text{tree}} - a) / (b - a). \quad (3)$$

208 Finally, the i WUE can be calculated as follows:

209
$$i\text{WUE} = (c_a b - \delta^{13}\text{C}_{\text{atm}} + \delta^{13}\text{C}_{\text{tree}}) / 1.6 (b - a). \quad (4)$$

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

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

217

218 **2.4 E-OBS daily climate data, CMI and SPEI calculation**

219 Daily climate data for precipitation (P), minimum (T_{\min}), mean (T_{mean}), and maximum (T_{\max})
220 temperature, as well as relative humidity (RH), were extracted from the E-OBS dataset on a regular
221 0.1-degree grid (Table 1). The data were obtained as netCDF files from
222 (http://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php). Using the RH and temperature
223 data, the vapour pressure deficit (VPD) in hPa was calculated based on the Tetens formula (Tetens
224 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
$$CMI = P/PET \quad (5)$$

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

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

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

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

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-

249 18 and 24 months) series from previous $(t-1)$ and current year (t) , using monthly response function in
250 the ‘DendroTools’ R-package (Jevšenak and Levanič, 2018).

251

252 **2.5 Growth trends and climate response**

253 We used Generalized Additive Mixed Models (GAMM) to study the long-term annual BAI and their
254 responses to changing climatic conditions, particularly concerning water balance within the growing
255 season (May-October) using SPEI indexes at the four study sites. We tested SPEI drought index at
256 1,3,6,9,12,18, and 24 months as the potential influence of drought on BAI. GAMM is a flexible
257 semiparametric method that allows the simultaneous modelling of linear and nonlinear relationships
258 between the response variable as a function of some explanatory variables (Wood, 2006) that allows
259 the treatment of autocorrelation and repeated measures (Wood, 2006). The variables included in the
260 model were the following:

261
$$BAI_i = s[year_i * (Site)] + s(age_i) + s(SPEI_i) + Z_i B_i + \epsilon \quad (5)$$

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

272

273 **2.6 Early warning signals of forest dieback**

274 For assessing stand resilience for each site and each time series of BAI, we computed the
275 autocorrelation at lag-1 (AC) and the standard deviation (SD) over the period 1965 to 2014 using a
276 15-year moving window (30% of the entire time series). These metrics are widely recognized
277 indicators of changes in time series and proximity to critical transitions to new states (Dakos et al.,
278 2012a; Camarero et al., 2015; Forzieri et al., 2022). The trend of AC and SD metrics over the
279 considered temporal window was computed by means of the non-parametric Mann-Kendall Tau
280 statistics. For each site, the significance of a positive (or negative) AC and SD trend was tested with
281 a one-sided t-test. We employed the R-package ‘early warnings’ (Dakos et al., 2012b) to compute the
282 selected metrics. All statistical analyses were conducted using the R-statistical software (R
283 Development Core Team, 2022)

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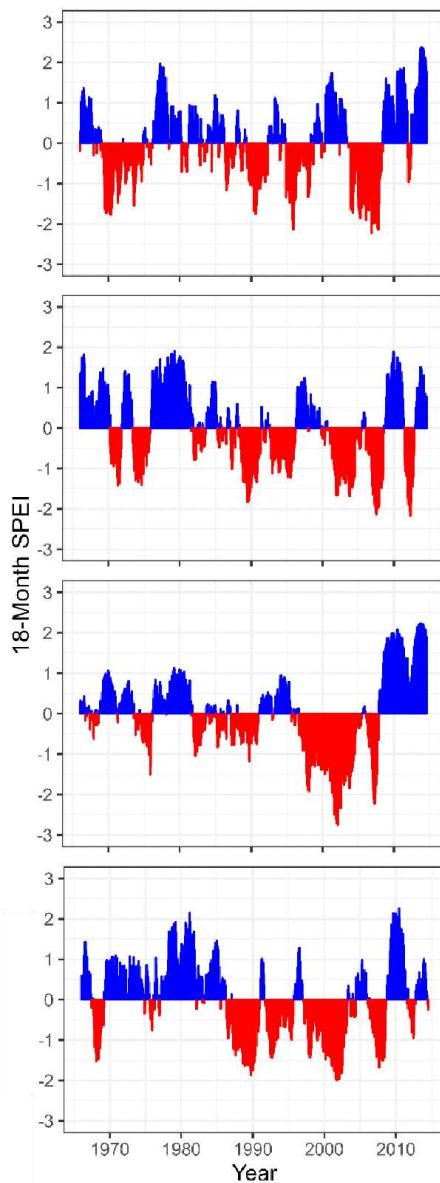
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286 **3 RESULTS**

287 **Climate trends and drought variability**

288 Annual precipitation (P) has increased significantly at TRE and CAM sites ($p < 0.01$, Figure S2a),
289 while LAZ showed a reduction in P trend during the period from 1965 to 2014 ($p < 0.05$, Figure S2a),
290 and CAL did not present any trend in P pattern. Notably, T_{\min} increased significantly in TRE, LAZ,
291 and CAM ($p < 0.001$, Figure S2b), whereas in the southern site (CAL), T_{\min} presented a pronounced
292 decrease ($p < 0.01$, Figure S2b). Simultaneously, both T_{mean} and T_{\max} exhibited a substantial and
293 significant increase across all sites ($p < 0.01$, Figure S2c and S2d). Interestingly, only at the
294 northernmost site (TRE), VPD increased drastically and significantly during the 2000s ($p < 0.001$,
295 Figure S2e), while at the southernmost site (CAL) VPD showed the opposite pattern (Figure S2e, p
296 < 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.

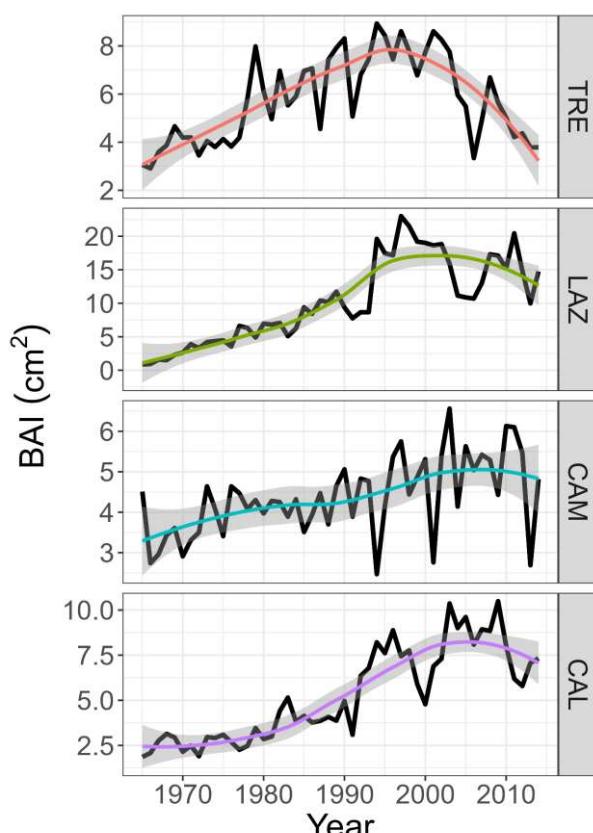
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306 **Long-term growth trends of *Fagus sylvatica* across the Italian Peninsula**

307 Mean TRW, the highest and the lowest growth rates were observed in LAZ and CAM sites,
308 respectively with statistically significant differences. Conversely, TRE and CAL showed similar
309 growth rates values ($p < 0.05$, Table S3). The age distribution of tree populations exhibited notable
310 differences across the four sites, with LAZ featuring the youngest trees and CAM the oldest trees (p
311 < 0.05 , Table S3).

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

315



316

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

320

321 **Growth response to climate variables**

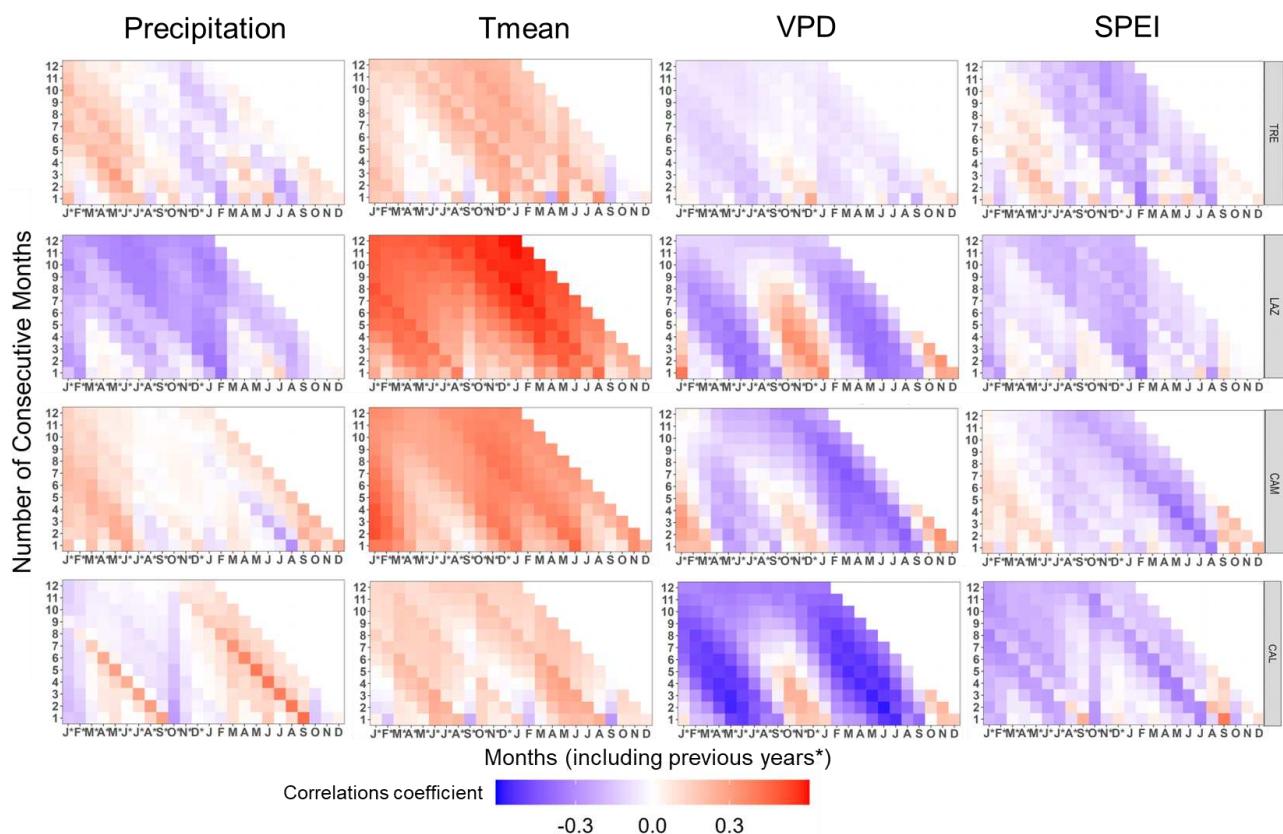
322 Basal area increment exhibited significant relationships with climatic variables in all study sites
323 (Figure 4). Overall, BAI was positively correlated with monthly P and T_{mean} and, notably, strongly
324 negative correlations with VPD were evident from May to September. This negative VPD correlation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



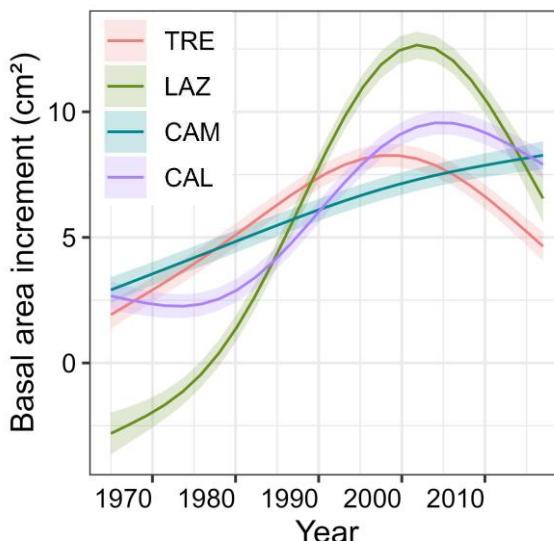
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340 **Figure 4.** Pearson's running correlations between BAI with monthly precipitation, mean temperature,
341 VPD, and SPEI1 for the current and the previous year (*) over the period 1965-2014 at each site. The
342 y-axis represents the time window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

344

345 **Growth trends of beech**

346 The GAMMs revealed different BAI trends of beech among the four sites (Figure 5, Table S4).
347 GAMM showed a monotonic increasing growth trend among the sites; however, they started to
348 diverge in the mid-1990s. Notably, the northernmost site (TRE) started to decline earlier than the
349 other sites (Figure 5). Secondly, LAZ exhibited the highest increase, followed by a drastic decline
350 during the 2000s – a similar pattern was also observed in CAL. In contrast, the oldest site CAM trees
351 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 $i\text{WUE}$ (Table 3, Figure 6). On the contrary, CAM (oldest site) showed the lowest value
359 of $i\text{WUE}$ (Table 3, Figure 6). LAZ and TRE on average presented similar $\delta^{13}\text{C}$ and $i\text{WUE}$ (Table 3).

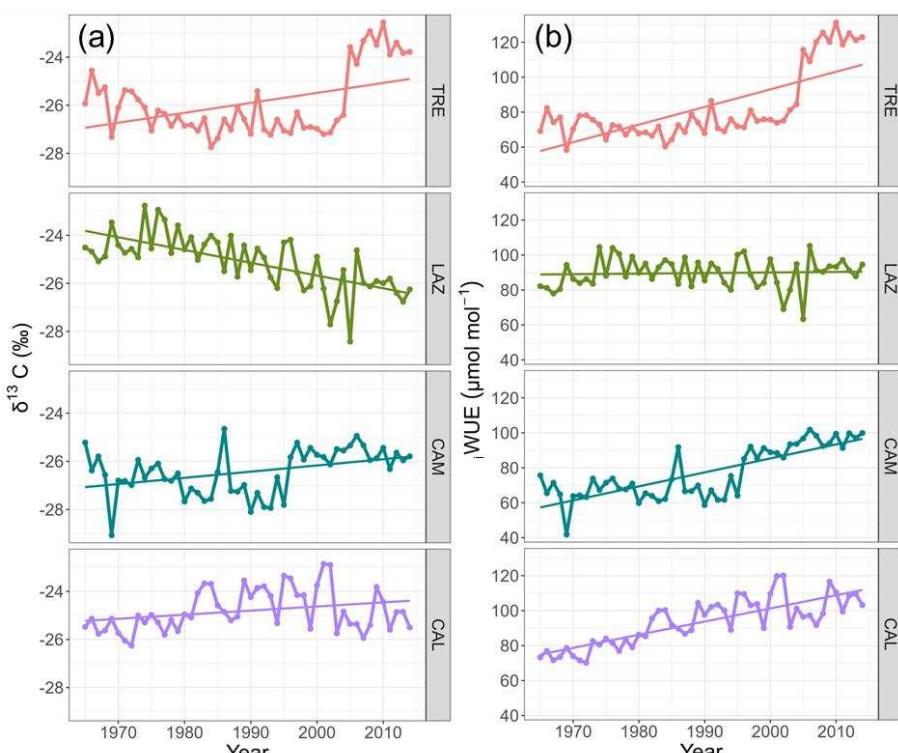
360

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

Site	$\delta^{13}\text{C}$ (‰)	$i\text{WUE}$ ($\mu\text{mol mol}^{-1}$)
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 iWUE , started to increase sharply after the drought of 2003.
367 Similarly, the southern sites CAM and CAL presented a steady increase in iWUE ($p < 0.001$, Figure
368 5). On the contrary, LAZ did not present any significant trend ($p = 0.701$).



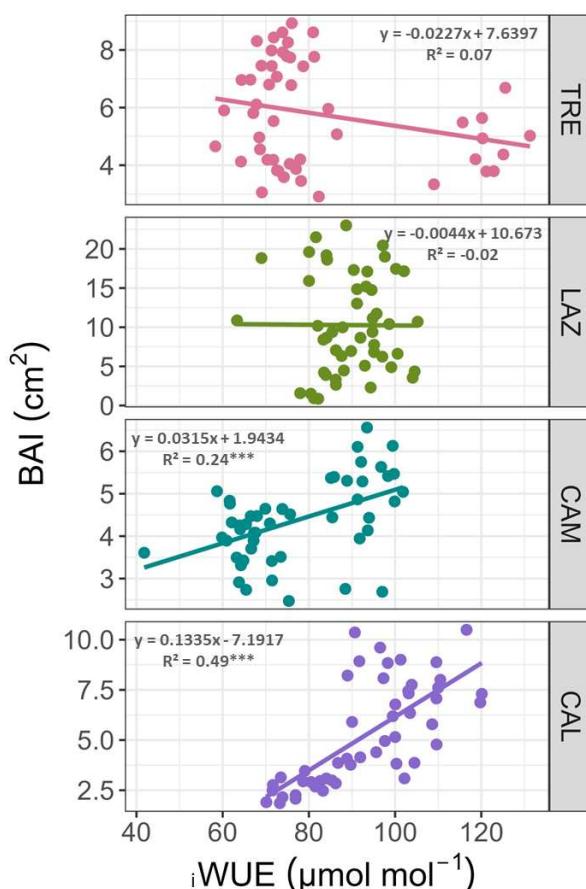
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370

371 **Figure 6** Trends of: a) $\delta^{13}\text{C}$ (‰), and b) iWUE , 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 iWUE
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 iWUE 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 **$\delta^{13}\text{C}$, iWUE, and climate relationship**

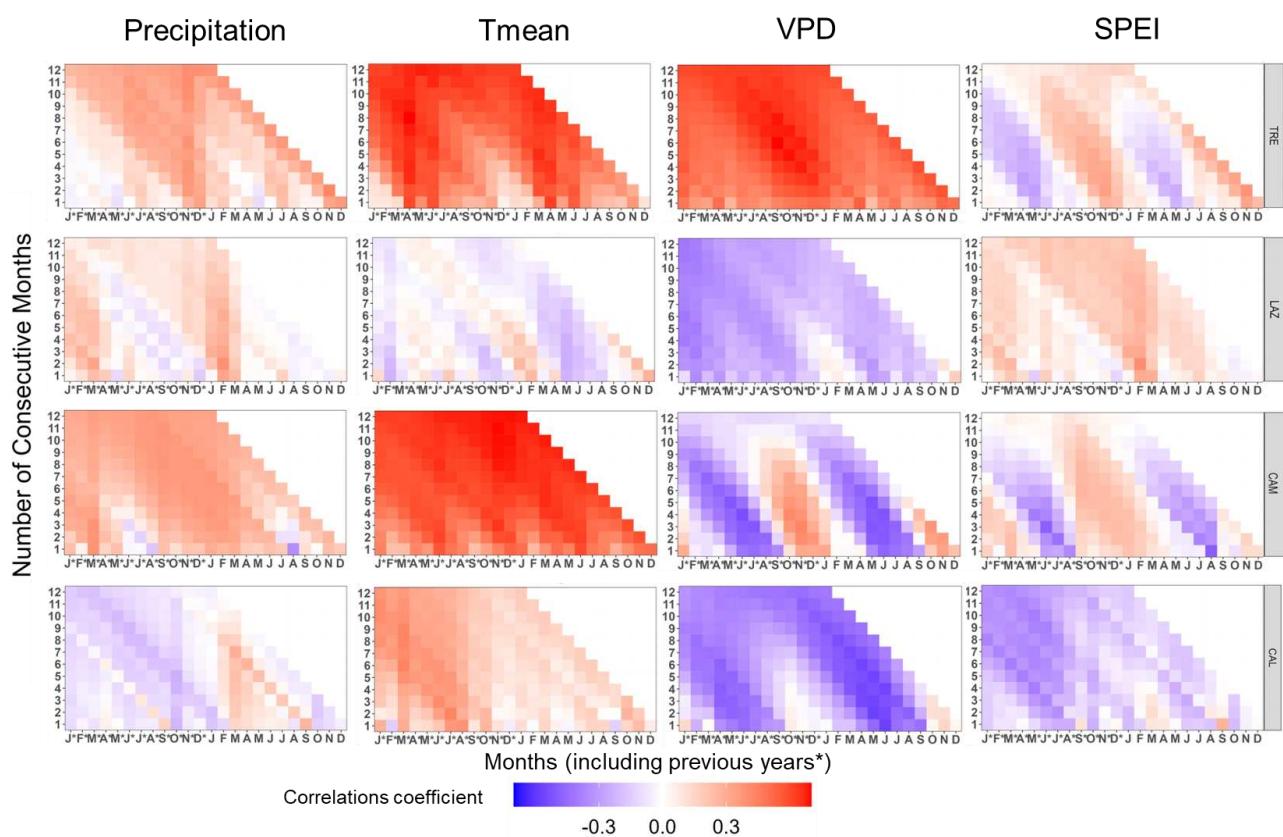
384 Carbon isotope composition ($\delta^{13}\text{C}$) and iWUE showed a similar relationship with climate variables.
385 However, iWUE presented stronger correlation with climate than $\delta^{13}\text{C}$ (Figure 8, Figure S4). An
386 exception was observed at LAZ, where $\delta^{13}\text{C}$ showed 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, i WUE was negatively and significantly correlated with VPD from March to November of
392 the current and previous year.

393 At CAM, i WUE 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 i WUE. On the contrary, i WUE 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, i WUE 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 i WUE from May to June (current and previous
400 year, Figure 8).



401

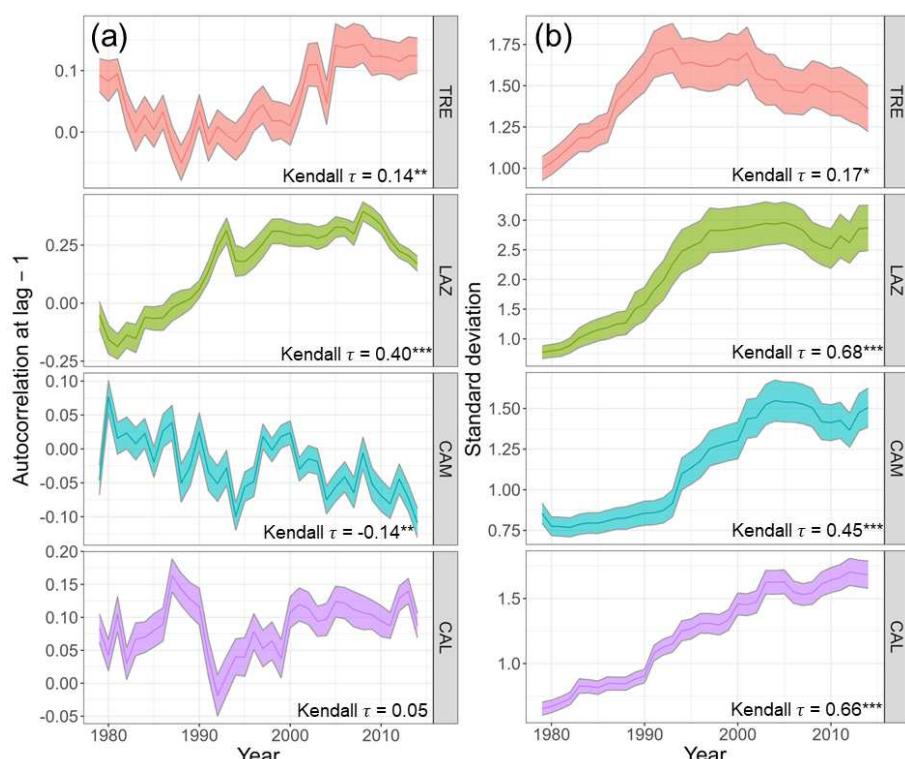
402 **Figure 8** Pearson's running correlations between i WUE with monthly precipitation, mean
403 temperature, VPD, and SPEI1 for the current and the previous year (*), over the period 1965-2014 at

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

406

407 **Early warning signals of declining forest resilience**

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



415
416 **Figure 9** Early warning signals: a) AR(1), first-order autocorrelation, b) SD, obtained using a 15-
417 year moving window for basal area increment (BAI) of *Fagus sylvatica* for four study sites for the
418 period 1965-2014. The statistics of BAI were calculated using the residuals of the time series after

419 removing the low-frequency signal (Gaussian filter) using 15-year-long windows (e.g. 1979
420 corresponds to the interval 1965-2014). The Kendall τ statistics indicate the strength of trends along
421 the time series for each variable and site. For each site, the bold line represents the mean of the
422 statistics among trees, and the shaded area is the standard error. (* $p < 0.05$, ** $p < 0.001$, *** $p <$
423 0.001).

424

425

426 4 DISCUSSION

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

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

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

442 Recent global-scale research by Yuan et al. (2019) highlighted the increase of VPD as a major
443 atmospheric driver affecting forest productivity by imposing water stress on photosynthesis. Water-
444 use strategies, particularly conservative/opportunistic responses within and across species, have been
445 closely linked to soil moisture availability (Moreno-Gutiérrez et al., 2012; Martínez-Vilalta et al.,
446 2014). Higher VPD and temperature accelerate soil moisture depletion causing a significant reduction
447 in carbon uptake (Sulman et al., 2016), elevating the risk of drought-induced dieback through
448 hydraulic failure and/or carbon starvation (Anderegg et al., 2016; Adams et al., 2017; Grossiord et
449 al., 2020).

450 Our results demonstrate a significant increase in VPD after the 2003 drought event in TRE, however
451 we found a weak negative correlation between VPD and BAI. We can hypothesise this might be
452 attributed to a lower soil water holding capacity (SWHC) at this site, potentially increasing
453 vulnerability to growth decline, as observed in our GAMM model. Conversely, LAZ exhibited higher
454 SWHC, likely contributing to higher transpiration rates and growth compared to other sites. CAM
455 and CAL sites presented moderate SWHC and a declining VPD trend, indicating less stress than the
456 TRE site. The GAMM model integrated responses to the SPEI index and individual age of each tree,
457 thus, we speculate that hydraulic strategies under drought significantly impact long-term growth rates,
458 reflecting site-specific and ontogenetic plasticity responses of the species. These findings may suggest
459 that young beech trees initially benefit from favourable climate conditions and higher transpiration
460 rates; however, this advantage depends on soil water availability and makes them susceptible to rapid
461 declines in growth during extreme drought events, as already observed in Switzerland (Vanoni et al.,
462 2016).

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

467 sensitivity to late frosts at the beginning of the growing season (Piovesan and Adams, 2001;
468 Castagneri et al., 2014; D'Andrea et al., 2021; Tonelli et al., 2023). Other studies have identified
469 lagged climate correlation with masting (Vacchiano et al., 2017). Additionally, Zimmermann et al.
470 (2015), in central Germany, found that beech growth was highly sensitive to summer temperatures
471 and extreme drought events after the 1980s.

472

473 **Drought sensitivity and water-use strategies effect on growth**

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

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

488 Our study highlights contrasting water use strategies of beech across the Italian peninsula. We
489 observed an increase of $\delta^{13}\text{C}$ and iWUE values in TRE, CAM, and CAL, indicating a conservative
490 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 iWUE 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 iWUE 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 iWUE 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 iWUE 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 iWUE 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 iWUE 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

517 southern range-edge distribution (Peñuelas et al., 2008). Recently, Qi et al. (2023) in China revealed
518 varying water use strategies among larch trees. Mature trees presented a more ‘conservative strategy’
519 (low g_s , constant assimilation rate (A)), whereas young trees maintained constant g_s and high A ,
520 indicating an opportunistic behaviour. Notably mature trees displayed a greater sensitivity to
521 atmospheric CO₂ concentrations than their young counterparts.

522 It should be pointed out that a major influence of photosynthetic rate on intercellular CO₂
523 concentration and $\delta^{13}\text{C}$, and the minor contribution of the regulation of stomatal conductance to
524 iWUE, were observed in other studies on the same species (Tognetti et al., 2014). These findings
525 suggest unclear patterns of potential increased drought-related tree decline signs in mountain beech
526 forests along the Italian latitudinal transect. Differences between leaf-level physiology and tree-ring
527 level processes may arise, reflecting potential variations in the (re)translocation patterns of non-
528 structural carbohydrates to organs (Martínez-Vilalta et al., 2016; Merganičová et al., 2019). Such
529 complexities make tree-ring analysis a challenging tool for decipher tree responses to fluctuating
530 seasonal conditions in the short term.

531

532 **Early Warning Signals of mortality**

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

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

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

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

563

564

565

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 iWUE
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 iWUE 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 iWUE 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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