



Bell-shaped tree-ring responses to air temperature drive productivity trends in long-lived mountain Mediterranean pines

Gianluca Piovesan^a, Angelo Rita^{b,*}, Franco Biondi^c, Michele Baliva^{a,d}, Marco Borghetti^e, Michele Brunetti^f, Giuseppe De Vivo^g, Alfredo Di Filippo^d, Anna Dinella^d, Tiziana Gentilesca^e, Maurizio Maugeri^h, Jordan Palli^{a,d}, Andrea Piottiⁱ, Emanuele Presutti Saba^d, Francesco Ripullone^e, Aldo Schettino^g, Giovanni G. Vendraminⁱ

^a Department of Ecological and Biological Sciences (DEB), University of Tuscia, Largo dell'Università, 01100 Viterbo, Italy

^b Dipartimento di Agraria, Università di Napoli Federico II, via Università 100, 80055 Portici, NA, Italy

^c DendroLab, Department of Natural Resources and Environmental Science, University of Nevada, Reno, USA

^d Department of Agriculture and Forest Sciences (DAFNE), University of Tuscia, Via S.C. de Lellis, 01100 Viterbo, Italy

^e Scuola di Scienze Agrarie, Forestali, Alimentari e dell'Ambiente, Università della Basilicata, Potenza, Italy

^f Institute of Atmospheric Sciences and Climate, ISAC-CNR, National Research Council (CNR), Bologna 40129, Italy

^g Ente Parco Nazionale del Pollino, Rotonda, PZ, Italy

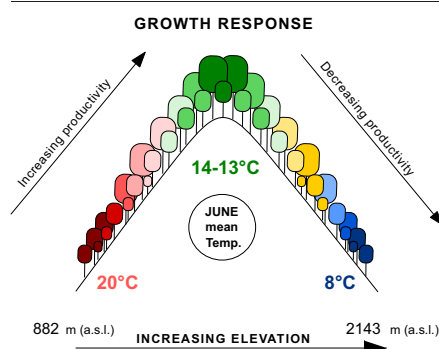
^h Department of Environmental Science and Policy, Università degli Studi di Milano, Milan 20133, Italy

ⁱ Institute of Biosciences and BioResources (IBBR), National Research Council (CNR), Via Madonna del Piano 10, 50019 Sesto Fiorentino, FI, Italy

HIGHLIGHTS

- Tree growth along an elevational gradient is non-linearly related to air temperature.
- The relation of pine growth with June and autumn temperature changes with elevation.
- June dendroclimatic response follows a bell-shaped thermal curve peaking at 13–14 °C.
- A positive response to April temperature drives acclimation of low-mountain pines.
- Old high-mountain pines have increased their stem productivity in recent decades.

GRAPHICAL ABSTRACT



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ABSTRACT

We investigated the dendroclimatic response of a *Pinus heldreichii* metapopulation distributed over a wide elevation interval (from 882 to 2143 m a.s.l.), spanning from low mountain to upper subalpine vegetation belts in the southern Italian Apennines. The tested hypothesis is that wood growth along an elevational gradient is non-linearly related to air temperature. During three years of fieldwork (2012–2015) at 24 sites, we collected wood cores from a total of 214 pine trees with diameter at breast height from 19 to 180 cm (average 82.7 ± 32.9 cm). We used a combination of tree-ring and genetic methods to reveal factors involved in growth acclimation using a space-for-time approach. Scores from canonical correspondence analysis were used to combine individual tree-ring series into four composite chronologies related to air temperature along the elevation gradient. Overall, the June dendroclimatic response followed a bell-shaped thermal niche curve, increasing until a peak around 13–14 °C. A similarly bell-shaped response was found with previous autumn air temperature, and both dendroclimatic signals interacted with stem size and growth rates, generating a divergent growth response between the top and the bottom of the elevation gradient. Increased tree growth in the

* Corresponding author at: Dipartimento di Agraria, Università di Napoli Federico II, via Università 100, IT-80055 Portici, Napoli, Italy.

E-mail addresses: piovesan@unitus.it (G. Piovesan), angelo.rita@unina.it (A. Rita), fbiondi@unr.edu (F. Biondi), m.baliva@unitus.it (M. Baliva), marco.borghetti@unibas.it (M. Borghetti), m.brunetti@isac.cnr.it (M. Brunetti), di Filippo@unitus.it (A. Di Filippo), maurizio.maugeri@mi.infn.it (M. Maugeri), jo.palli@unitus.it (J. Palli), francesco.ripullone@unibas.it (F. Ripullone), aldo.schettino@parconazionalepollino.it (A. Schettino), giovanni.vendramin@ibbr.cnr.it (G.G. Vendramin).

upper subalpine belt was consistent with the consequences of increasing air temperature under no drought stress. A positive link was uncovered between pine growth at all elevations and April mean temperature, with trees growing at the lowest elevations showing the strongest growth response. No elevational genetic differences were found, hence long-lived tree species with small geographical ranges may reverse their climatic response between the lower and upper bioclimatic zones of their environmental niche. Our study revealed a high resistance and acclimation capability of Mediterranean forest stands, and such low vulnerability to changing climatic conditions highlights the potential to store carbon in these ecosystems for the coming decades.

1. Introduction

The response of tree growth and stand productivity to climatic factors is a key performance indicator of forest ecosystem functioning, which has direct consequences for forest resistance and resilience to future environmental changes (Hessburg et al., 2019). Increasing concentration of atmospheric CO₂ associated with changing temperature and precipitation patterns are likely to trigger differential impacts on natural and managed forests across biomes (Huang et al., 2019; Piao et al., 2020; Pretzsch et al., 2020). For instance, forest growth has increased in recent times in subalpine trees and forests (Salzer et al., 2014; Silva et al., 2016), and certain species may be able to further acclimate with increasing air temperature even in the humid tropics (Bennett et al., 2021a). However, forest response to future circumstances is uncertain, particularly in Mediterranean regions, which is an area with complex climate patterns (Tuel and Eltahir, 2020). Here, heatwaves and dry spells may result in widespread productivity loss and increased mortality (Rita et al., 2020), even though the impact of drought on tree growth is generally limited to a single year (Gazol et al., 2020).

Climatic impacts on forests have often been investigated using dendrochronological data, even for scaling up from individual trees to entire ecosystems (Jeong et al., 2021; Babst et al., 2018). Traditional dendroclimatic methods rely almost entirely on linear statistical models of varying complexity (St. George, 2014; Zang and Biondi, 2015). However, recent studies using tree-ring records as a proxy for stand productivity have highlighted diverging responses along elevation gradients, thus suggesting an important acclimation capacity of the trees (Jevšenak et al., 2020; Jochner et al., 2018; King et al., 2013; Li et al., 2020; de Sauvage et al., 2022; Sidor et al., 2015; Tardif et al., 2003). Geographical and topographical gradients are considered natural laboratories for understanding plant acclimation and local adaptation (Frei et al., 2014; Opgenoorth et al., 2021). In many cases, growth of both conifer and hardwood species is positively correlated with air temperature at higher elevations because temperature can limit photosynthesis and meristematic activity (Schröter and Oberhuber, 2021). At lower elevations, increasing temperature has a more varied impact, possibly because of other environmental and bioecological factors (Cuapio-Hernández et al., 2022).

Ecological theory and experimental studies have pointed out that organisms respond to environmental gradients in a variety of ways (Austin, 2007), including bell-shaped patterns (Austin and Smith, 1989; Westman, 1980). This also applies to wood growth in connection with air temperature, even though this nonlinear response ultimately depends on the macroecological and biogeographical context (D'Arrigo et al., 2004; Escobar-Sandoval et al., 2021; Wu et al., 2019). Assuming that every other factor remains constant, a key role in defining air temperature thresholds above which stand productivity starts decreasing is played by temperature-induced growth stress (de Boer et al., 2019). The existence of optimum air temperatures for ecosystem productivity has been recently investigated across global biomes (Wu et al., 2019).

Endemism hotspots are particularly useful to evaluate potential responses to climate change scenarios. Among them, *Pinus heldreichii* H. Christ presents a scattered and fragmented distribution range restricted to the Balkan Peninsula and southern Italy. *P. heldreichii* populations of southern Italy are distributed along an elevation gradient larger than 1200 m (from 882 to 2143 m a.s.l.), from sub-Mediterranean stands up to subalpine cliffs. Stands are typically open, on rocky ledges with shallow soils (Osman,

2018) and located in remote mountain areas where anthropogenic disturbances are extremely low or absent (Todaro et al., 2007; Piovesan et al., 2019). In such open-grown stands there is almost no competition for light. Indeed, because of the absence of growth allocation differentiation among trees (e.g., Trouvé et al., 2015), stem growth trajectories can be analyzed without the interference of tree competition.

Plant traits may be confounding factors in studying climate-growth responses along environmental gradients as they are shaped during the long ontogenetic cycle by genotype-environment interactions (Berzaghi et al., 2020). This issue is particularly relevant when statistical relationships are calibrated over many decades and the subsequent climate reconstructions cover multiple centuries, because past demography and gene flow patterns may then influence dendroclimatic responses and reconstructions (Avanzi et al., 2019; Halbritter et al., 2018; King et al., 2013). Promising evidence for understanding climatic-driven acclimation and adaptive capacity of individual trees over time have been obtained from recent studies linking genetics with dendroecology (Heer et al., 2018; Ohlemüller et al., 2008; Venegas-Gonzalez et al., 2022). Considering the multi-century lifespans of trees commonly sampled for tree-ring analysis, and the long times required to reach the old stage of their ontogenetic cycle, common garden experiments, which have been used to reveal elevational clines (e.g., de Villemeruil et al., 2016; Vitasse et al., 2019), are unfeasible. And yet, the long-standing ecological question of distinguishing functional phenotypic plasticity from genetic ecotypes needs to be further investigated with respect to dendroclimatic relationships. Such basic knowledge on tree biology and ecology is essential for understanding the ability of different populations to withstand environmental changes.

In this study, we expanded our research on climate-driven growth responses in a metapopulation of *P. heldreichii* in southern Italy by specifically sampling along an elevation gradient from the montane to the subalpine Mediterranean environment. The availability of high-resolution climatology studies (Brunetti et al., 2014; Crespi et al., 2018) as well as of a network of high-quality meteorological records (Brunetti et al., 2006, 2012; Simolo et al., 2010) provided enhanced opportunities for reliable dendroclimatic analyses. By taking into account the effect of possible confounding factors (e.g., tree age/dimension, genetics), we used this extremely wide elevational gradient to test hypotheses on non-linear relationships between climate and wood growth (Cuapio-Hernández et al., 2022). Our main questions were (i) is wood growth along an elevational gradient non-linearly related to summer air temperature? and (ii) do non-linear tree-growth responses during other seasons also influence dendroclimatic signals as elevation changes?

2. Materials and method

2.1. Study area

Our study focused on 24 sites occupied by a *Pinus heldreichii* (H. Christ) metapopulation distributed throughout Pollino National Park in the southern Apennines (Italy). The sampled pines were located within forest patches along the elevation gradient, including an amphitheater-like high mountain formation extending ca. 6.6 km² (Todaro et al., 2007). Overall, our study sites cover a 1261-m elevation gradient, from 882 to 2143 m above sea level (a.s.l.) (Fig. 1, Table S1). A bedrock of greyish limestone (dolomite) with shallow rendzina-like soil characterizes all sampled sites.

Increment cores were collected over three years of fieldwork (2012–2015) from a total of 214 trees with diameter at breast height

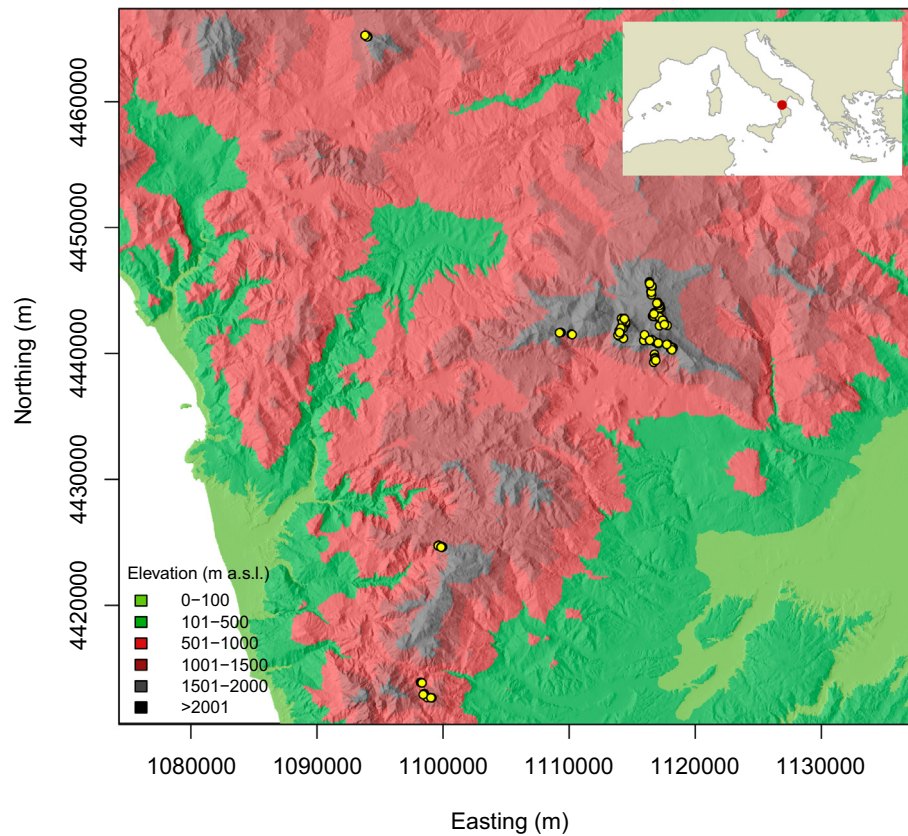


Fig. 1. Tree-ring network distribution within the study area ($\sim 15 \text{ km}^2$; red dot in map inset). Geographical coordinates are in Universal Transverse Mercator (UTM) units, zone 32 N, and topographic relief is shown using pseudo-colored elevation intervals. Sampling sites (yellow dots) spanned a $\sim 1260\text{-m}$ elevation gradient from low montane to subalpine Mediterranean environments.

(D.B.H.) spanning from 19 to 180 cm (average: 82.7 cm; standard deviation: 32.9 cm). Large, sampled trees ($> 50 \text{ cm}$ D.B.H.) included individuals with dead spike top, strip-bark formations, and few live crown patches in the lower-middle part of the stem.

2.2. Climatic data

We accurately reconstructed climate variability at each site by exploiting the spatial density and time coverage of data available over the past two centuries (Brunetti et al., 2006, 2014; Crespi et al., 2018). The global coarse-scale climatological datasets widely used in dendroclimatology as primary predictors to understand climate-growth relationships (e.g., Gao et al., 2022) lack representativeness at local scales, and this is even truer when remote sites are considered, because a meteorological station is rarely available. In our analysis, monthly temperature and precipitation series for remote mountain tree-ring sites were reconstructed by applying the anomaly method (Mitchell and Jones, 2005; New et al., 2000), which employs interpolation techniques able to capture the leading role of complex orography, as described in Brunetti et al. (2012; see also Supplementary Methods).

The climatology of the study area indicated an overall elevation gradient from 16.3 to 7.5 °C for average annual temperature, and from 1498 to 2055 mm for total annual precipitation. The annual cycle of mean air temperature and total precipitation followed similar patterns at all elevations (Fig. S1), with a relatively dry summer (June–August) and wetter conditions during the rest of the year.

2.3. Tree-ring data

Increment cores were mounted, mechanically sanded, and polished with a scalpel, then ring widths were measured to the nearest 0.01 mm

using a CCTRMD (Computer Controlled Tree Ring Measure Device; Aniol, 1987) interfaced with the software CATRAS (Aniol, 1983). Ring-width measurement series were cross-dated through visual and statistical (GLK; t-values) synchronizations (Stokes and Smiley, 1996). After cross-dating, age-related growth trends were removed using the detrendR package (Campelo et al., 2012) for the R numerical environment (R Core Team, 2021). A 100-yr cubic smoothing spline was fit to each entire ring-width series, and the resulting ring indices were then pre-whitened by applying an autoregressive model (Supplementary Table S2). The statistical quality of chronologies was evaluated using first-order autocorrelation (AR1), Gini coefficient (Biondi and Qeadan, 2008a), mean correlation between series (Rbar), and Expressed Population Signal (EPS; Wigley et al., 1984).

Basal area increment (BAI) was used as a proxy for annual biomass production (Di Filippo et al., 2012). Ring-width chronologies were converted into tree basal area increments (BAI) using the bai.out function (Biondi and Qeadan, 2008b) of the dplR package (Bunn, 2008) as follows:

$$\text{BAI}_t = \pi r_t^2 - \pi r_{t-1}^2$$

where BAI_t is the annual ring area; and r_t and r_{t-1} are the stem radii at the end and beginning of the annual increment, respectively. BAI minimizes the age effect associated with stem geometry, reduces low-frequency variability, and minimizes the need for detrending (Biondi and Qeadan, 2008b).

2.4. Environmental data analysis

A canonical correspondence analysis was performed (CCA; ter Braak, 1986) because of the wide elevational gradient (from 882 to 2143 m a.s.l.; Ashiq and Anand, 2016; ter Braak and Smilauer, 1998). With respect to

other multivariate ordination techniques, CCA has been used to model spatial and temporal ecological responses along environmental gradients (Siefert et al., 2012). CCA was computed between pre-whitened ring-width series and site-specific environmental variables, namely average annual temperature, topographic aspect (Northness = $\cos(\text{aspect})$; Eastness = $\sin(\text{aspect})$), and total annual precipitation. Scores from the first CCA axis (CCA1) were thus used to combine tree-ring series into four composite chronologies (Table S1 and Fig. 2) based on the following thresholds: ≤ -0.050 (belt 1, upper subalpine environment; 42 trees, average elevation 2031 m a.s.l.); -0.049 to 0 (belt 2, lower subalpine environment; 79 trees, average elevation 1996 m a.s.l.); 0.001 to 0.049 (belt 3, high mountain environment; 53 trees, average elevation 1856 m a.s.l.); ≥ 0.050 (belt 4, low mountain environment; 40 trees, average elevation 1284 m a.s.l.). The threshold of -0.05 and 0.05 grouped around 20 % of the trees located respectively at the upper and lower limits of the gradient, thus highlighting the differences in climatic signals.

Growth-climate relationships over the common time period (1966–2015) were then computed via bootstrapped response and correlation functions with 1000 replications using the treeclim R package (Zang and Biondi, 2015). The four composite chronologies were used as

predictands, while site-specific monthly air temperature (mean, maximum, and minimum) and total precipitation were the predictors.

In addition, the June temperature response curve of site scores from the first CCA axis (CCA1) was smoothed with three-knot thin plate regression splines using the *gam* function of the *mgcv* package (Wood and Wood, 2015). The CCA1 grouping factor was specified as a random smooth term in a Generalized Additive Mixed Model (GAMM; Hastie and Tibshirani, 1990; Wood, 2017). The level of complexity (nonlinearity) of model terms was determined by the estimated degrees of freedom of the smoother by using the approximate Restricted Maximum Likelihood (REML) method, with low REML values representing the best compromise between model complexity and fit to the observed data (Wood and Wood, 2015). We then tested for changes of this nonlinear pattern using the first derivative of the estimated trend, calculated using the method of finite differences.

The response of BAI to average temperature during selected months was also investigated using a Generalized Additive Mixed Model (GAMM). Previous-year growth (BAI_{t-1}) was included as a model term to take into account autocorrelation between subsequent years. A group-level term that was derived from the CCA analysis of the prewhitened ring-width chronologies, i.e., CCA1 group ≥ 0.050 (low mountain environment) and CCA1

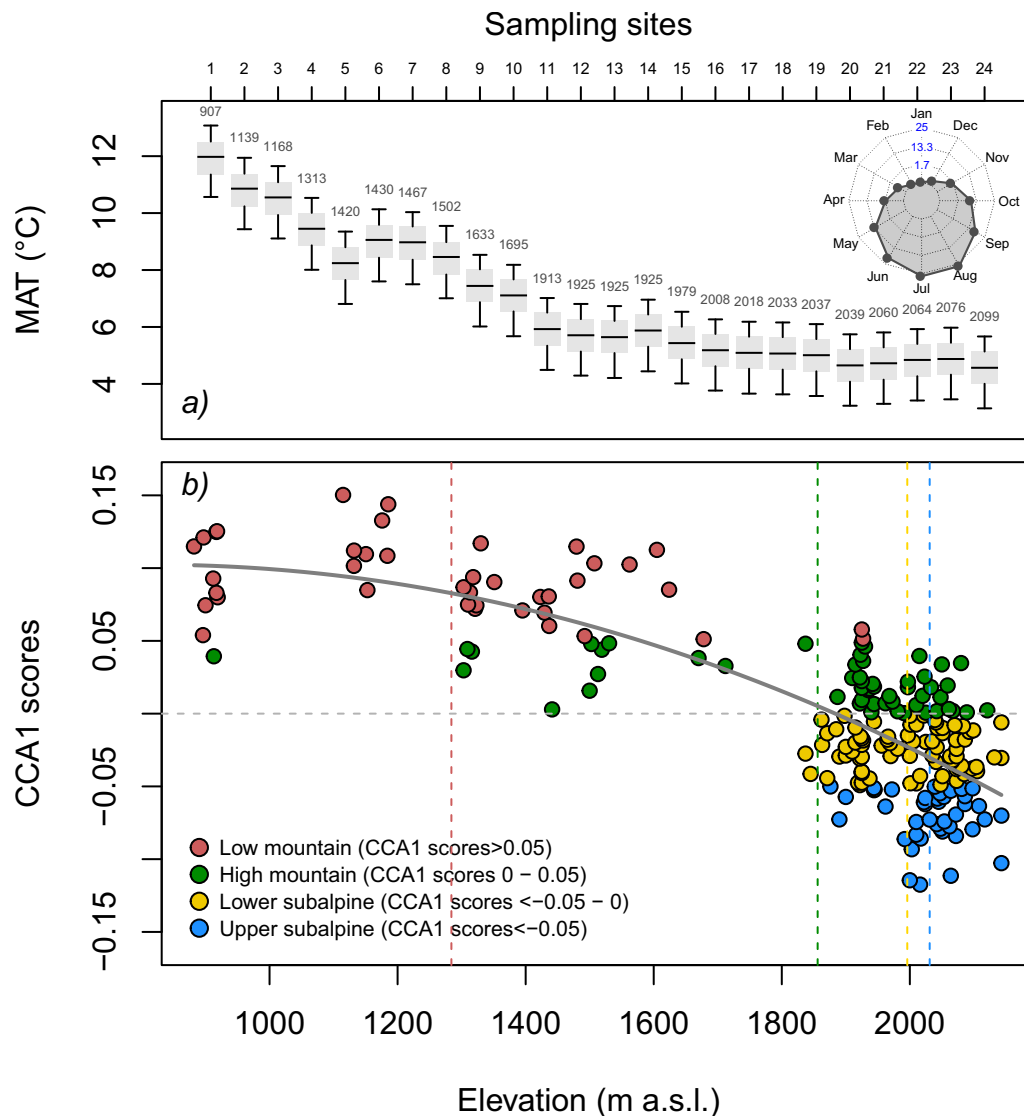


Fig. 2. a) Mean annual temperature (MAT, °C) of sampling sites along the elevation gradient. Numeric values above boxplots are the site-specific average elevations (m a.s.l.). The spider-web graph inset shows the monthly mean pooled MAT (grayscale dots and segments). b) CCA1 scores of prewhitened ring-width series against elevation, with different colors for the four bioclimatic belts. Dashed vertical lines, also color-coded, indicate the mean elevation of each belt. A second-degree polynomial fit to all scores ($R^2 = 0.64$) is shown in dark grey.

group ≤ -0.050 (subalpine environment), was added to fit different trend adjustments over time. Two-dimensional thin-plate splines were used for the interaction between Northness and Eastness and included as a random factor. Because BAI values represent repeated measures over the same individuals, we included a random effect of tree ID on the intercept and slopes to account for tree-specific noise. We used the REML method to estimate model coefficients and smoothing parameters.

2.5. Genetic analysis

To describe the genetic structure of *Pinus heldreichii* populations, 515 individuals from 15 populations covering a subset of our tree-ring network (Table S7) were genetically characterized at neutral molecular markers (i.e., nuclear microsatellites, nSSRs). Specifically, all sampled individuals were genotyped at 12 unlinked and null allele free nSSRs (pEST2669, pEST8, Steinitz et al., 2011; B4F08, Guevara et al., 2005; epi3, Budde et al., 2014, PtTX3116, Elsik and Williams, 2001; PHA_33235, PHA_16653, PHA_5323, PHA_6426, PHA_4497, PHA_6062, PHA_15897, Leonarduzzi et al., 2016) arranged in two multiplexes. The DNA extraction and amplification procedures are reported in Leonarduzzi et al. (2016). Genetic distances (G_{ST}) were estimated by calculating both G_{ST} among populations and the multi-locus estimate of pair-wise relatedness (r) among individuals (Smouse and Peakall, 1999). The relationship between differences in elevation and genetic distances at both individual and population levels was assessed through partial Mantel tests, evaluating the correlation between the matrices of genetic and elevation distance while controlling for the effect of linear distance. All calculations were performed by using GenAlEx (Peakall and Smouse, 2006) and partial Mantel tests were carried out by the *mantel.partial* function in the R package *vegan* (Oksanen et al., 2018).

3. Results

Tree-ring series ordination (period 1966–2015) through CCA highlighted a bioclimatic component driven by temperature variation along the elevation gradient. Site scores from the first CCA axis of the prewhitened ring-width series (CCA1) explained 74.7 % of the original variance in tree-ring data (214 trees). Mean annual air temperature was the leading environmental factor (Pearson correlation $r = 0.79$) for CCA1 tree scores, while aspect contributed to a lesser extent (Eastness: $r = 0.20$; Northness: $r = 0.20$). CCA1 scores ranged approx. from -0.15 to 0.15 , showing a non-linear inverse relationship with tree elevation (Fig. 2). CCA2 (25 %) had no correlation with temperature and elevation. Very similar results were obtained using BAI series (data not shown). The Mann-Whitney test (Table S1) showed that Eastness of the two higher bioclimatic belts (1 and 2) was significantly different than the lowest one (belt 4), while no significant difference was found for Northness (Table S1). Some overlap existed in terms of elevation between CCA1 classes (Fig. 2b). For instance, between 1950 and 2050 m there were trees categorized as belts 1–3 (Table S6), i.e., high mountain (19 trees), lower subalpine (26 trees), and upper subalpine (16 trees). Limited difference in mean annual temperature ($\sim 1^\circ\text{C}$) was found between the 14 sites sampled at the upper elevations, ranging from ~ 1900 to ~ 2100 m (Fig. 2a).

The average tree-ring series length was 366 years ($SD = 213$ years), with four individuals exceeding 900 years of age. Average tree age increased with elevation while the opposite trend was found for BAI (Table S1). On average, trees at the highest elevations (belt 1, upper subalpine) showed significantly lower BAI than trees belonging to other belts (Table S1). While BAI values between 1966 and 2015 for trees growing in the low mountain environment (belt 4) leveled out post-1990, trees at higher elevations (belts 1–3) were characterized by an overall increasing BAI trend (Fig. S2 and Table S1). Average tree age was greater in the three higher belts (1, 2, and 3), where the longest-lived trees were found, compared to the lowest one (belt 4; Table S1). Average composite chronologies of ring-width and BAI had EPS >0.85 for the study period (1966–2015) (Tables S2 and S3). Site chronologies from the highest and

the lowest belts (1 and 4) showed no statistical synchronization with each other (Table S4).

Dendroclimatic response functions pointed to air temperature as the leading climate variable affecting tree growth variability along the elevation gradient (Fig. 3). Signs of response function coefficients between tree growth and average monthly temperature reversed along the elevation gradient. The low mountain (belt 4) chronologies had an overall negative relationship with monthly temperature, while the opposite case was found, especially in June, for chronologies from the upper subalpine environment (belt 1; Fig. 3a). Subalpine pines were limited by cold June temperatures, especially with regard to the minima (Figs. S3–S4). The BAI chronology for the upper subalpine environment (belt 1; Table S3b), when compared to mean annual temperatures calculated from the previous September to the current August, was characterized by an increasing growth trend in parallel with climate warming (Fig. S8).

All four elevation belts were positively related to April mean temperature, but the response was statistically significant only for trees growing at the lowest elevations (belt 4; Fig. 3a). Total precipitation is still relatively abundant in spring even at the lowest elevations (>50 mm/month on average), hence no relevant water stress is expected (Fig. S1). Warmer air temperature makes late frost less likely to happen, and may speed up snowpack melting, which increases soil moisture. Tree growth of the two subalpine belts (1–2) was significantly and positively correlated to February mean temperature (Fig. 3a). October–November temperatures in the previous year were also significantly and positively related with chronologies from middle and high elevations (Figs. S3 to S6). Total precipitation was less connected with tree growth than mean air temperature (Fig. 3). A relationship with previous June–July precipitation (negative for the lowest belt, positive for the three higher belts) was the only significant connection (Fig. 3b).

We found no significant relationship between genetic distance and elevation both at the individual and population levels (Fig. S7).

Relationships between growth parameters and environmental variables detected by GAMM (Fig. 4) included a positive link between BAI and April mean temperature. Mean air temperature in June and in November–December of the previous year had connections with BAI that were opposite for upper subalpine (positive) and low mountain environments (negative; Fig. 4 and Table S5), revealing the importance of gradient-based analyses. The positive dendroclimatic association with February temperature for the two subalpine elevation classes did not appear in GAMM results, and it remains unclear given that average monthly air temperatures were normally below zero during those months at the highest elevations (Fig. S1). Overall, the fitted model explained about 85 % of total variance, as also shown by the graphical match between predicted and observed data (Fig. 4b).

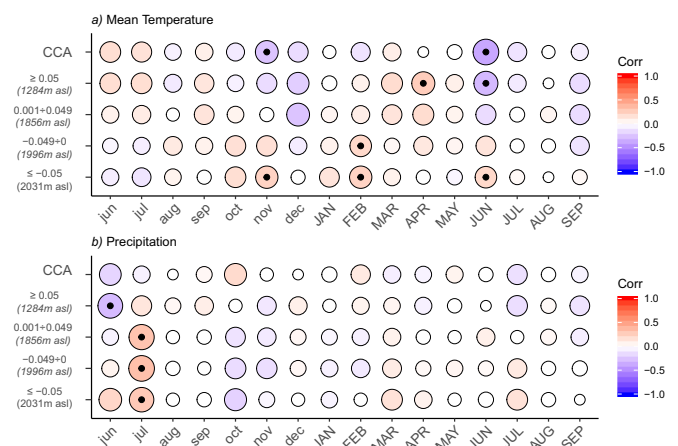


Fig. 3. Bootstrapped response functions of CCA1 scores, derived from prewhitened ring-width chronologies, against a) monthly mean temperature, and b) monthly total precipitation. The average elevation of each belt is shown on the vertical axis. Lowercase month abbreviations on the horizontal axis refer to the prior year.

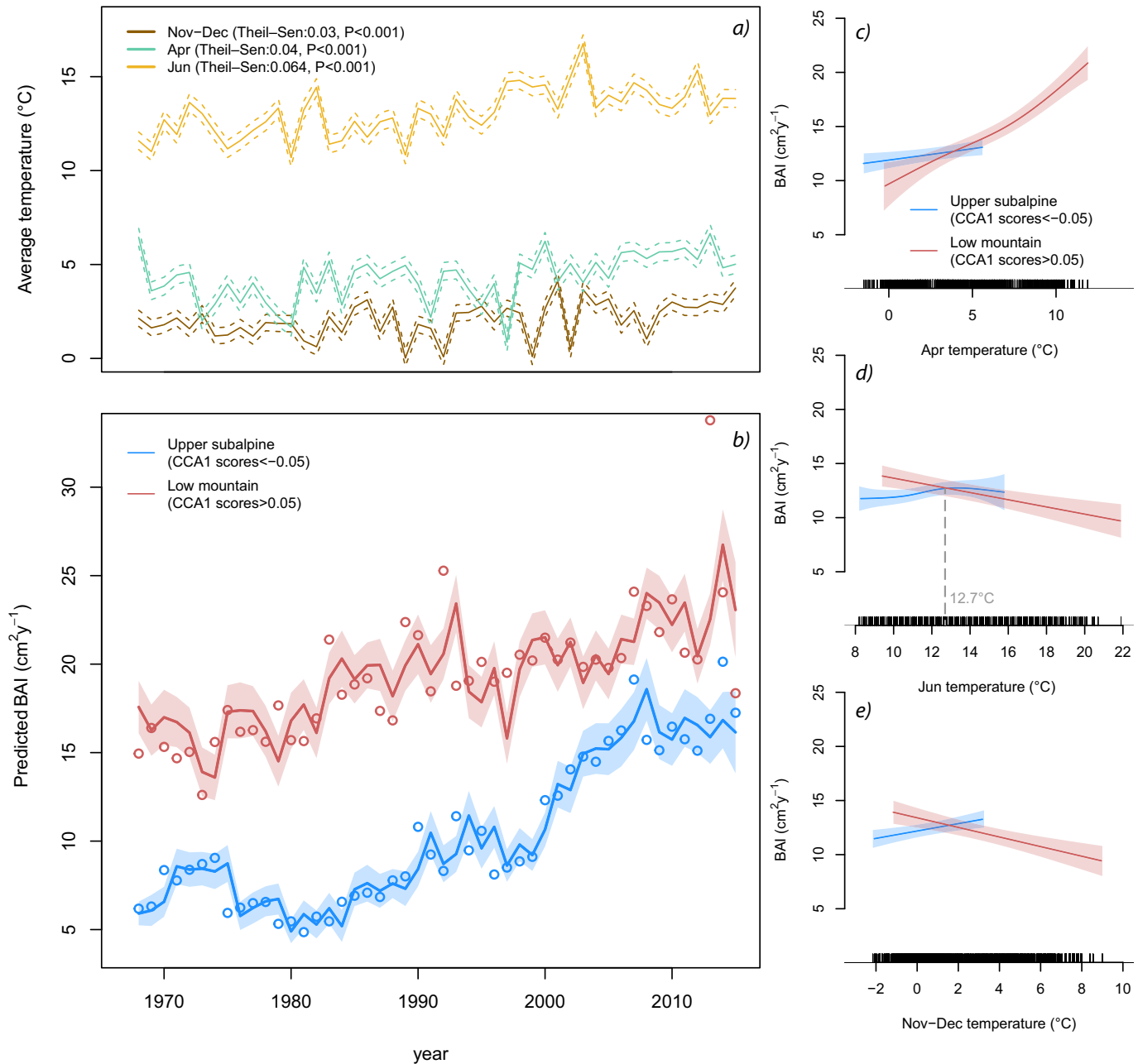


Fig. 4. a) Time-series patterns during 1966–2015 of mean air temperature in November–December, April, and June, which were all increasing based on the non-parametric Theil–Sen slope test (Sen, 1968). b) Predicted GAMM (lines) and observed (dots) average basal area increment (BAI) chronologies from the upper subalpine and the low mountain environment, as defined by the CCA1 scores of prewhitened ring-width chronologies. Shaded areas around the lines represent their standard error. Fitted (excluding random terms) GAMM trends for the BAI response to average air temperature in (c) April, (d) June, and (e) November–December of the previous year. In this analysis, which used only trees from the top and bottom of the elevational gradient, an intersection point was found for June mean temperature of 12.7 °C (grey dashed vertical line in d).

Prewhitened ring-width chronologies displayed a bell-shaped relationship with June mean air temperature (Fig. 5). An inflection point was suggested by the first derivative of the GAMM fitted trend, corresponding to a mean June temperature of 14 °C (Fig. 5). Comparing the temperature response of trees growing only at the top and bottom of the elevational gradient (Fig. 4d) revealed a lower turning point, around 13 °C (12.7 °C; Figs. 4d – 5).

4. Discussion

Average tree growth decreases with elevation in European mountains, a bioclimatic pattern previously discussed by Di Filippo et al. (2012). Our

study confirmed that growth gradient for *Pinus heldreichii* on a Mediterranean massif (Mt. Pollino, southern Italy) from 1966 to 2015, so that pines of the subalpine zone (belt 1) are characterized by the lowest levels of wood growth. However, in the most recent decades all sampled pines have increased their annual growth rates, and this trend has been greater at the higher elevations, to the point that BAI of the lowest-elevation trees (belt 4) has become comparable with that of belt 3 and 2 (Fig. S2). The positive relationship with air temperature was most pronounced in the upper subalpine environment, suggesting that climate warming in temperate mountains may be responsible for these elevation-dependent growth trends. While it has been argued that increased air temperature may restrict the area of cold-limited forests (Pompa-García et al., 2021), the increased

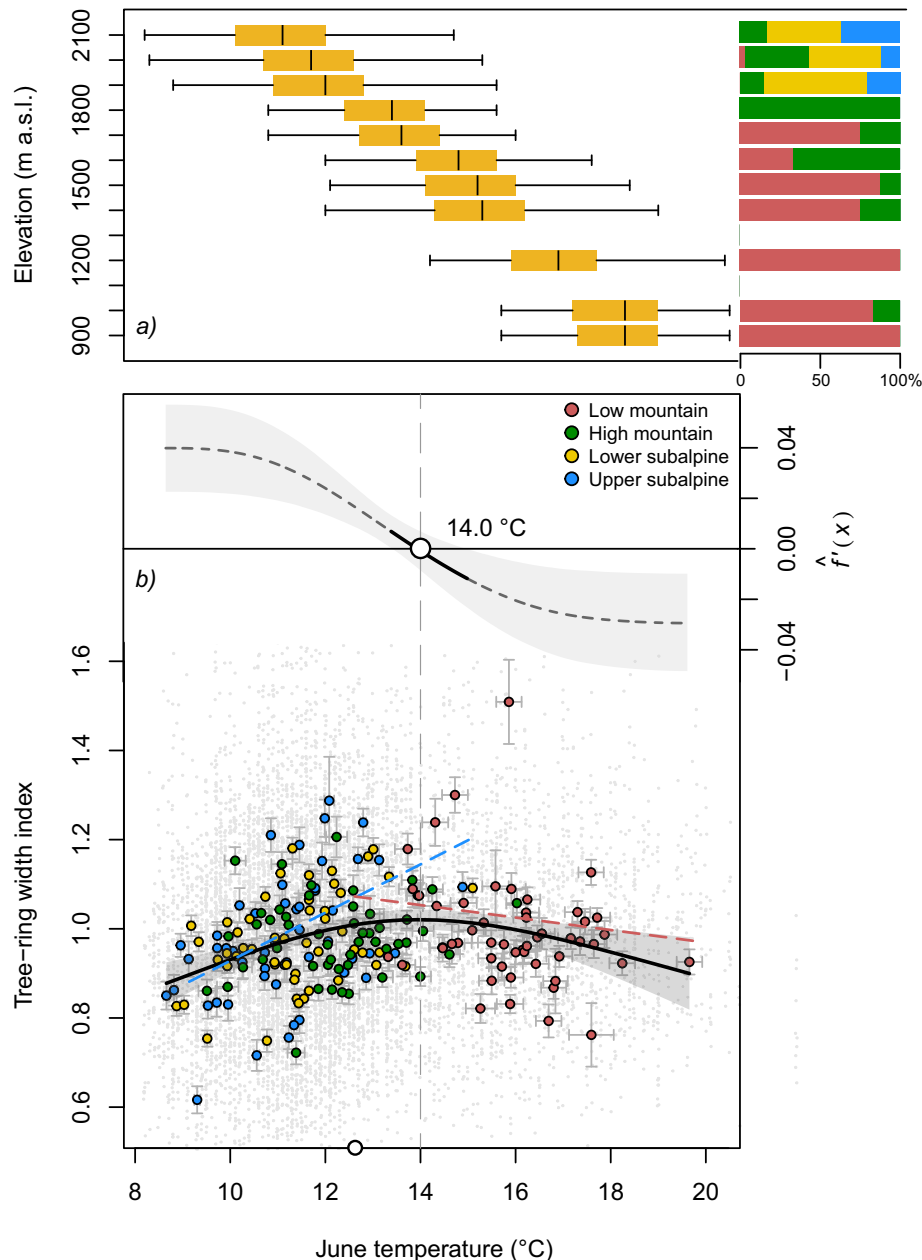


Fig. 5. a) Box-plot diagrams showing distribution of June air temperature with elevation of the 24 sampled sites grouped by elevation (11 groups from 900 to 2100 m, each group covering a 100-m interval). Horizontal bars to the right represent proportion of sampled trees at each of these 11 groups for each of the 4 elevation belts, color-coded as in Fig. 2b. b) Generalized additive mixed model (GAMM) fit between prewhitened ring-width series and average June air temperature. In the upper portion, the smooth line shows the first derivative ($f'(x)$) of the fitted trend, with a turning point at 14 °C. The grey area around the line represents a 95 % confidence interval. In the lower portion, the fitted model (solid black line) and its 95 % confidence interval (grey shaded area) are overlaid on the mean values (solid dots) and their standard errors (grey bars) of CCA1 scores, color-coded as in Fig. 2. Light-grey dots represent the whole tree-ring width data. Blue and red dashed lines represent linear growth-temperature regression of trees from the upper subalpine environment and low mountain environment, respectively. The two dashed lines intersect at ~12.7 °C (white dot on x-axis). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

productivity of trees growing at higher elevations is consistent with climate warming scenarios under no drought stress (Büntgen et al., 2014; Dorado-Liñán et al., 2017; Vitasse et al., 2019). Increased growth has similarly been reported for the last decades in treeline stands of *Pinus uncinata* (Spain) and *Pinus longaeve* (USA) (de Boer et al., 2019; Galván et al., 2014).

Tree size was also affected by bioclimatic conditions. The largest stem diameters were found in the lower subalpine environment (belt 2), where *P. heldreichii* trees experience their ecological optimum – sensu Ellenberg (1988) – and are now expanding into abandoned grasslands (Piovesan, 2019). The subalpine belt is also characterized by ecological conditions that favor extreme longevity, hence millennium-old trees are present

(Piovesan et al., 2019; Piovesan and Biondi, 2021). Dendroclimatic signals pointed out the primary role of air temperature in driving pine growth responses along the elevation gradient, while precipitation in these open stands played a minor role. Despite its Mediterranean climate, the study area is not characterized by severe and extended summer drought (Fig. S1), especially in the subalpine environment. Furthermore, drought events can be offset by occult moisture (fog banks, low clouds) coming from the relatively near Thyrrenian and Ionian seas (Todaro et al., 2007). Dendroclimatic analysis of CCA1 composite chronologies revealed the leading climatic signal of June air temperature, conditioning growth rates at the top and at the bottom of the elevation gradient. A warm June was

associated with higher tree growth in the subalpine stands while the opposite relationship was uncovered at the lowest elevations. Water from melting snowpack and fog banks is likely to provide enough moisture during early summer in the subalpine environment (Todaro et al., 2007), so that pine trees can take advantage of a mild/warm June, as it has been reported for subalpine environments outside the Mediterranean basin (Dusenge et al., 2019; Pretzsch et al., 2020; Sidor et al., 2015). June temperature has been found to regulate conifer xylogenesis in mountain environments when maximum transpiration and growth rates occur in coincidence with the period of maximum day length (Rossi et al., 2006). At low elevations, instead, warmer June temperatures may induce drought stress due to increasing evapotranspiration (Buermann et al., 2018; Pretzsch et al., 2020). Tree growth limitation due to drought is common in the Apennines for both conifers (e.g., fir) and angiosperms (e.g., beech, oaks) growing on hilly and mountain sites (Piovesan et al., 2005; Colangelo et al., 2021).

P. heldreichii growth was related to June temperature according to a bell-shaped “thermal niche” curve, nonlinearly increasing to a peak around 13–14.0 °C. Such a turning point is consistent with studies of optimum air temperature for ecosystems under cold climates in the boreal biome (Huang et al., 2019; Yin et al., 2022), and it is slightly higher than the temperature thresholds estimated for growth decline of spruce populations at treeline in Alaska (11–12 °C, mean July temperature; Wilmsking et al., 2004) and in Canada (11.3 °C, mean July–August temperature; D’Arrigo et al., 2004). Growth decline as a consequence of summer temperatures exceeding 13–16 °C was described also for spruce in the Carpathians and Norwegian forests (Andreassen et al., 2006; Sidor et al., 2015).

P. heldreichii differentiated from Mediterranean pines in the Tertiary (Saladin et al., 2017), developing specific adaptations to the Mediterranean-montane climate (Schirone et al., 1991). Therefore, it is plausible that growth temperature thresholds of our sampled stands could be higher than those reconstructed for taiga forests (D’Arrigo et al., 2004; Wilmsking et al., 2004) because of the long evolutionary adaptation to the Mediterranean climate. With regard to maximum air temperatures, the turning point found at ~18 °C (Fig. S9) is consistent with the optimum air temperature assigned to evergreen needle-leaved forests of the boreal hemisphere (Liu, 2020). Our dendroecological results are consistent with other remote sensing and eddy covariance studies revealing that growth–temperature relationships can be described by a convex parabola with detectable temperature optimum specific for each ecoregion (Bennett et al., 2021b). Since the shape of that curve is also affected by environmental covariates (e.g., available water, solar radiation, disturbances), we highlight the necessity to consider the local sensitivity of tree growth to temperature to improve current land-surface models. In this study, the optimal temperature for wood growth confirms that subalpine/ boreal forest ecosystems have the lowest temperature values with respect to other forest types (Liu, 2020; Bennett et al., 2021b), highlighting the key role of climatic constraints in shaping functional evolution in trees. *P. heldreichii* acclimation capacity should also be noted, as it is demonstrated by the wide elevational gradient it occupies, from near treeline descending into low mountain rocky slopes where it mixes with the Mediterranean evergreen vegetation.

In the absence of water deficit stress, warm air temperature promotes photosynthetic capacity up to an optimum threshold above which temperature decreases photosynthesis (Dusenge et al., 2019; Huang et al., 2019). Such an optimum depends on the physiology of the species, although it typically occurs in the 30–40 °C range at the leaf level in absence of other limiting factors (Huang et al., 2019). Recent findings suggest that turgor plays a key role in the wood formation process, with a decrease in growth rates of spruce above 11 °C that can be explained by water pressure deficit (VPD; Peters et al., 2021). The nonlinear growth–temperature relationships we uncovered could thus be due to varying ecological conditions along the elevation gradient because VPD can induce lower turgidity at the reported threshold temperatures (12–14 °C), negatively affecting tree growth, as was reported for *Pinus longaeva* at treeline in the White Mountains of North America (Beck et al., 2011; de Boer et al., 2019) and for the boreal biome (Yin et al., 2022).

Although a positive relationship between air temperature and tree growth at high elevation has been widely recognized, the response to June temperatures interacted with stem size and growth rates. In particular, trees growing within a narrow elevation interval, between 1950 and 2050 m, could be classified as belts 1–3, but with significantly different mean D.B.H. and BAI among such classes (Table S6), suggesting that the temperature gradient along the elevation and the site aspects were not the only factors controlling the dendroclimatic response. In other words, given the limited changes in climate that would be expected in the subalpine environment over 100 m of elevation difference (Fig. 2a), the separation between tree responses to June temperature was most likely driven by individual tree size and growth variability, possibly interacting with microtopography. Positive correlation to June temperature characterizes slow growing and smaller pines confirming the growth/size-modulated climate sensitivity that was found in other subalpine forest species (e.g., Carrer and Urbinati, 2004; Campbell et al., 2021). The overlap of bioclimatic belts for trees growing at the highest elevations was also plausibly linked to topographic influences (e.g., Bunn et al., 2018) that might confound the trees’ responses to climate in the complex Mediterranean mountain environment.

Differences in climatic responses along the elevational gradient could be due to natural phenotypic plasticity and the ability of the species to acclimatize, or to local adaptation despite high gene flow (e.g., Ruiz Daniels et al., 2019). The reported absence of genetic structure at nSSR loci was likely due to substantial reshuffling of neutral genetic variation through gene flow along the investigated elevation gradient (Fig. S7), and excludes a general impact of past demography on subsequent results about the relationship between growth parameters and environmental variables. Differential effects of climate warming on trees growth have been recognized for temperate tree species at the edge of their ecological gradient (Cai et al., 2020; Jochner et al., 2018; Pretzsch et al., 2020). Studies linking genomic and dendrophenotypic variation can explore the biological mechanisms behind stress-tolerant phenotypes in tree populations (e.g., Heer et al., 2018; Martínez-Sancho et al., 2020), and the ecological settings of our investigation represent a valuable resource for future genomic investigation. Our research highlighted the capacity of *P. heldreichii* to acclimate to warmer conditions, as also shown in another study that involved a subset of our samples together with additional tree species living in old-growth forests of the same region (Colangelo et al., 2021).

A positive link was uncovered between pine BAI at all elevations and April mean temperature (Figs. 3a–4c). Trees growing at the lowest elevations showed much stronger growth response to April temperatures. In Mediterranean mountains, spring (March–April) is characterized by progressive snowpack melting beginning at low elevation, and the occurrence of seasonal and orographic rain that ensure water availability (Latron et al., 2009). Spring warmer air temperature makes late frost less likely to happen, and may speed up snowpack melting, which increases soil moisture spurring fast growth resumption. Hence, tree growth could be favored at all elevations, and low elevation stands could particularly benefit from early spring warmth (Häusser et al., 2023). The growth increase experienced in 2013 by pines at the lowest elevations (Fig. 4b) could then be related to the April mean temperature, which in that year exceeded the overall 1966–2015 average by 2.4 °C. In the subalpine environment (belts 1–2), April mean temperatures are usually below the threshold for wood growth, which ranges between 5.5 °C and 7.5 °C (Andreu-Hayles et al., 2020; Körner, 1998; Rossi et al., 2007), and late frost events could still occur in this month (Fig. S1). On the other hand, as a consequence of widespread temperature increase, montane stands may undergo phenological anticipation whose benefits are then offset by increased summer temperature and/or drought stress (Buermann et al., 2018; Dow et al., 2022).

Pines growing in the subalpine environment were positively influenced by mean air temperature in February and in previous-year November–December (Figs. 3a–4e). Autumn warm temperatures can affect the metabolic carbohydrate pool that trees will exploit during the current year (Tardif et al., 2003), most likely triggering growth responses in the early growing season (Todaro et al., 2007).

5. Conclusions

We investigated the role of bell-shaped bioclimatic niches on a meta-population of open-grown *P. heldreichii* growing along a wide elevation gradient in the Southern Italian Apennines, where no elevational genetic structure was detected. Mean annual temperature and topographical aspect were the main predictors of annual tree-ring variability along the gradient, but responses to monthly air temperature revealed diverging patterns between low mountain and subalpine pines. Opposite dendroclimatic responses between the top and bottom of the elevation gradient have led to reduced differences in stem growth (BAI) along the elevation gradient. Pines growing at the highest elevations have reached stem growth (BAI) comparable to that of lower-elevation sites, whose growth has instead not benefited from warmer air temperatures during early summer and previous autumn. The increased productivity of trees in the upper subalpine belt is consistent with the consequences of climate change scenarios under no drought stress. However, at the lowest elevations, a positive response to April temperature may be counterbalancing the negative impact on pine growth of increasing air temperature during those other two seasons. This high resistance and acclimation capability along Mediterranean elevation gradients suggest a low vulnerability to changing climatic conditions, supporting the potential to store carbon for the coming decades.

Average June air temperature was a key factor influencing tree growth, and we showed evidence for a bell-shaped thermal niche curve, nonlinearly increasing until a peak around 13–14 °C. Such a turning point is consistent with global studies that have identified optimum air temperature for tree growth under cold climates, and our analysis suggests that even species found within relatively small geographical ranges may reverse their climatic response between the lower and upper bioclimatic zones of their environmental niche, thereby revealing a high resistance and acclimation capability of old-growth forest stands.

CRedit authorship contribution statement

Gianluca Piovesan: Conceptualization, Methodology, Project administration, Supervision, Investigation, Writing – original draft, Writing – review & editing. **Angelo Rita:** Conceptualization, Formal analysis, Software, Validation, Writing – original draft, Writing – review & editing. **Franco Biondi:** Conceptualization, Supervision, Writing – original draft, Writing – review & editing. **Michele Baliva:** Conceptualization, Investigation, Data curation, Writing – review & editing. **Marco Borghetti:** Conceptualization, Writing – review & editing. **Michele Brunetti:** Conceptualization, Data curation, Formal analysis, Software, Validation, Writing – review & editing. **Giuseppe De Vivo:** Conceptualization, Writing – review & editing. **Alfredo Di Filippo:** Conceptualization, Investigation, Writing – review & editing. **Anna Dinella:** Conceptualization, Data curation, Writing – review & editing. **Tiziana Gentilesca:** Conceptualization, Data curation, Writing – review & editing. **Maurizio Maugeri:** Conceptualization, Data curation, Writing – review & editing. **Jordan Palli:** Conceptualization, Data curation, Formal analysis, Software, Validation, Writing – review & editing. **Andrea Piotti:** Conceptualization, Investigation, Data curation, Writing – review & editing. **Emanuele Presutti Saba:** Conceptualization, Investigation, Writing – review & editing. **Francesco Ripullone:** Conceptualization, Writing – original draft, Writing – review & editing. **Aldo Schettino:** Conceptualization, Investigation, Writing – review & editing. **Giovanni G. Vendramin:** Conceptualization, Data curation, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.164103>.

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