



Mediterranean old-growth forests exhibit resistance to climate warming

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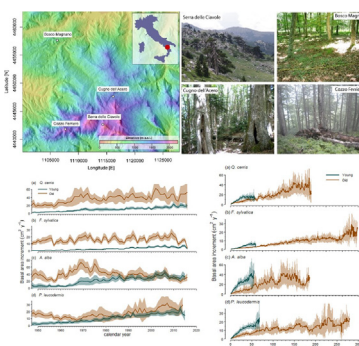
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HIGHLIGHTS

- We characterized radial growth dynamics in old-growth forests.
- Climate-growth relations of young and old trees were assessed.
- Younger trees grew faster than their older conspecifics.
- Growth sensitivity to climate differed between young and old trees.
- Old trees showed stable growth rates and were resilient to climate warming

GRAPHICAL ABSTRACT



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ABSTRACT

Old-growth mountain forests represent an ideal setting for studying long-term impacts of climate change. We studied the few remnants of old-growth forests located within the Pollino massif (southern Italy) to evaluate how the growth of conspecific young and old trees responded to climate change. We investigated two conifer species (*Abies alba* and *Pinus leucodermis*) and two hardwood species (*Fagus sylvatica* and *Quercus cerris*). We sampled one stand per species along an altitudinal gradient, ranging from a drought-limited low-elevation hardwood forest to a cold-limited subalpine pine forest. We used a dendrochronological approach to characterize the long-term growth dynamics of old (age > 120 years) versus young (age < 120 years) trees. Younger trees grew faster than their older conspecifics during their juvenile stage, regardless of species. Linear mixed effect models were used to quantify recent growth trends (1950–2015) and responses to climate for old and young trees. Climate sensitivity, expressed as radial growth responses to climate during the last three decades, partially differed between species because high spring temperatures enhanced conifer growth, whereas *F. sylvatica* growth was negatively affected by warmer spring conditions. Furthermore, tree growth was negatively impacted by summer drought in all species. Climate sensitivity differed between young and old trees, with younger trees tending to be more sensitive in *P. leucodermis* and *A. alba*, whereas older *F. sylvatica* trees were more sensitive. In low-elevation *Q. cerris* stands, limitation of growth due to drought was not related to tree age, suggesting symmetric water competition. We found evidence for a fast-growth trend in young individuals compared with that in their older conspecifics. Notably, old trees tended to have relatively stable growth

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rates, showing remarkable resistance to climate warming. These responses to climate change should be recognized when forecasting the future dynamics of old-growth forests for their sustainable management.

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1. Introduction

Humans have inhabited and transformed European forest ecosystems for thousands of years (Parfitt et al., 2010). As a result, current European landscapes form a complex and heterogeneous mosaic of agricultural fields, urban regions, and forested areas with different degrees of naturalness (Ellis et al., 2012). In this scenario, well-preserved, old-growth forests (long-established woodland habitats, partially retaining their original attributes sensu Peterken, 1996) are often restricted to small and isolated patches (Wirth et al., 2009). European old-growth forests are estimated to occupy only 0.7% of the total forested area (Sabatini et al., 2018). These fragmented forest patches are mainly confined to remote mountain areas with low levels of human pressure (Mikoláš et al., 2019).

Old-growth forests are of prime ecological value (Peterken, 1996; Frelich and Reich, 2003; Bauhus et al., 2009), as they represent small vestiges of how Europe's past primeval forest may have looked (Chytrý et al., 2010). In addition, old-growth forests provide various ecosystem services, such as biodiversity maintenance, long-term carbon storage, and landscape uniqueness (Farrell et al., 2000; Luysaert et al., 2008; Stephenson et al., 2014; Millar and Stephenson, 2015; Pederson et al., 2015; Büntgen et al., 2019). Further, a common feature of old-growth forests is that they contain large, and often old, trees, that is, trees of monumental height and/or diameter and long lifespans, which in many cases were established before the beginning of the Industrial Age (Lindenmayer and Laurance, 2017). In addition, natural stochastic disturbance has facilitated the establishment of new cohorts (Piovesan et al., 2005), resulting in uneven aged stand structures (Di Filippo et al., 2017). Therefore, old-growth forests represent valuable natural laboratories for evaluating how conspecific young and old trees respond to global change drivers, including climate warming and land use changes (Petritan et al., 2014).

Atmospheric CO₂ and N concentrations have steadily increased over the last century, leading to rising air temperatures and improving soil fertility, respectively (IPCC, 2013). It remains unclear whether conspecific young and old trees display similar plasticity in response to the rises in air temperature, carbon availability, and soil fertility that have been observed over the last few decades. That is, it remains unclear whether these changing factors can have positive, neutral or negative effects on tree growth and whether such effects vary between regions. Old trees that were established in lower temperatures, atmospheric CO₂ concentrations, and soil fertility should have grown less than their younger conspecifics established over the last 50–100 years (Phillips et al., 2008; Camarero et al., 2015a). However, climate change poses great challenges for the conservation of old forests, particularly in regions such as the Mediterranean Basin, where warming can exacerbate the negative impacts of drought on tree growth (Piovesan et al., 2008; Dorado-Liñán et al., 2019). Drought stress can lead to declines in growth and increased tree mortality, thus compromising the survival of older trees, leading to a reduction in the woody carbon stocks of old-growth forests (Körner, 2017; Büntgen et al., 2019; Martín-Benito et al., 2020). Old-growth forests represent a valuable setting in which long-term growth trends and age-specific impacts can be investigated in relation to changing environmental factors, such as climate.

Exploring how conspecific young and old trees respond to climate warming presents several challenges. First, if longevity arises as a trade-off to growth rate, large old trees may display lower growth rates than younger individuals of the same size, simply due to different growth trajectories that integrate the complexity of recruitment dynamics, suppression phases, and disturbance events throughout forest development (e.g., Di Filippo et al., 2017). Moreover, if “fast growers” tend to die

when they are young and do not reach old age, the cohort of old trees will be composed of individuals that displayed low growth rates in the past (Brienen et al., 2012; Piovesan et al., 2019a). Indeed, trees that survive to old age tend to exhibit slower early growth than that of younger trees (Black et al., 2008; Bigler and Veblen, 2009; Roskilly et al., 2019). Further, several components of global change covary (e.g., temperature and CO₂), resulting in increasing, decreasing, or neutral growth trajectories for both old and young individuals (Gedalof and Berg, 2010). For instance, generally, CO₂-fertilization effects on tree growth have not been detected under natural conditions, often because other constraints, such as drought, overwhelm any fertilization effect (Peñuelas et al., 2011; Camarero et al., 2015a, 2015b; Jiang et al., 2020).

integrate the complexity/intensity of recruitment dynamics, suppression phases and disturbance events throughout forest development.

Climatic variability can exert disparate effects on tree growth depending on the tree species considered, stand structure, and local climatic conditions of the regions they inhabit (Babst et al., 2013). Warming trends have been accentuated since the 1980s (Ballantyne et al., 2017) and have relaxed the constraints that temperature exerts on tree growth in cold biomes at high latitudes and altitudes (e.g., Tardif et al., 2003; Babst et al., 2019). Drought stress has become a more relevant growth constraint at low-elevation regions subjected to seasonal water shortages (Babst et al., 2019; Pompa-García et al., 2021). Moreover, the occurrence of drought-induced growth reduction in mountain forests has also been reported (e.g., Piovesan et al., 2008; Galván et al., 2014). However, it remains unclear whether large old trees are more sensitive to the observed changes in climate than their younger conspecifics. Few studies have examined the potential response of coexisting large, old trees and younger individuals to warming trends in conifers (e.g., Camarero et al., 2015a) and hardwood species (e.g., Piovesan et al., 2019a, 2019b) located at different altitudinal levels (but see Johnson and Abrams, 2009).

One of the few remnants of old-growth Mediterranean forests is located in the Pollino National Park (southern Italy), where several tree species have lifespans of at least 500 years, including silver fir (*Abies alba* Mill.), Bosnian pine (*Pinus heldreichii* var. *leucodermis* Antoine L., hereafter *P. leucodermis*) and European beech (*Fagus sylvatica* L.) (Blasi et al., 2010) (e.g., Di Filippo et al., 2015; Piovesan et al., 2018; Piovesan et al., 2019a). Notably, some of the oldest dated trees in Europe (*P. leucodermis*, *F. sylvatica*) have been found in the Pollino massif (Biondi, 1992; Piovesan et al., 2018, 2019a). These ancient stands are restricted to mountain sites characterized by irregular topographic conditions (i.e., steep slopes and shallow soils), which allowed them to be nearly untouched for centuries. The very few cases of traditional livestock and silvicultural activities were abandoned over the past century, contributing to their transition to increasingly natural conditions. In this study, we aimed to use this unique natural setting to evaluate how old and young individuals of two evergreen conifers (*A. alba* and *P. leucodermis*) and two deciduous hardwood species (*Q. cerris* and *F. sylvatica*) grow and respond to climate variability. In these four different stands, where each tree species was selected from only one site, we sampled coexisting old and young individuals and compared their growth trajectories and responses to climate. We hypothesized that old trees would present lower growth rates than their younger conspecifics, partially reflecting a trade-off between growth vigor and longevity. Regarding the response of tree growth to climate over the past decades (1950 to present), we expected that old individuals of *P. leucodermis* inhabiting high-elevation cold sites would be less sensitive to increases in temperature than their young, fast-growing conspecifics. We also expected those old individuals of species inhabiting mesic sites (e.g., *A. alba*) would be more sensitive to summer drought partially reflecting the aggravation of drought stress as climate warms.

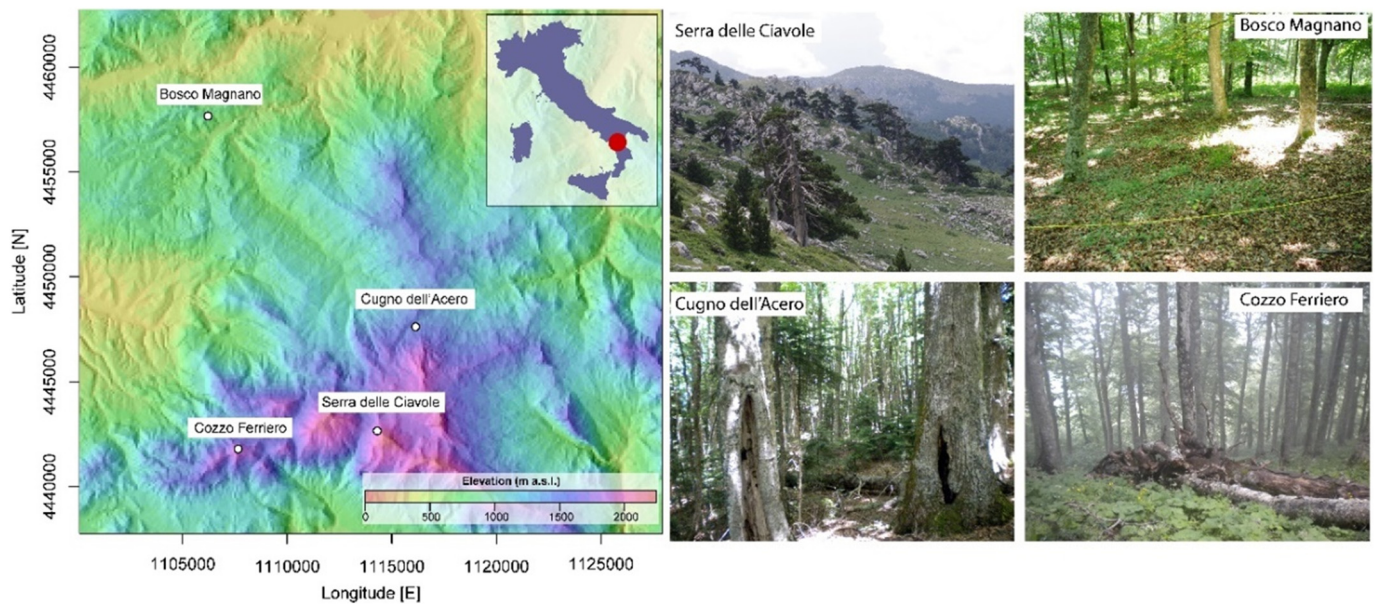


Fig. 1. Location and view of the four study sites in the Pollino National Park, southern Italy. The colour scale represents site elevation. Views of study sites: Serra delle Ciavole site: scattered individuals of *Pinus leucodermis* near the upper tree line; Bosco Magnano: monospecific canopy layer of *Quercus cerris*; Cugno dell'Acero: dominant old individuals of *Abies alba*, and Cozzo Ferriero: uneven aged stand of *Fagus sylvatica*.

2. Material and methods

2.1. Study area

The study area was located in the Pollino National Park (hereafter “Pollino NP”) (39° 55' N, 16° 06' E, southern Apennine mountains, Fig. 1), which is the largest protected area in Italy, covering approximately 192,000 ha, with the majority of the territory belonging to the montane belt (i.e., from 800 to 2000 m above sea level). Despite widespread logging over the past few centuries, the Pollino NP area harbors remnants of old-growth forests dominated by late-successional tree species. Four study sites were identified and characterized by the presence of large trees, standing dead trees, abundant woody debris on the ground, and high structural heterogeneity, a consequence of reduced anthropogenic pressure in recent decades (Di Filippo et al., 2004, 2017; Blasi et al., 2010).

The climate of the Pollino massif is modified by its topographical complexity (elevation, slope, and aspect) and is influenced by its proximity to the Tyrrhenian and Ionian seas. In particular, the southeastern Ionian area displays higher temperatures and short but intense rainfall, with an annual average rainfall of approximately 600 mm, whereas the western Tyrrhenian side is characterized by lower temperatures and more frequent and regular rainfall, with annual rainfall averages reaching up to 2000 mm (Ciancio, 1994). The area is characterized by a mountain-Mediterranean climate of cool winters and mild, dry summers, where temperatures have been rising since 1980 (Table 1, Fig. S1). In the interior of the park, at an altitude of 2000 m, the mean winter temperature is -3.2 °C, while the mean summer temperature is 13.8 °C, with average annual rainfall reaching 1560 mm.

In the lowermost site (e.g., *Q. cerris*), the mean annual temperature is 12.3 °C with an annual precipitation of 1206 mm. In the mesic, mid-

elevation sites (e.g., *A. alba* and *F. sylvatica* sites), the mean annual temperatures range from 7.0 °C to 9.2 °C, and annual precipitation varies from 1441 to 1617 mm. In the high-elevation *P. leucodermis* site, the mean annual temperature is 6.1 °C with an annual precipitation of 1649 mm.

All stands were high-forest and unevenly aged, exhibiting unique ecological features that merit inclusion in the “Natura 2000” network, which is the largest coordinated network of protected areas in the world. Among the four stands, the beech forest of Cozzo Ferriero has recently been recognized as “UNESCO World Heritage” site. The site was selected for its biological and ecological values, representing an exceptional example of an intact and ancient forest in Europe. Monumental trees grow in this area, reaching ages of over 500 years, representing the more long-lived broadleaved trees in Europe (Piovesan et al., 2019a).

At low altitudes, the Bosco Magnano forest extends to approximately 1000 ha, including an old-growth forest patch (~18 ha). The latter contains several vegetation types, with *Q. cerris* as the dominant species, forming a monospecific canopy layer and monumental trees reaching 52 m in height and 150 cm in diameter at the breast height (DBH) in some cases. Other broadleaf species, such as *Carpinus betulus* L., *Alnus glutinosa* (L.) Gaertn., and *Acer campestre* L., have also been identified. The shrub layer is composed of several species, including *Rubus hirtus* Waldst. & Kit. and *Ilex aquifolium* L.

The Cugno dell'Acero forest occupies approximately 1000 ha, constituting the largest mixed forest in the central-southern Apennines. In fact, *A. alba* and *F. sylvatica* share the dominance of the upper arboreal layer and show equivalent coverage index values. In some patches, the dominant and old individuals of *A. alba*, mostly in good condition, reach more than 80 cm DBH and 35 m height (Ripullone et al., 2016). Scattered *I. aquifolium* individuals grow in the understory.

Table 1

Geographical characteristics of the study sites and number of sampled trees in the Pollino massif, southern Italy – Mediterranean biome. Bioclimatic classification was defined following Piovesan et al. (2005).

| Site | Tree species | Lat. (N) | Long. (E) | Elevation (m a.s.l.) | Bioclimate type | Slope range (%) | No. sampled young trees | No. sampled old trees |
|---------------------|--------------------------|----------|-----------|----------------------|-----------------|-----------------|-------------------------|-----------------------|
| Bosco Magnano | <i>Quercus cerris</i> | 40.051 | 16.104 | 900 | Low elevation | 10–30 | 20 | 16 |
| Cugno dell'Acero | <i>Abies alba</i> | 39.954 | 16.210 | 1450 | Mountainous | 10–30 | 17 | 18 |
| Cozzo Ferriero | <i>Fagus sylvatica</i> | 39.908 | 16.106 | 1785 | High-mountain | 25–70 | 28 | 27 |
| Serra Delle Ciavole | <i>Pinus leucodermis</i> | 39.911 | 16.184 | 1970 | Subalpine | 15–60 | 25 | 25 |

The Serra delle Ciavole covers around 100 ha. Here, *P. leucodermis* stands are formed by scattered individuals coexisting with *Juniperus communis* L. in the understory and on subalpine limestone grasslands. This conifer is considered a relic of the oro-Mediterranean conifer forests in the Balkan and Italian peninsulas. In this area, several individuals of *P. leucodermis* have reached 1000 years of age (Piovesan et al., 2018).

2.2. Field sampling

Five circular plots (radius = 20 m) were randomly located in each of the four sampled stands. These plots were chosen after excluding a 20-m wide buffer area running along the internal border of the stand (see Sabatini et al., 2018). In these 20 plots, we characterized the stand structure (tree density and basal area) and species composition by sampling trees in three concentric circular areas with a 4, 13, and 20 m radius if their DBH was above 2.5, 10.0, and 50.0 cm, respectively (Blasi et al., 2010). DBH was measured on all trees using a tree caliper (Haglof, Sweden).

Regarding dead wood, we recorded the presence of stumps, coarse woody debris, dead standing, and downed trees using the protocol proposed for the European ICP forest level-II monitoring areas (Motta et al., 2006) and measured their diameter, length, and height to determine the volume of dead wood (Table 2). Lastly, to characterize stand structural diversity, that is, tree diameter inequality, we calculated the Gini-Simpson index per hectare using the DBH values of trees from all circular plots together (Burrascano et al., 2018; Jost, 2006; Lexerød and Eid, 2006).

2.3. Dendrochronological methods

We used dendrochronology to estimate age and quantify the past growth rates of large old and young individuals of the four studied species (Fritts, 1976). Sampled trees were cored at breast height (1.3 m) using increment borers. For coring, dominant trees with a good state of vigor were selected among all DBH classes present within the five circular plots (radius = 20 m). Specifically, young trees were selected in small gaps to avoid suppression by surrounding larger individuals. A total of 176 trees were sampled from the four species (see Table 1). For each tree, two wood cores were extracted to the pith and, where possible, perpendicular to the slope to avoid stem eccentricity caused by a wood reaction, and each core was prepared according to standard dendrochronological procedures. Given the large size of some trees, an 80 cm increment borer (Haglöf, Sweden) was used to reach the pith.

In the laboratory, the cores were air-dried, glued, and polished using a series of sand-paper grids until the tree-ring boundaries were clearly visible. Cores were visually cross-dated and measured to the nearest 0.01 mm using a LINTAB digital positioner and TSAP-Win software (Rinntech, Heidelberg, Germany). Cross-dating accuracy was checked using the COFECHA software (Holmes, 1983). These data were used to calculate the basal area increment (BAI) to remove the trend of decreasing ring width with increasing stem size over time (Biondi and Qeadan, 2008).

Tree age was estimated at 1.3 m using the cores that passed through the stem pith (80% of cores in *A. alba*, *F. sylvatica*, and *Q. cerris*, and 66% of cores in *P. leucodermis*), or when the innermost rings showed a curved arc (11% of cores in *A. alba*, 16% of cores in *F. sylvatica*, 9% of cores in *Q. cerris*, and 12% of cores in *P. leucodermis*). We classified the trees into young (age ≤ 120 years) and old (age > 120 years) cohorts

(hereafter age class). The 120-year threshold was chosen because a stand is considered mature beyond that age. We fitted a template of concentric circles to the curve of the innermost rings to estimate the number of missing rings (Duncan, 1989). We calculated two chronofunctional indicators of old-growth forests following Di Filippo et al. (2017) related to tree age: the mean age of the five (Age5) and ten (Age10) oldest trees.

Ring width measures were also used to calculate the mean indexed series (chronologies) for old and young trees of each species. Individual ring width series were detrended using a cubic regression spline with a frequency response of 0.5, at a wavelength of 32 years, to obtain yearly values of detrended ring width indices. Then, autoregressive modeling was used to remove most of the first-order autocorrelation (pre-whitening). Chronologies were obtained by averaging the pre-whitened individual series using a bi-weight robust mean. These procedures were performed using the dplR package in R (Bunn, 2008).

To assess climate-growth relationships, we calculated Pearson correlations between the chronologies of old and young trees of each species and monthly climate data. Due to the lack and heterogeneity of some local climate data, we used 0.25 °C-gridded climate data from the E-OBS dataset ver. 13.0 for the period 1990–2016 (Haylock et al., 2008). Monthly temperature and precipitation data were extracted to quantify climate trends and climate-growth associations. We also obtained mean and summed values of temperature and water balance (P-PET, difference between precipitation and potential evapotranspiration) for spring (March to May) and summer (June to August), respectively.

2.4. Statistical analyses

Variables calculated for old and young trees (DBH, BAI, Age5, and Age10) were compared using the Mann-Whitney test. We used generalized additive mixed models (GAMM; Wood, 2006) to compare growth (BAI) trajectories of old and young individuals of the four species studied during the early years (~45 years) of their lives. We selected this period because the younger trees for each species were around that age. Using this method, we can evaluate how BAI varies with the increase in cambial age and DBH, and subsequently compare the observed growth trajectories with those projected by the models. We modeled the BAI of the young individuals of each species as a function of DBH and age. A two-dimensional tensor product smooth, including thin plate splines for the interaction between age and DBH, was included as the fixed part (k) of the model (with basis dimensions of 4 and 6, respectively, to control model rigidity), while tree identity was included as a random factor as BAI values represent repeated measures over the same individuals. The model equation was conducted as follows:

$$\text{BAI} = (\text{age, dbh, } k = c(4, 6)) + \text{random} = 1 | \text{tree identity} \quad (1)$$

These models were used to project BAI trajectories from 1 to 45 years of age in 999 randomly simulated individuals with DBHs in the range of the sampled DBHs for young individuals. Put simply, we used the model to create 999 simulated trees with sizes and growth trends comparable to those observed in young individuals of each species. For each of the observed (old and young) and randomized (young only) individuals, we calculated the average BAI as the mean of BAI values for the study period (from 1 to 45 years). Therefore, we

Table 2

Main structural characteristics of the old-growth forest sites (values are means ± SE). The Gini-Simpson structural diversity index was calculated for 5-cm DBH classes. Different letters indicate significant differences at the 0.05 level based on Mann-Whitney tests.

| Species | Basal area (m ² ha ⁻¹) | Density (ind. ha ⁻¹) | Living wood volume (m ³ ha ⁻¹) | Dead wood volume (m ³ ha ⁻¹) | Gini-Simpson index |
|-----------------------|---|----------------------------------|---|---|--------------------|
| <i>Q. cerris</i> | 36.9 ± 4.4b | 1267 ± 9.1c | 556.8 ± 39.3b | 23.3 ± 19.3a | 0.50 ± 0.05c |
| <i>A. alba</i> | 67.8 ± 7.9d | 1830 ± 22.3d | 897.0 ± 31.3c | 46.7 ± 15.5b | 0.18 ± 0.02a |
| <i>F. sylvatica</i> | 53.5 ± 2.5c | 385 ± 6.0b | 501.2 ± 17.1b | 22.4 ± 8.4a | 0.30 ± 0.03b |
| <i>P. leucodermis</i> | 27.0 ± 4.8a | 72 ± 0.7a | 201.9 ± 16.5a | 35.7 ± 15.1a | 0.55 ± 0.08c |

compared whether the observed average BAI for old trees was within the range of the expected average BAI for young trees. This was done by counting the number of simulated young individuals (999) that presented growth values lower or equal to the mean growth in old trees, and expressed as the probability that the mean observed growth in old trees is higher than the simulated growth in young individuals.

We used linear mixed effect models (LME; Pinheiro et al., 2018) to quantify recent growth trends (1950–2015) and responses to climate for the old and young trees of the four studied species. We ran separate models for each species using tree identity as a random factor. Growth trends were quantified by including calendar year as an explanatory variable. Since BAI trajectories can vary depending on tree age, we included interactions between year and age class. Preliminary analyses

of the relationship between growth variability (detrended ring width indices) and monthly climate showed the importance of summer precipitation, temperature, and spring temperature for the growth of the species (Fig. S2). Therefore, to test for the effect of climate variation on BAI, we included the average maximum temperature for spring, which accounted for the impact of spring temperature on growth rate during the early growing season, and the water balance for, which accounted for the impact of drought on growth in the models. Furthermore, to account for the differences in response to climate as a function of longevity, we included interactions between temperature and water balance with age class. Finally, to control for ontogenetic and tree-size factors, DBH values were included in the fixed part of the models. The BAI was log-transformed ($\log(x + 1)$) before the analyses to achieve normality

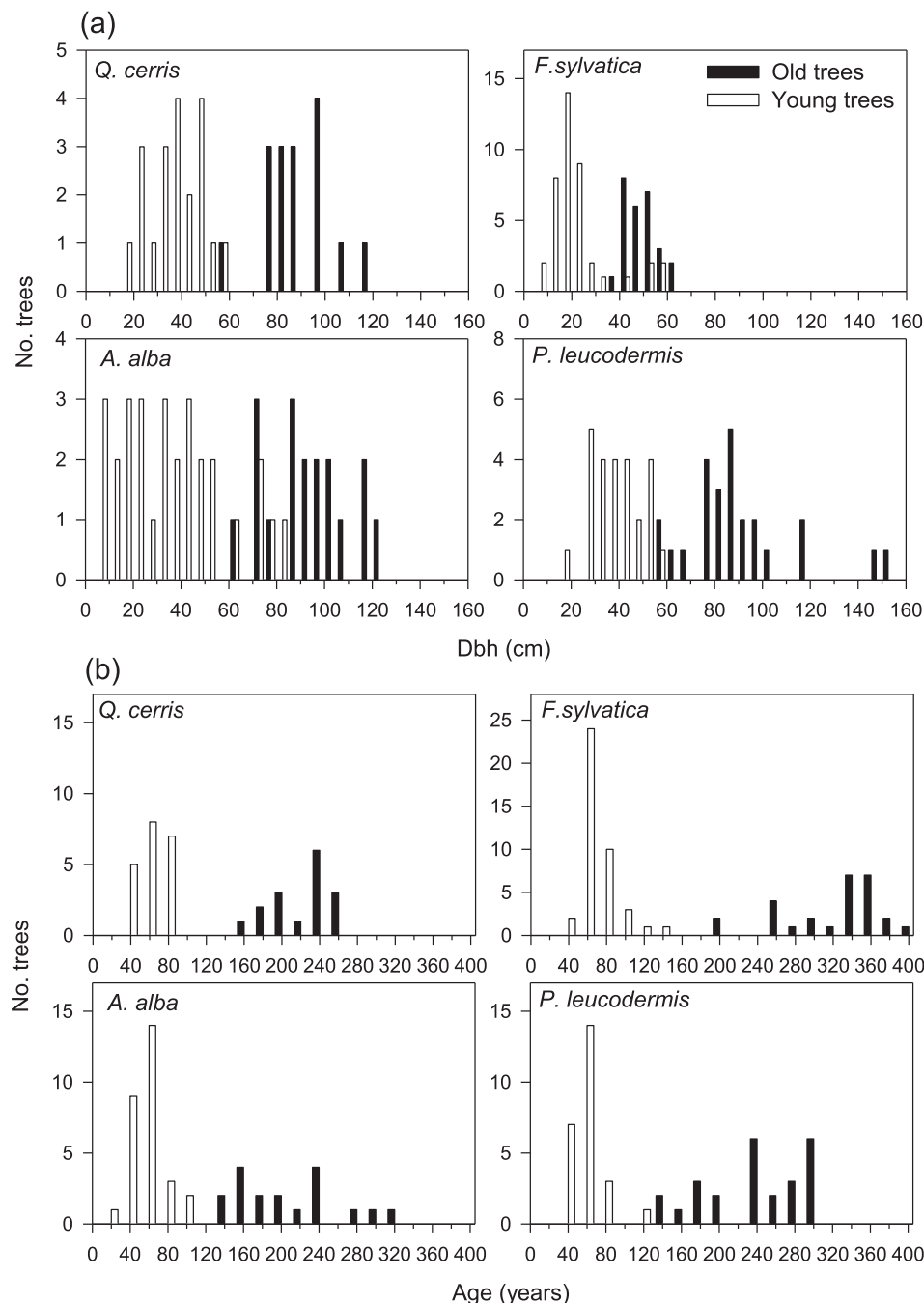


Fig. 2. Histograms showing the distribution of old and young trees grouped as a function of their diameter at breast height (a) and age (b).

Table 3

Structural variables (diameter at breast height (DBH), age of the 5 (Age 5) and 10 (Age 10) oldest trees), and basal area increment (BAI) calculated for young and old trees between 1950 and 2016 (values represent means \pm SE). Different letters indicate significant differences at the 0.05 level between young and old trees based on Mann-Whitney tests.

| Species | Type of individual | DBH (cm) | Age 5 (years) | Age 10 (years) | BAI (cm ²) | Height (m) |
|-----------------------|--------------------|-----------------|---------------|----------------|------------------------|-----------------|
| <i>Q. cerris</i> | Young | 37.9 \pm 2.4a | 51 \pm 3a | 42 \pm 2a | 12.0 \pm 1.3a | 30.8 \pm 1.4a |
| | Old | 89.2 \pm 3.6b | 254 \pm 3b | 243 \pm 4b | 29.9 \pm 5.2b | 39.8 \pm 1.7b |
| <i>A. alba</i> | Young | 37.0 \pm 4.1a | 42 \pm 2a | 37 \pm 3a | 23.6 \pm 2.6a | 19.6 \pm 1.8a |
| | Old | 94.1 \pm 4.0b | 280 \pm 16b | 250 \pm 13b | 35.6 \pm 3.3b | 27.0 \pm 0.5b |
| <i>F. sylvatica</i> | Young | 22.7 \pm 2.0a | 56 \pm 2a | 52 \pm 2a | 3.4 \pm 0.4a | 16.2 \pm 0.7a |
| | Old | 49.4 \pm 1.2b | 376 \pm 7b | 365 \pm 5b | 15.1 \pm 1.7b | 27.7 \pm 0.7b |
| <i>P. leucodermis</i> | Young | 39.0 \pm 1.9a | 49 \pm 2a | 45 \pm 2a | 9.9 \pm 0.9a | 7.6 \pm 1.3a |
| | Old | 91.5 \pm 4.5b | 299 \pm 2b | 290 \pm 4b | 14.8 \pm 3.2b | 13.8 \pm 0.5b |

assumptions. We included a first-order autocorrelation structure (AR1) to account for the dependency of the BAI in year t (i.e., year of growth) on the BAI of the previous year ($t - 1$).

We applied a multi-model inference approach to select the most parsimonious models (Burnham and Anderson, 2002). We listed the models according to their Akaike Information Criterion (AIC) values, and selected the most parsimonious model among those models with a difference lower than two AIC units from the model with the lowest AIC. The fit of the final selected model was quantified by calculating the marginal (R^2_m) and conditional (R^2_c) R^2 values, which account for the variance explained by the fixed effects and by the fixed and random effects, respectively (Nakagawa et al., 2017). Potential evapotranspiration was calculated using the Penman-Monteith equation in the SPEI package of R (Vicente-Serrano et al., 2010). The mgcv package in R (Wood, 2006) was used to fit the GAMMs. The LMEs were fitted using the nlme package (Pinheiro et al., 2018), while model selection was performed using the MuMIn package (Barton, 2012). All analyses were performed using R software (R Core Team, 2018).

3. Results

3.1. Stand structure

The highest and lowest basal area and density values were found in the *A. alba* and *P. leucodermis* sites, respectively (Table 2). The volume of dead wood reached minimum values in the *F. sylvatica* site with a global mean value of 32.0 m³ ha⁻¹; however, the *P. leucodermis* site presented the lowest volume of living wood. Finally, the Gini-Simpson reached maximum values in the *P. leucodermis* and *Q. cerris* sites, indicating the highest structural diversity and DBH inequality, while the *A. alba* site showed the lowest structural diversity (Table 2).

Shade-tolerant species, such as *F. sylvatica*, showed a less distinct separation of DBH distribution between young and old trees than that of shade-intolerant species such as *P. leucodermis* (Fig. 2). The highest DBHs of old trees were recorded in *A. alba* and *P. leucodermis* (Fig. 2a, Table 3), while the oldest ages were observed in *F. sylvatica* (Fig. 2b, Table 3). The oldest tree was a *F. sylvatica* individual, which was determined to be at least 398 years old. Aged *F. sylvatica* trees were older than the rest of the studied species (Table 3). *Q. cerris* and *A. alba* trees were, on average, the youngest among the four species.

3.2. Growth and age patterns and trends

The time series of BAI since 1950 were characterized by fluctuating trends with stable growth behavior, or growth increase in the case of *P. leucodermis* (Fig. 3a). When comparing growth trends at the same age, substantial differences in BAI were found between young and old individuals of the four species studied (Fig. 3b). Both *A. alba* and

Q. cerris displayed the highest BAI values, whereas the lowest growth rate was observed for *F. sylvatica* (Fig. 3 and Fig. S3).

Young trees of the four studied species tended to grow faster than their older conspecifics during the first decades of their lifespan (Fig. 3b). During the first years of their life (1 to 45 years), old trees presented BAI values lower than expected by the model created with the young individuals for all species except *F. sylvatica* (Fig. 4 and Fig. S4).

According to the fitted models, we found marked differences in the recent (1950–2016) growth trajectories between young and old individuals of the four studied species (Fig. 5). Young individuals presented steeper growth trajectories, whereas the trajectories of old trees varied from not significantly negative (*A. alba*) to a markedly significant positive (*P. leucodermis*) effect (Tables S1 and S2). Tree age was inversely correlated with growth for all species, while DBH had a positive effect on BAI in *Q. cerris* and *F. sylvatica*, but not in *A. alba* and *P. leucodermis*.

3.3. Growth responses to climate in old vs. young trees

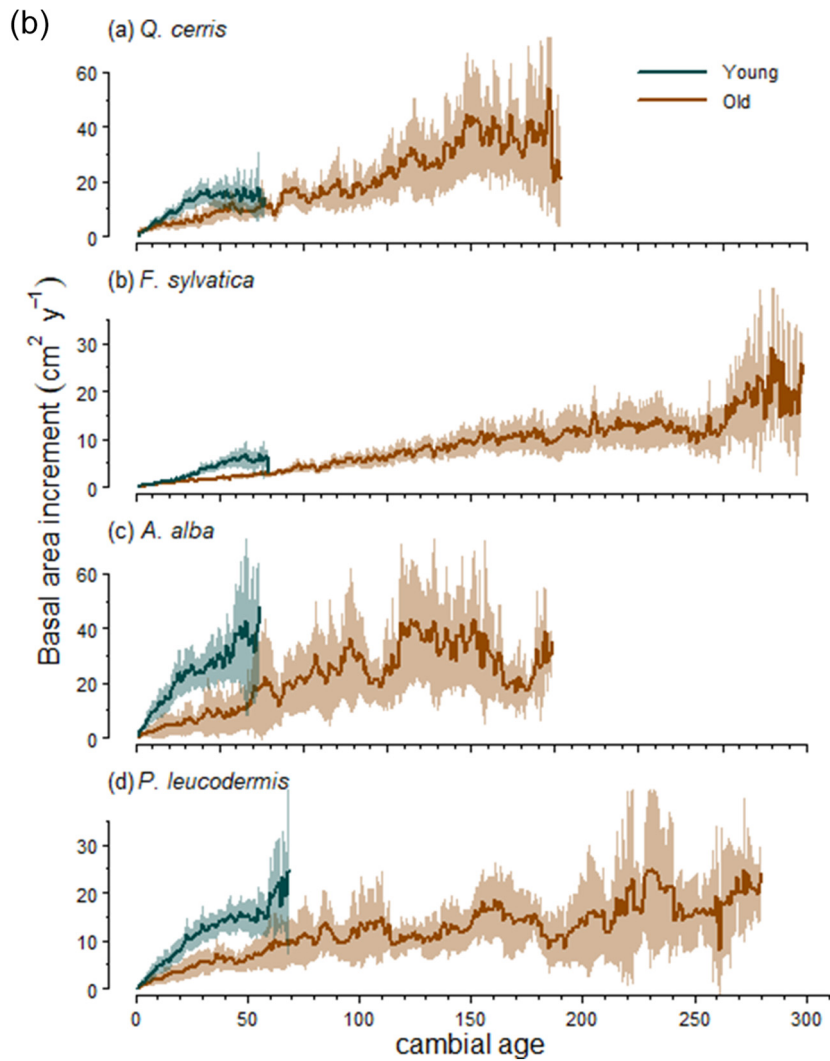
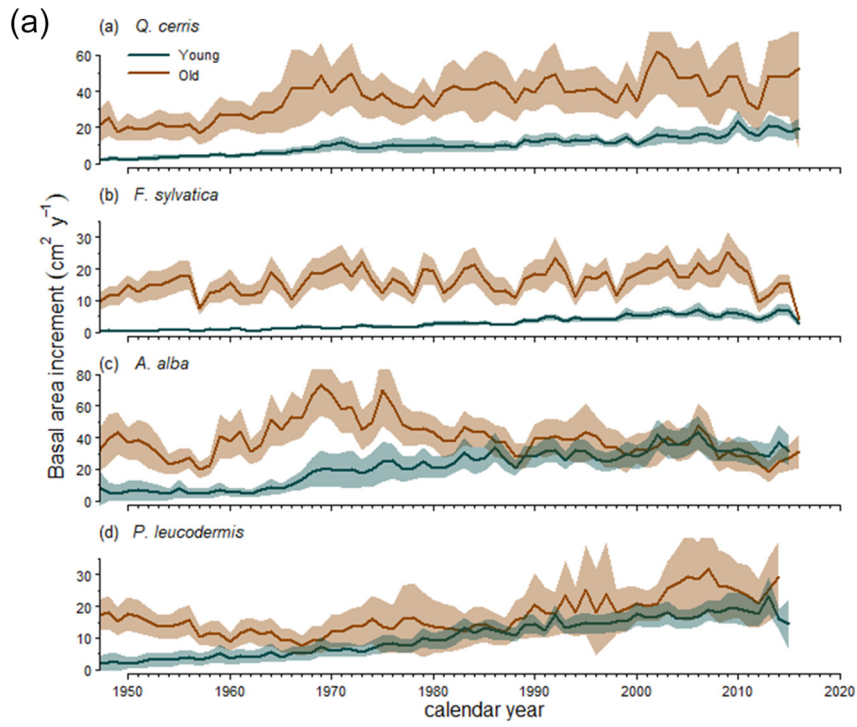
The growth of *A. alba* and *Q. cerris* responded negatively to elevated summer temperatures and positively to summer precipitation (Fig. S2). A higher water balance in June and July was positively related to *Q. cerris*, *F. sylvatica*, and *A. alba* growth rates, whereas *P. leucodermis* growth was enhanced by warm summer conditions (Table 4, Fig. S2). When evaluating the individual response to climate, we found significant interactions between age class and water balance in *A. alba* and *P. leucodermis*, with the growth of young trees being more constrained by low water balance, while the opposite effect emerged for *F. sylvatica* (Fig. 6, Table 4). Young *P. leucodermis* trees responded more positively to warmer April temperatures than their old conspecifics, while young *F. sylvatica* trees were less impacted by a warmer April.

4. Discussion

According to our hypotheses, we found evidence for a fast-growth trend in young individuals compared with that in older conspecifics. Our results revealed a stable growth trend for most old trees, except for *P. leucodermis* trees at the highest elevation site, the growth of which has increased in the last three decades (Fig. 3). We also found different responses to climatic variation between young and old conspecifics.

The leveling of growth and production in *F. sylvatica*, *Q. cerris*, and *A. alba* could be due to the more frequent droughts and heat waves occurring in southern Europe in the last decades (Spinoni et al., 2017; Zhang et al., 2020). Although all the study species were sensitive to June–July water balance (see Table 4), growth trends revealed a capacity of large and ancient trees growing in old-growth forests of Mediterranean

Fig. 3. Series of basal area increments as a function of calendar year (a) and cambial age (b) considering young (blue lines) and old (brown lines) trees of each studied species. Lines represent means and the shadow area represents standard errors.



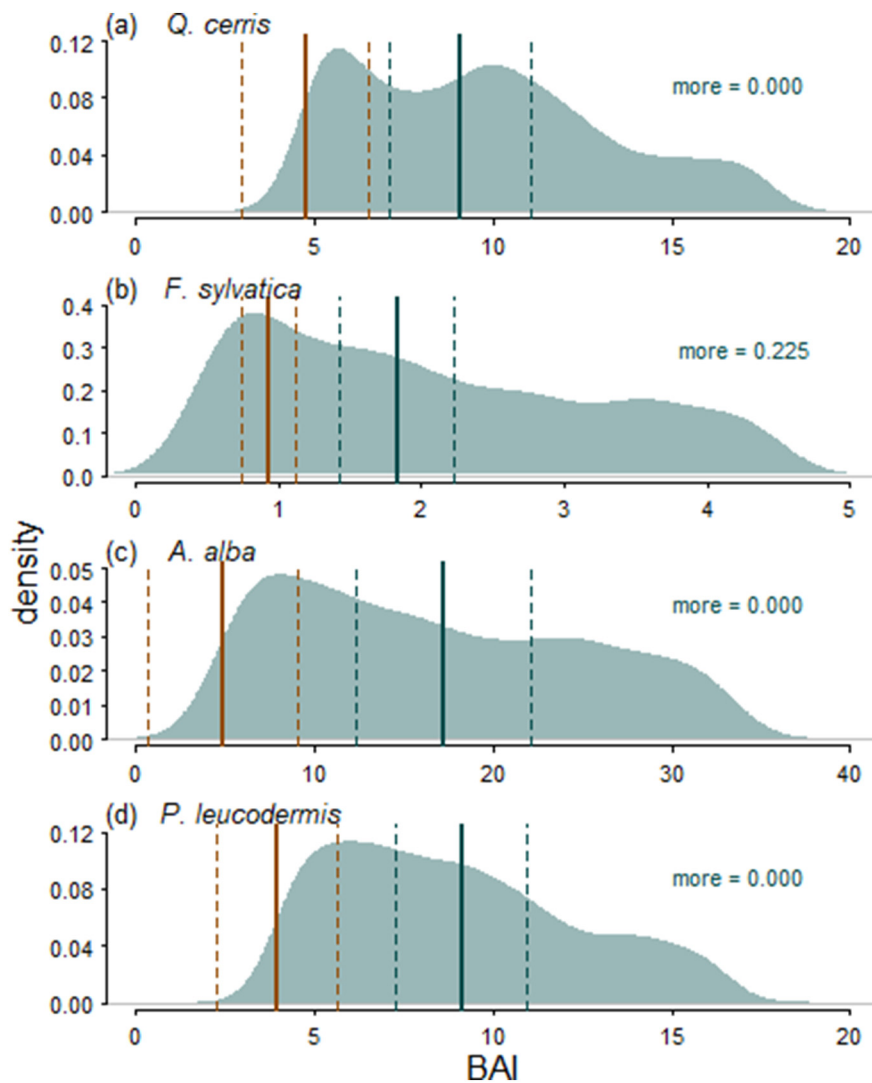


Fig. 4. Growth (average basal area increment, BAI) observed in old (brown lines) and young (blue lines) trees and growth for simulated young individuals (blue shaded area) during the first 45 years of life. Continuous and dashed lines represent the mean and 95% coefficient interval respectively for old (brown) and young (blue) trees. The observed BAI of old individuals was compared with the randomized BAI of young individuals ($n = 999$ randomizations): “more” represents the expected likelihood that an old tree grows in the range of young trees (i.e. the probability that the mean observed growth in old trees is higher than the simulated growth in young individuals). The larger the value the higher the number of simulated young individuals that show values lower or equal to the mean growth in old individuals (e.g. 225 out of 999 simulated individuals in *F. sylvatica*).

mountains for growth acclimation to climate warming. Conversely, heat waves and drought spells have caused widespread dieback phenomena in managed or degraded forests in the same region (Colangelo et al., 2017; Ripullone et al., 2020), confirming the need for further monitoring studies on the role of land use and other climatic and environmental factors in mitigating the impact of such extreme climate events.

As hypothesized, old trees presented lower growth rates than younger conspecifics during the 1950–2016 period, reflecting a trade-off between growth vigor and longevity (Piovesan and Biondi, 2021). Such high growth rates were not observed in the shade-tolerant *F. sylvatica*, in which slow-growing individuals were found in both young and old age classes (Di Filippo et al., 2017). Conifer species (*A. alba*, *P. leucodermis*) responded to climate warming with a much more marked growth enhancement than deciduous hardwood species (*F. sylvatica*, *Q. cerris*), whose growth was mainly limited by summer drought. However, the positive growth trend of old *P. leucodermis* contrasted with the absence of a significant trend in old *A. alba* trees. This difference in growth behavior can be linked to local climate conditions. In the mountainous mesic sites dominated by *A. alba* stands, the advance of early spring is counterbalanced by summer drought, while in the subalpine

P. leucodermis stands, climate warming stimulates photosynthetic activity and wood production during the vegetative period in a cooler and wetter environment. This increasing growth trend has previously been reported in other mountain areas, highlighting the role of long-lived trees as long-term carbon pools (Büntgen et al., 2019). In contrast, old *F. sylvatica* trees showed persistently low growth rates, as observed in previous studies in Mediterranean mountain forests (Piovesan et al., 2008), renewing interest in the roles of phenotypic plasticity and genetic variability as adaptive mechanisms to tolerate drought, particularly at the southernmost edge of the species distribution area (De Lafontaine et al., 2013).

Our results confirm that climate variation differently impacts on young and old trees. Warming temperatures drove growth of young *P. leucodermis* trees in the high-elevation sites, which may have benefited more from an earlier advancement of the spring onset. In the case of deciduous hardwood species such as *F. sylvatica*, they may be less responsive to climate warming because the bursting onset depends on temperature but also on photoperiod (Menzel et al., 2006). In conifers, climate warming may lead to more similar spring phenology patterns, regardless of site elevation (Vitasse et al., 2018).

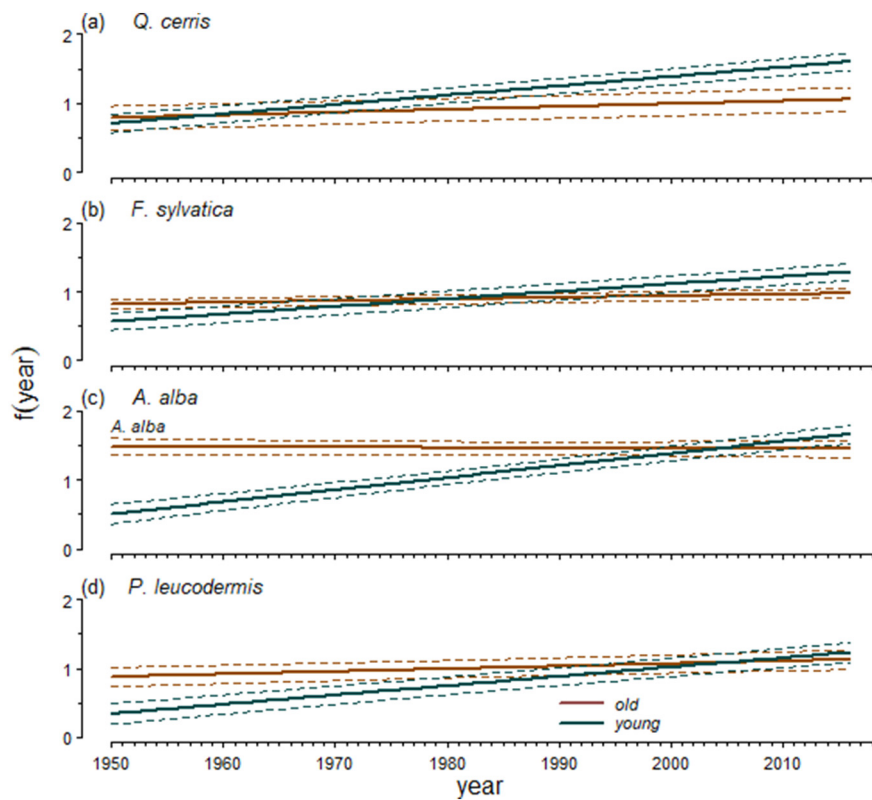


Fig. 5. Different growth trends established as a function of year ($f(\text{year})$) in young (blue lines) and old (brown lines) trees of each species. Continuous and dashed lines indicate the mean responses and their 95% confidence intervals, respectively.

Regarding the limiting factors of our study sites, the growth of *A. alba* young trees may have been constrained by low summer precipitation (Ripullone et al., 2016). In addition, Rita et al. (2014) reported that milder winter temperatures favor the growth of *A. alba*, suggesting substantial investment from carbon and nutrient reserves formed during the year prior to ring formation. Furthermore, mild winter and spring temperatures could be associated with a lower snowpack and an earlier spring onset, providing a longer growing period without water stress, which could enhance growth. Other studies have found *A. alba* dieback in some regions of southern Europe (Camarero et al., 2011; Cater and Levanic, 2019). This phenomenon was more marked in low-elevation sites subjected to higher temperatures and evaporative demand during late summer (e.g., Gazol et al., 2015); however, the mesic conditions of this study area make *A. alba* less vulnerable to recent climate warming and summer drought. Lastly, the existence of fast growers that became old may be explained by the local provenance of *A. alba* (Giacobbe,

1973), which may be established in large canopy gaps, making the Pollino NP an ideal setting for preserving old stands of this species (Ripullone et al., 2016). These results seem to deviate from the commonly reported trade-off between growth rates and longevity; however, sustained growth rates, when conditions allow it, are another requirement for trees to achieve their maximum longevity that enhances its lifespan (Piovesan and Biondi, 2021), explaining why fast-growing *A. alba* can attain old ages. Climate warming has a negative impact on *F. sylvatica* growth in Mediterranean mountains subjected to seasonal drought and frequent spring frosts (Piovesan et al., 2008; Rubio-Cuadrado et al., 2018). In the old-growth forest site of the present study, *F. sylvatica* stands appeared in shallow soils near the mountain ridge and on steep slopes (Table 1). The presence of such shallow soils can determine the ability of trees to access soil water, which can partially explain why *F. sylvatica* growth depends strongly on summer water balance (Ripullone et al., 2020). However, we found that younger *F. sylvatica* trees were less affected by summer drought, a finding which merits further consideration in relation to the old-growth structure. We observed a clustered distribution of young individuals in old-growth stands, which could be a product of the openings of canopy gaps that originated due to the fall of large trees, a distinctive trait of old-growth dynamics (Wirth et al., 2009; Petritan et al., 2017). These canopy openings allow new recruitment, which determines an uneven age structure and a complex vertical and horizontal structure. This has been illustrated in old-growth *F. sylvatica* forests across Italy (Di Filippo et al., 2017). It should be emphasized that the old-growth *F. sylvatica* and *P. leucodermis* stands of the current study were nearly untouched over the last centuries because of their remoteness from towns and the harsh topographic conditions.

Interestingly, *F. sylvatica* growth was negatively affected by spring temperature, a relationship that was more intense in older trees (Fig. 6). *F. sylvatica* growth is also sensitive to the occurrence of spring frost events that can damage recently unfolded leaves (Vitasse et al., 2019). This effect can be modulated by climate warming because

Table 4

Results of the linear mixed effect models fitted to growth (BAI) as a function of long-term trends (year) and climate variables (JJ P-PET, June to July water balance; April TMax, mean maximum April temperature). Models were fitted as a function of tree diameter (DBH), and considered old and young trees (type). Marginal (R^2_m) and conditional (R^2_c) R^2 values represented the variances explained by the fixed effects and the fixed and random effects, respectively. Significance levels: * $p < 0.05$, ** $p < 0.01$.

| Variables | <i>Q. cerris</i> | <i>F. sylvatica</i> | <i>A. alba</i> | <i>P. leucodermis</i> |
|------------------|------------------|---------------------|----------------|-----------------------|
| Year | 4.19** | 8.24** | -0.39 | 3.89** |
| DBH | 6.07** | 8.47** | --- | --- |
| Type | 1.94 | 0.33 | -5.18** | -2.20* |
| JJA P-PET | 10.80** | 10.24** | 5.15** | -0.38 |
| MAM TMax | --- | -10.90** | --- | 3.25** |
| Year*type | 6.89** | 17.42** | 9.10** | 6.58** |
| JJA P-PET * type | --- | -3.29** | 5.15** | 4.48** |
| MAM TMax * type | --- | 6.81** | --- | --- |
| R^2_m (%) | 0.63 | 0.69 | 0.43 | 0.20 |
| R^2_c (%) | 0.74 | 0.85 | 0.5 | 0.68 |

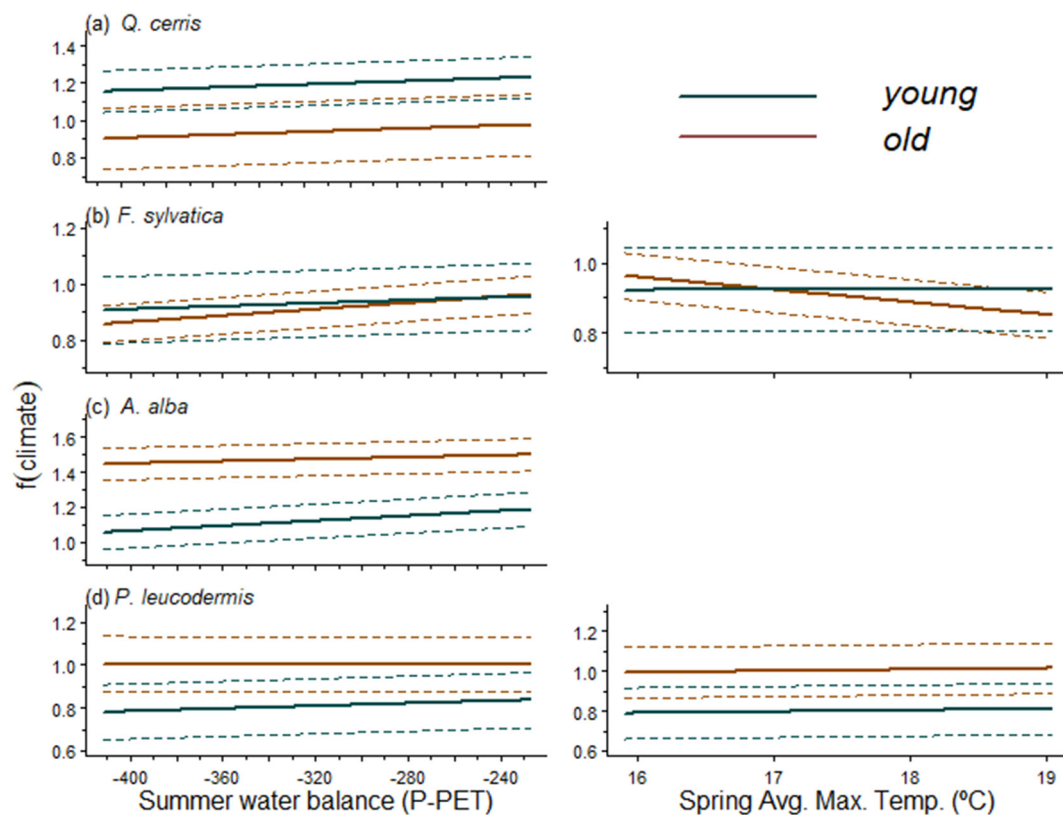


Fig. 6. Different growth responses to selected climate variables (Spring –MAM–mean maximum temperature in *P. leucodermis*; Summer (JJA) water balance in the rest of species) estimated for young (blue lines) and old (brown lines) trees. Continuous and dashed lines indicate the mean responses and their 95% confidence intervals, respectively.

temperature partially constrains leaf unfolding at high elevations (Vitasse and Basler, 2013). Elevated temperatures during April can advance leaf unfolding, exposing young leaves to the occurrence of late frost events and subsequently reduce radial growth (Piovesan et al., 2005; Sangüesa-Barreda et al., 2021). The potential impact of late frost on beech growth in the Pollino NP needs to be considered in addition to its sensitivity to drought occurrence, as these factors can cause significant changes in forest composition, structure, and functioning (Nolè et al., 2018; see also Piovesan, 2019).

In the case of *Q. cerris*, recurrent droughts may lead to a growth decline, particularly in the case of old trees (Colangelo et al., 2017), but no sign of growth decline was observed in the old-growth stands of this study. Interestingly, no differences in growth response to summer water balance were found between old and young *Q. cerris* trees, which suggests a relevant role of size-symmetric water competition processes under recurrent summer dry conditions (Zang et al., 2012). Old and young *Q. cerris* significantly differed in size, and it has been shown that large trees are more prone to drought-induced mortality than smaller individuals (e.g., Stovall et al., 2019; Stovall et al., 2020); however, in Mediterranean oak species, several studies have found greater drought sensitivity in smaller individuals (e.g., Galiano et al., 2012; Colangelo et al., 2017). The lack of differences in growth sensitivity to climate between old and young oak trees, together with the strong influence of summer water balance on growth (Fig. 6), suggest that drought plays an important role in determining *Q. cerris* performance in the Pollino NP.

The positive growth trajectory of *P. leucodermis* contrasts with the lack of such growth trends in *A. alba* and the low growth rates of *F. sylvatica*. As expected, shade-intolerant conifer species in cold, high elevations, whose growth is mainly limited by low temperatures, have experienced marked growth enhancement compared with shade-

tolerant, hardwood species whose growth is more limited by summer drought. Climate warming extends the growing season and increases the growth rate of trees, particularly at cold sites at high altitudes or latitudes, which could enhance the growth of similar high-elevation pine forests (Sánchez-Salguero et al., 2017; Piovesan et al., 2019a). Consequently, warming trends had a marked influence on the growth of large old trees in the case of *P. leucodermis*, which grows in an open forest landscape where tree competition is absent or very low. Young *P. leucodermis* trees responded more positively to warmer April temperatures than that of their old conspecifics, confirming the relevant role of tree age in determining the BAI slope (Piovesan et al., 2019b). This is most likely due to a greater reactivity in the physiology of young trees in the last three decades, which may respond through an advancement of cambial resumption in spring in conjunction with higher growth rates (Rossi et al., 2008).

Finally, some caveats should be considered in our approach. We could not reconstruct changes in tree-to-tree competition and mortality, which is not feasible at such long-term scales. Alternatively, we opted to compare growth trajectories and responses to climate in coexisting old and young trees of the same species. When comparing the growth of old and young trees during the first decades of life, a relevant sampling bias should be considered (Duchesne et al., 2019), as fast-growing trees die earlier (e.g., tree longevity is associated to low radial growth rates; Di Filippo et al., 2017; Piovesan and Biondi, 2021). Although younger trees also include fast growers that typically do not get old, the growth behavior of young trees deserves further investigation to disentangle their acclimatization capacity. The ideal situation would be to sample young and old stands in the same location, but due to the legacies of past management that is unfeasible. In future studies it would be interesting to study the response of young and old individuals along altitudinal and site quality gradients. Other long-term drivers of

tree growth, such as CO₂ concentrations, increased N deposition, changing soil fertility, and forest structure should be considered in future studies (Gentilesca et al., 2018).

5. Conclusions

In this study, we found that old and young trees coexisting in old-growth forests showed different growth trajectories and responses to climate warming. These differences depended on tree taxa and local climatic conditions. *P. leucodermis* showed marked growth enhancement in response to warming at cold sites; however, old trees of low-elevation hardwood forests showed stable growth behavior, highlighting the ability of *F. sylvatica*, *A. alba*, and *Q. cerris* to acclimate to warming in the Mediterranean mountains. Studying and monitoring the growth performance of young trees in association with old trees is a strategic task to track old-growth functioning in the face of global change. The conservation of mountain ecosystems represents an important target (15.4) of Agenda 2030.

The progress towards sustainable development is monitored through two specific indicators to protect the integrity and functionality of ecosystems inside protected areas. Our findings have relevant applied implications in the carbon cycle mitigation and in biodiversity conservation supporting programs for preserving old-growth stands and restoring forest naturalness in order to improve their resistance and resilience to global changes.

CRedit authorship contribution statement

Michele Colangelo, J. Julio Camarero, Antonio Gazol and Francesco Ripullone: Conceptualization, Methodology, Software. **Michele Colangelo, J. Julio Camarero, Antonio Gazol, Francesco Ripullone and Gianluca Piovesan:** Data curation, Writing- Original draft preparation. **Michele Colangelo, J. Julio Camarero and Antonio Gazol:** Visualization, Investigation. **Michele Colangelo, J. Julio Camarero, Francesco Ripullone and Gianluca Piovesan:** Supervision. **Antonio Gazol and Angelo Rita:** Software, Validation. **Francesco Ripullone, Gianluca Piovesan, Marco Borghetti, Angelo Rita, Michele Baliva, Tiziana Gentilesca, Aldo Schettino:** Writing- Reviewing and Editing.

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.2021.149684>.

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