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The return of tall forests: Reconstructing the canopy resilience of an extensively harvested primary forest in Mediterranean mountains

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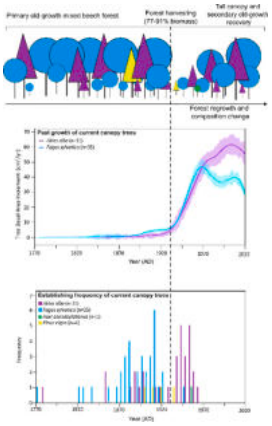
HIGHLIGHTS

- Passive rewilding is functional to restore the ecological integrity of massively perturbed Mediterranean forests.
- Survivor trees and post-harvesting fir regeneration were the pillars of biomass restoration.
- Silver fir (mixed forest) accelerated and facilitated ecological restoration.
- Larger and older trees are currently resisting climate warming.
- Forest dynamics and stand acclimation may lead to negative productivity trends in advanced rewilding stages.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding recovery times and mechanisms of ecosystem dynamics towards the old-growth stage is crucial for forest restoration, but still poorly delineated in Mediterranean. Through tree-ring methods, we reconstructed the return of a tall canopy after severe human disturbance in a mixed beech (*Fagus sylvatica*) and silver fir (*Abies alba*) forest, located at a mountain site in the southern edge of both species' range (Gariglione, south Italy). The primary forest was extensively harvested between 1930 and 1950, removing up to 91 % of the biomass. Growth histories, climate-growth relationships and time-series of growth dominance in Gariglione were compared with a network of protected mature and old-growth beech forests distributed along a wide elevational gradient in the same region. We found that the renewed tall canopy of Gariglione is mainly composed of remnant trees, which include uncut trees and saplings, and the post-harvesting regeneration mostly represented by fir. Canopy beech trees reached maximum basal area increment (BAI) in the 1970s, 40–50 years after cutting. Then, beech BAI

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PDSI
Rewilding

shifted towards negative trends in phase with drying climate (PDSI), while fir maintained a sustained growth until 2000. This growth asynchrony between the two species conferred community stability over the last decades. The network comparison highlighted the common negative impact of summer drought on high-frequency growth signals of beech in south Italy. However, analysis of long-term mean growth trends indicates decreasing BAI limited to Gariglione beech, revealing relevant differences due to site ecology and its interactions with legacy effects of past management in driving growth responses to climate change. Indeed, lowland mature beech forests showed increasing BAI in the last decades, while primary high-mountain forests displayed a remarkably stable low oscillating growth. In all the Mediterranean forests we studied, large and old trees showed a marked growth acclimation despite ongoing climate warming, demonstrating the effectiveness of landscape rewilding.

1. Introduction

Understanding the mechanism of species and ecosystem resilience to large-scale perturbations and assessing patterns and processes of forest ecosystem recovery is a key issue in global change studies (Seidl and Turner, 2022). The restoration of composition, structure and functionality attributes of old-growth forest stands has significant implications in biodiversity conservation and climate change mitigation programs for implementing international environmental agendas, such as the Global Biodiversity Framework (Crouzeilles et al., 2016; Mo et al., 2023; Piovesan et al., 2022; Rayden et al., 2023). However, multiple uncertainties remain around conceptualization, planning and assessment stages of ecological restoration projects for implementing effective recovery of forest habitats (Marshall et al., 2023).

Ecological studies revealed that after deforestation or extensive harvesting of tropical forests, the recovery of biomass and species composition requires >10–12 decades to achieve old-growth traits (Poorter et al., 2021). Temperate forests seem to be characterized by similar recovery times of carbon storage (e.g., Allen et al., 2016) but other forest attributes, such as the presence of large and tall trees, may require longer (>200 years) (Albrich et al., 2021; Sutherland et al., 2016). In this context, there is a need to delve deeper into the dynamics of old-growth forest restoration focusing on dynamics of compositional, structural and functional recovery (Manhães et al., 2022; Hua et al., 2022).

In temperate regions, primary and old-growth forests are sparse and fragmented because of the long-term widespread land use and land use changes, which produced cultural landscapes and simplified forest ecosystems. In Europe, only a few patches of old-growth forests have survived in remote mountain areas (Mikoláš et al., 2023). Conserving these relicts requires ad hoc mapping, monitoring, and strict protection measures through National Parks and other protected areas. A leading example of protection and restoration of natural forest ecosystems on a continental scale is the Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe UNESCO World Heritage Serial Site. However, in temperate regions, protecting the existing fragmented old-growth ecosystems may not be enough to halt the loss of biodiversity and ensure adequate ecosystem services to future generations (Chiarucci and Piovesan, 2020). Conserving and restoring old-growth forests and connecting natural forest areas with wildlife corridors and stepping stones will contribute to bending the curve of biodiversity loss (Barton and Keeton, 2018; Case et al., 2023). Current targets for nature conservation are designed to expand protected areas (e.g., 30 by 30) and restore ecological integrity of degraded ecosystems (Zeng et al., 2022).

Defining recovery times and mechanisms of forest dynamic towards the old-growth stage are crucial issues. Tree growth trajectories relate the age of a tree to its size and are influenced by local-scale factors such as site natural history, past uses (legacy effects), landscape configuration and global changes (Chazdon et al., 2016; Pretzsch et al., 2022; Verheyen, 2022; Vilà-Cabrera et al., 2023). Global studies have demonstrated that temperate and boreal forests are the largest carbon sinks (Yang et al., 2023), with a prevalent role of young and middle-aged (50–140 yr) stands, but the growth processes of rewilding deciduous stands towards old-growth stages are still overlooked. Furthermore, climate change can impact temperate forest dynamics diverting recovery dynamics from historical reference systems and opening an uncertain future, e.g. novel ecosystems (Corlett, 2016; Dollinger et al., 2023; McDowell et al., 2020). Studies suggest that forest stability is increasingly at risk from a range of global change factors that can cause forest dieback in consequence of drought, fire, biotic agents, and other disturbances (Anderegg et al., 2020; Hartmann et al., 2022). Large scale models have shown a widespread decline in forest resilience, driving an increasing vulnerability of carbon stocks (Forzieri et al., 2021; Koch and Kaplan, 2022; Uribe et al., 2023) caused for example by critical transitions from tall forests to alternative low biomass states such as dwarf shrubby vegetation in the case of the tropics (Flores et al., 2024). Drought is considered a leading factor in shifting the range of northern temperate species towards cold and wet regions (Astigarraga, 2023) while bigger negative impacts on tree growth are expected in hotspot regions of climate warming located at the rear edge of forest species distributions (Forzieri et al., 2021). The rewilding mountain landscape of Mediterranean mountains, a hotspot of biodiversity but also of climate change, is an interesting opportunity to study forest resilience reconstructing tree growth trajectories of ecosystem integrity recovery.

In the southern Apennines (Italy) large areas covered by nearly intact forests were present until the early 20th century, when extensive and intensive timber harvesting activities began to respond to the market's growing demand for wood (Iovino and Menguzzato, 2014). After the harvesting period, some of these forests were not cut anymore and have now developed high forest functionality and biomass stocks (Piovesan et al., 2022). The presence of historical records describing local forests before the intense wood harvest along with detailed documentation about cutting operations, offer a unique chance to describe patterns of forest biomass recovery after extensive and intensive disturbance. Also, Apennine mixed beech-fir forests are fragmented and vulnerable habitats of high conservation interest and ecological value (Palli et al., 2022). Thanks to their ability to mitigate climate change in a biogeographically vulnerable area (i.e., the Mediterranean hotspot of climate change), old-growth mixed forest stands represent strategic ecosystems for conserving a unique biodiversity (linked to refuge areas), from genetic structure to the community (Palli et al., 2022; Piotti et al., 2017). The mixed beech forest of the Gariglione State Forest represents a case study of special interest. Here, the primary forest was extensively harvested in the first half of the century and then managed using conservation practices that led to passive rewilding in recent decades. Today, almost a century later, the forest has a tall canopy with renewed old-growth attributes (Piovesan et al., in preparation), providing the possibility to perform a retrospective study and describe the resilience trajectories of a mixed beech-fir forest in the Mediterranean mountain environment.

Using tree-ring records, we reconstructed lifetime growth trajectories (i.e., diameter growth time series) of canopy trees in the Garglione Forest, a Mediterranean forest ecosystem, that is returning to tall structure and old-growth stage after intensive and extensive forest harvesting. We characterize mechanisms of canopy recovery and stand growth dynamics of rewilding mixed beech-fir forest. Being the highest layer of the vertical forest structure, the canopy is the area of greatest energy input into the forest ecosystem thus generating most of the net

primary production (up to 90 % and more of the above ground biomass increment in closed forest ecosystems; Martin-Benito et al., 2022). Moreover, tall and complex canopies are effective climatic insulators, providing thermal buffering (De Frenne et al., 2019) and harboring a unique biodiversity (Walter et al., 2021). We reconstructed the impact of the past disturbance, the long-term tree canopy growth, and the response to climate change of European beech (*Fagus sylvatica*) and silver fir (*Abies alba*), two late successional species, and then compared the growth performances with a regional network of old-growth and mature beech forests, focusing on the role of climate variations in growth dynamics. Specifically, we addressed the following research questions:

- How did tree recruitment in a mountain mixed primary Mediterranean forest change after being extensively harvested?
- How did lifetime diameter growth trajectories develop during the ecological restoration of a tall old-growth beech forest mixed with fir?
- How has climate change impacted tree canopy growth during forest recovery towards secondary old-growth stages?
- How stable have growth-diameter (or age) relationships of canopy trees been over the last 50 years?

2. Materials and methods

2.1. Study area: the Calabrian beech tree-ring network

Gariglione State Forest, in Sila National Park (Calabria, Southern Italy) (Fig. 1) covers 1717 ha along the slopes of mount Gariglione

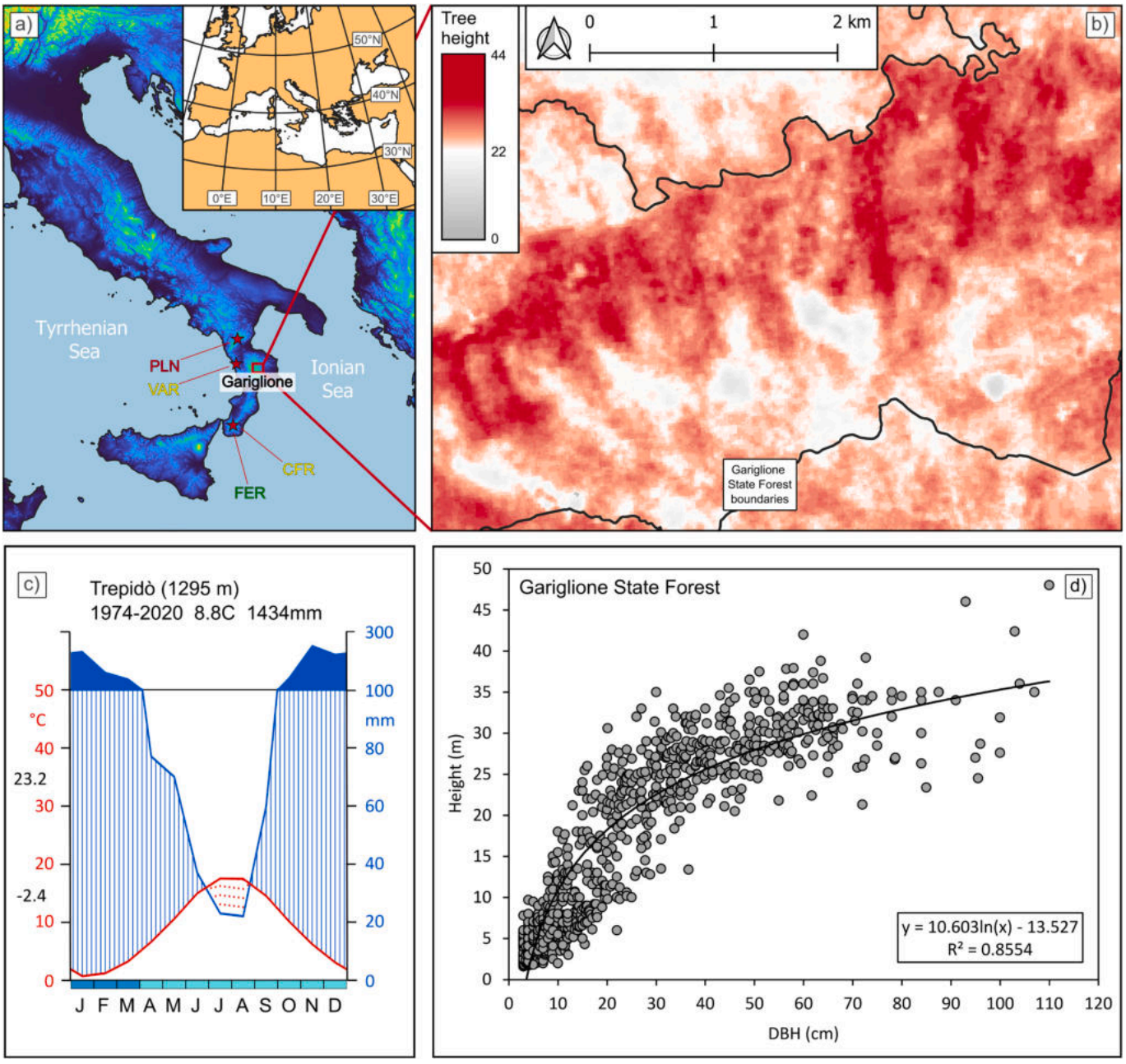


Fig. 1. Study site. a) Location of the study area in the Mediterranean basin (inset) and in the Italian peninsula. The beech forests included in the Calabrian beech network (PLN, VAR, CFR, FER) (Table 1) are also shown. b) Focus on the area within the Gariglione State Forest boundaries that was subjected by inventory sampling; the color gradient indicates the canopy height (data from Lang et al., 2023). c) Bagnouls-Gaussen thermo-pluviometric diagram from Trepidò located at 1295 m, 6 km away from the Gariglione Forest. d) Height-diameter relationship of beech and fir trees in the Gariglione forest.

(1765 m a.s.l.) and is entirely included within the park boundaries (Zone A, i.e., strictly protected). The Gariglione forest is a hotspot of climate change and biodiversity (i.e., the southernmost distribution of temperate mountain ecosystem in Europe). Two priority forest habitats of the Natura 2000 Network (EU Habitats and Birds Directives) are present in the Gariglione Forest (codes 9220*, 9530*). Trees were sampled in the upper part of the State Forest area, along an elevational gradient from 1300 to 1750 m a.s.l. The forest ecosystem has an average canopy height above 30 m and some trees exceeding 45 m (Fig. 1b, d), making the Gariglione a tall forest (Huang et al., 2023). The forest is characterized by a multilayer vertical profile and high levels of biomass (Di Matteo et al., 2023). The rich biodiversity is evidenced by the presence of distinct fauna of conservation interest such as carabid beetles (Mazzei et al., 2017). The forest canopy is dominated by European beech (*Fagus sylvatica*, hereafter "beech") mixed with silver fir (*Abies alba*, hereafter "fir"). Other tree species scattered throughout the Gariglionie Forest are black pine (*Pinus nigra* subsp. *laricio*), aspen (*Populus tremula*), alders (*Alnus cordata; Alnus glutinosa*), hornbeam (*Carpinus betulus*), maples (*Acer* spp.), and Turkey oak (*Quercus cerris*) at lower elevation. The bedrock of the Gariglione Forest is composed of metamorphic and intrusive magmatic rocks. The most diffuse lithological types are biotic gneiss, amphibolite, pyroxenite, pegmatite, siliceous marbles (Lorenzoni and Zanettin Lorenzoni, 1983). Soils are deep and characterized by high fertility and are classified as Dystrudepts according to the Taxonomic Classification of Soils (ARSSA, 2003).

At the beginning of the twentieth century, Gariglione was an old-growth forest with a high carbon stock forest (circa 1000 m^3/ha), diffuse presence of old, very large and tall trees (up to >2 m in diameter and 40 m in height) and widespread presence of deadwood and large and decaying trees (Douglas, 1915; Carullo, 1952). Starting from 1930 up to the 1950s, the Gariglione forest underwent extensive harvesting with the goal of adapting the old-growth stand to timber production. From 77 % to 91 % of the total volume was harvested (Carullo, 1952). Only 30 ha were left untouched to preserve the original status of the forest. In 1968, the Gariglione forest was included in the Calabria National Park, today incorporated in Sila National Park. In 1977 the forest was declared a biogenetic reserve and managed by the State Forest Service (today Carabinieri Forestali) with a passive rewilding approach. The Gariglione Forest is located in a region with particularly clean air (Becchetti et al., 2023), which implies that pollution or the deposition of nitrogenous fertilizers has not influenced the ecosystem recovery.

Growth trends of canopy trees in the Gariglione Forest were compared to a network of mature and old-growth beech stands distributed along a latitudinal (ca. 200 km) and altitudinal (ca. 1500 m) gradient in the Calabrian-Lucanian Apennine (Fig. 1a; Table 1) to differentiate growth trajectories (Di Filippo et al., 2017) and climatic response of canopy trees living in different site conditions (Piovesan et al., 2005). All sites have had no direct human impact since 1970. Old-growth stands are characterized by the natural death of dominant trees, and new cohorts establishing in gaps and entering the canopy. Stands were catalogued as primary old-growth if they had a long, continuous history of natural disturbance and regeneration, and as secondary old-growth stands if they had been logged in the past and then left to natural dynamics for multiple decades (Di Filippo et al., 2017; Vandekerkhove et al., 2022).

2.2. Tree-ring methods

A suite of tree-ring methods was used to reconstruct the resilient responses of the human perturbed old-growth forest by studying trees in the current canopy. A resilient response is an emergent ecosystem property conferred by different mechanisms at work at differing levels of biological organization that can be summarized in the following sequential processes from individuals to community: persistence/resistance, recovery, and reorganization/adaptability (Falk et al., 2019; Strickland et al., 2024). In this study, the resilience of the forest canopy following extensive cutting was first examined by means of dendroecology, to reconstruct the tree recruitment, the disturbance ecology, and the growth history. Then, we performed dendroclimatological analyses including beech forests of the Calabrian tree-ring network to assess the effect of climate variations on tree growth (Fritts, 1976; Piovesan et al., 2005).

2.2.1. Sample collection and processing

Cored trees were selected according to a sampling design using plots and transects in an inventory program aimed at monitoring and reporting the structure (preliminary height data are reported in Fig. 1), composition and functionality of the Gariglione Forest (Piovesan et al. in prep). This study was focused on canopy recovery, i.e., current trees with diameter at breast height > 37.5 cm as described in dendroecological methods applied to beech ecosystems (Peters, 1997; Di Filippo et al., 2017).

Increment cores were extracted at breast height (1.3 m above the ground) using a Pressler increment borer. A total of 186 canopy trees were sampled: 72 trees were sampled in the Gariglione Forest (39 beech and 33 fir), 60 beech trees in the high mountain belt, 24 beech trees in the low mountain belt and 30 beech trees at hilly elevation (Table S1 in Supplementary Material 1).

Tree-ring widths were measured to the nearest 0.01 mm using a Computer Controlled Tree-Ring Measure Device (CCTRMD) and core series were visually and statistically cross-dated using the interfaced with the software CATRAS (Aniol, 1983, 1987). Cross-dated tree ring-width series were checked for accuracy of dating using the COFECHA computer program (Holmes, 1983). Additionally, the expressed population signal (EPS) was computed with the R package Detrender (Campelo, 2012) and used to measure site chronology reliability over a moving 50 yr window (Table S1 in Supplementary Material 1). Tree-ring series displaying poor statistical fit with the average curve were rejected.

2.2.2. Dendroecology

Cross-dated tree-ring series were used to estimate tree establishment period and reconstruct current canopy growth dynamics. Only trees with pith centered or partially centered were included. The relationships between age and current DBH were analyzed by fitting linear and

Table 1
Site and stand attributes of the Calabrian beech network.

Site	Protected area	Naturalness	Bedrock	Elevation range (m a.s.l.)	Elevation belt
Pollinello (**PLN**)	Pollino National Park	Primary old-growth forest	Limestone	1890–2005	High mountain
Gariglione (**GAR**)	Sila National Park	Mature and secondary old-growth forest	Metamorphic and intrusive magmatic rocks	1300–1750	Mountain
Ferraina (**FER**)	Aspromonte National Park	Secondary old-growth forest	Gneiss	1267–1414	Low mountain
Cinquefrondi (**CFR**)	Aspromonte National Park	Mature	Shale, phyllites and marbles	570–640	Hilly
Varconcello (**VAR**)	Catena Costiera Regional Park	Mature	Gneiss and granitic	470–620	Hilly

nonlinear models generated using the software PAST (Hammer et al., 2001) and picking the model with the lowest Akaike Information Criterion (AIC). Tree establishment event dates which in our study indicate the year of first tree ring produced at 1.30 m height (pith date), were computed and grouped into 5-year bins. Since the tree establishment period is calculated at 1.30 m, tree age might be underestimated of circa 10 years for post-harvesting regeneration or even more in the case of advanced regeneration shaded by overstory in the old-growth stand (Piovesan and Biondi, 2021). However, this uncertainty does not determine any substantial change in the discussion of canopy recovery mechanisms.

Chrono-functional indicators proposed by Di Filippo et al. (2017) were used to assess the level of naturalness of the forests included in this study.

Growth histories were reconstructed for cores including the pith. DBH growth over time was calculated at yearly intervals by using tree-ring series multiplied by a constant factor (DBHf/DBHtr) to account for the discrepancy between the measured DBH in the field (DBHf) and the diameter calculated summing tree-ring width (DBHtr) (e.g., asymmetric growth around the pith; Speer, 2010).

Radial growth patterns of all increment cores collected in the Gariglione Forest were analyzed in association with tree establishment for reconstructing past disturbance events (e.g., past harvesting period and natural disturbances in recent years). Growth releases after disturbances in the Gariglione Forest were first assessed through the method of Nowacki and Abrams (1997) which is based on the intensity of growth change (%GC) using the following formula:

$$\%GC = [(M2 - M1)/M1] \bullet 100$$

where M1 is the mean annual diameter growth of the preceding 10-yr period (including the current year), and M2 is the mean annual diameter growth of the subsequent 10-yr period. A 10-yr timespan tends to average out short-term growth responses related to high frequency climate variations (Leak, 1987) and amplify the medium-term growth changes commonly associated with canopy disturbance (e.g., cuttings in managed forests or natural death). We analyzed moderate (%GC between 50 %–99 %) and major growth releases (%GC >100 %).

We also employed the boundary-line method (Black and Abrams, 2003) to scale the percent growth change, according to growth rate prior to disturbance, defining moderate and major releases as those falling within 25–49.9 % and 50–100 % of the boundary line, respectively. We compared the calculated boundary lines with those developed for beech in the Apennines (Ziaco et al., 2012) and for fir in the Dinaric Mountains of Bosnia and Herzegovina (Nagel et al., 2014). All calculations were performed through the R package TRADER (Altman et al., 2014) and dplR (Bunn, 2008). Beech and fir data were analyzed separately.

2.2.3. Dendroclimatology

The impact of climate variations on tree growth was analyzed by means of dendroclimatology (Cook and Peters, 1981).

Basal Area Increments (BAI) were calculated from tree-ring width time series and interpreted as a proxy of wood production (Anderson-Teixeira et al., 2022; Dye et al., 2019; Piovesan et al., 2008; Vospernik, 2021). For each individual series, past annual BAI was progressively reconstructed starting from the outside bark diameter using the following formula:

$$BAI_t = \frac{\pi}{4} \cdot \left[DBH_t^2 - (DBH_t - 2\mathrm{RW}_t)^2 \right]$$

where DBHt is the stem diameter at the end of year t and RWt is the tree-ring width.

The climatic signals embedded in tree-rings of the Calabrian beech network were searched for by analyzing the different frequencies of the BAI series. RW and BAI series were detrended through a cubic smoothing spline with a 50 % frequency response over a 50-year period, to remove age/diameter-related effects and enhance the short-term climate variations influencing growth. A third-order autoregressive model was used to remove the autocorrelation from each BAI series (pre-whitening).

Pre-whitened BAI series were ordered through Principal Component Analysis (PCA) following methods reported in Piovesan et al. (2005) to extract common growth variations (i.e., climatic signal) for the period 1970 to 2020. PC1 scores were correlated with monthly self-calibrated Palmer drought severity (scPDSI) index using the R package Treeclim (Zang and Biondi, 2015) to estimate the high-frequency climatic signals (bootstrapped correlation functions). scPDSI were downloaded for each site (0.5°*0.5° grid), from the KNMI Climate Explorer web application (CRU scPDSI 4.05 early dataset) provided by the Climatic Research Unit at the University of East Anglia (Barichivich et al., 2021). Bootstrapped correlation functions were calculated for the period 1970–2020 using a 17-month scPDSI window from June of the previous year to October of the current year, to account for monthly climatic variables which may influence growth variations via direct effects on photosynthesis or indirect effects (e.g., mast seeding; Selås et al., 2002).

The long-term impact of scPDSI on low-frequency BAI variation was visually emphasized by filtering the series with a cubic smoothing spline with a 50 % frequency response over a 30-year period (Cook and Peters, 1981).

2.2.4. Growth dominance coefficient (GDC)

We applied the growth dominance coefficient (GDC), which is based on the principle of Lorenz curve (e.g., Gini coefficient; West, 2014), to measure tree growth behavior among trees and analyze temporal trends in the allocation of stand growth depending on tree size (from smaller to larger trees; Binkley et al., 2006; Bose et al., 2022) and between young and old trees. To this purpose, we constructed the growth dominance curves for each site and species arranging in ascending order the DBH or the age (x axis) of individual trees and the cumulative increment in stem basal area (y axis). GDC was calculated using the following formula:

$$GDC = 1 - \sum_{i=1}^{n} (\%G_i - \%G_{i-1}) \cdot (\%BAI_i + \%BAI_{i-1})$$

where n is the number of trees in the stand, $\%G_i$ is the cumulative proportional stem basal area or age of $tree_i$, and $\%BAI_i$ is cumulative proportional basal area increment of $tree_i$.

GDC can take theoretical values between 1 and −1 (Binkley et al., 2006):

- GDC > 0 disproportionate growth - higher relative growth rates - of big/old tree (asymmetric growth dominance).
- GDC = 0 proportional growth (neutral dominance)
- GDC < 0 disproportionate growth of small/young trees (inversely asymmetric).

PCA scores calculated for yearly GDC time-series were used to compute bootstrapped correlation functions with scPDSI following the same methods described in the Section 2.2.3 “Dendroclimatology”.

3. Results

3.1. Mechanisms of canopy recovery in the Gariglione Forest

3.1.1. Forest age structure

In the Gariglione Forest the mean age of canopy trees is 118 yr (±40 yr SD), and the median is 112 yr. Beech display significantly higher median age (124 yr) compared to fir (84 yr) (Table S2b in Supplementary 1), while there is no difference between median DBH in beech and fir (Table S2a in Supplementary 1). Age-DBH relationship in fir can be described by a Hill’s sigmoid function which reaches the asymptote around 80 cm of DBH and 100 yr of age (Fig. 2a). Canopy beech trees

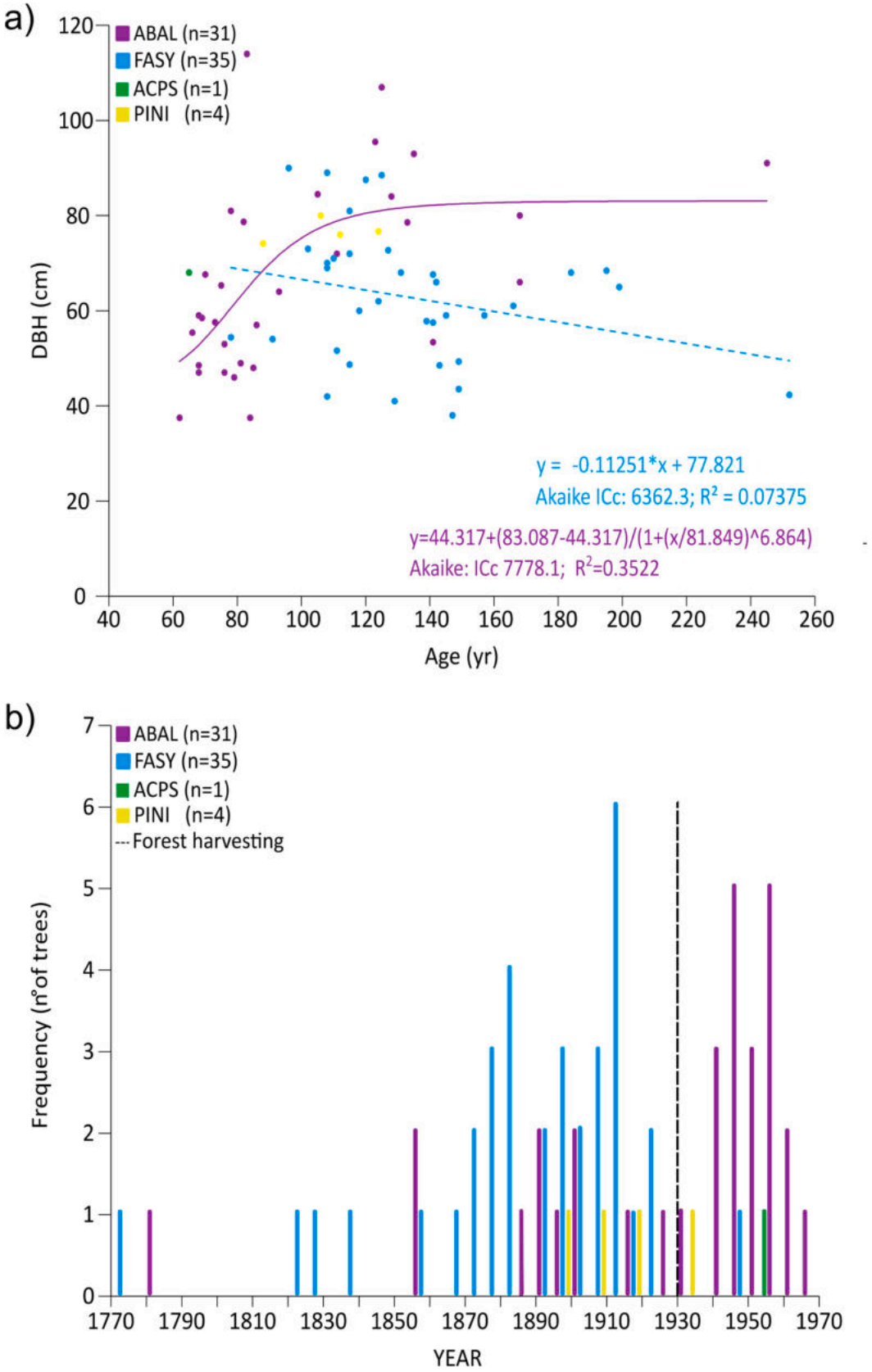


Fig. 2. Stand age structure and establishment dates of the Gariglione Forest. a) Age vs DBH in FASY (beech, *Fagus sylvatica*), ABAL (fir, *Abies alba*), ACPS (maple, *Acer pseudoplatanus*) and PINI (black pine, *Pinus nigra* subsp. *laricio*). Dashed blue line indicate the non-significant linear regression in FASY age-DBH relationship. Solid purple line indicates the Hill's sigmoid function in ABAL. Equations of the regressions, R^2 values and the Akaike information criterion are shown in the lower right corner. b) Five-year bins of tree establishment frequency. Dashed vertical line indicate the breakpoint year of the extensive forest cut in the Gariglione Forest (1930).

show no age-DBH correlation because trees with diameter of 40–50 cm can range from 78 to over 250 years old (Fig. 2a; Table S1).

Establishment frequencies indicate that at least 69 % of current canopy trees were living in the primary old-growth (Fig. 2b). All but one of the beech trees were at least 1.30 m high in 1930 (Fig. 2b). In contrast, 65 % of the sampled fir trees were not established or were smaller than 1.30 m before the forest cuts in 1930 (Fig. 2b). The Gariglione Forest is currently dominated by late successional species (beech and fir). Scattered light-demanding large trees, such as maples or black pine, established in large gaps, today survive in the canopy because of their very fast growth rates (Fig. 2a, b).

3.1.2. Disturbance ecology

Both beech and fir display a sharp increase in average tree-ring growth following 1930 (Fig. 3a), as a consequence of major growth releases (Fig. 3b). Overall, growth releases were greater in fir than beech. Fir %GC peaked in 1936 with an average value of 236 %, while beech peaked the following year, in 1937, reaching 169 % (Fig. 3b). Major growth releases of individual trees were recorded by fir and beech from approx. 1930 to 1955 in coincidence with the harvesting period (Fig. 3c, d, Fig. S1 in Supplementary 2). Moderate and major growth releases between 1930 and 1940 involved 69 % of trees of both species, demonstrating the widespread impact of forest cutting (Fig. 3c, d, Fig. S1 in Supplementary 2). Since 1960, growth releases temporarily ceased, indicating no relevant disturbances, in agreement with changes of forest management approach towards conservation strategies. Since approx. 1980, moderate releases are recorded especially for beech; these new phases of growth increase can be interpreted as the transition to a natural disturbance regime characterized by canopy gaps opening in consequence of natural agents of tree mortality (Fig. 3c, d). During the last 50 years fir trees show an overall greater growth (Fig. 3a).

3.2. Growth history: Gariglione Forest vs a regional network of beech forests

In Gariglione, growth history curves highlight faster mean DBH growth of fir than beech (Fig. 4a). Such a difference is due to the contribution of numerous young fir trees (<90 years) that are characterized by very fast DBH growth rates (Fig. 4b, c). Mean DBH growth rates of fir trees are placed between the late-successional beech and the shade-intolerant black pine (Fig. 4a). However, when the sample is divided into age groups, it appears that the older fir and beech trees (>120 years) have grown in the primary forest with similar slow growth rates until about 1930, when growth rates start increasing (Fig. 4b). The youngest trees (<90 years), which established in the perturbed forest, showed the fastest growth rates (Fig. 4b, c).

The multi-site comparison of DBH growth reconstructions underscore the exceptional growth increase in Gariglione that followed the beginning of cuts in 1930 (Fig. 4d). After that extensive disturbance, DBH growth rates of beech changed from values coherent with its intermediate mountain bioclimatic belt to faster DBH growth rates characteristic of beech forests located at low mountain elevation (Fig. 4d).

The Gariglione Forest showed a resilient response following extensive cutting (removal of up to 90 % of aboveground biomass, comparable to a stand replacing disturbance). The forest stand experienced an outstanding growth spurt in the following decades. Today the canopy has renewed chronological indicators in line with secondary old-growth beech forest (Table 2). The other beech forests from the Calabrian network are also characterized by an overall forest functional naturalness typical of secondary or primary old-growth (Table 2). However, the median diameter and age are significantly lower at hilly elevations (Table S2 in Supplementary 1) highlighting a less advanced stage of rewilding in these stands (mature phase). On the other hand, the high mountain site can be ascribed to primary old-growth forest characterized by much higher median ages because of the presence of extremely old trees (Table S2b in Supplementary 1).

3.3. Climatic signals in tree growth

The Gariglione Forest showed the lowest climatic-related dendrochronological parameters (e.g., Mean correlation coefficient with master chronology and mean sensitivity) and high radial growth increments (Table S1 in Supplementary Material 1). Site chronologies used in the dendroclimatic investigations have an Expressed Population Signal (EPS) >0.85 (Table S1 in Supplementary Material 1), meaning that tree ring series represent the population signal with sufficient quality.

The Principal Component Analysis (PCA) performed on prewhitened BAI site chronologies reflect the common growth variations (PC 1) of mountain and hilly elevation sites (Fig. 5a, see also Fig. S2 in Supplementary Material 2). Hilly and high mountain sites are anticorrelated on the PC2 component (Fig. 5a). Bootstrapped correlation function of PC1 scores identified a set of drought signals during the current summer and the early autumn (Fig. 5b; see also Fig. S3 in Supplementary Material 2). The bioclimatic ordination and responses of the Calabrian beech network is consistent with other beech forests distributed along a similar elevation gradient in the Apennines (Piovesan et al., 2005).

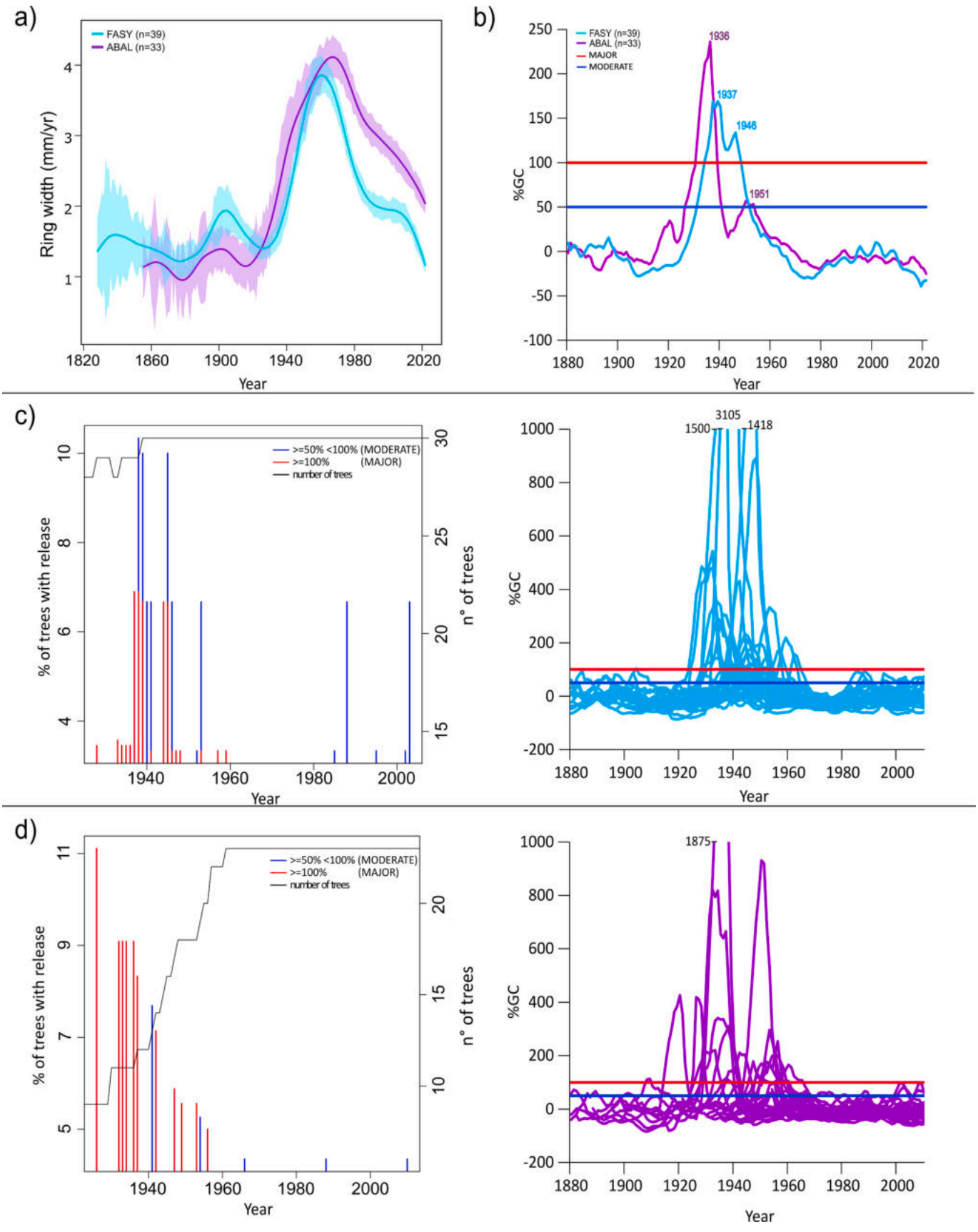
Low pass filter of BAI highlighted a fast growth in the Gariglione with a culmination around 1970 in beech, while fir maintained a sustained BAI until 2000, revealing relevant differences in growth trends in the last decades (Fig. 6a; Table 3) that remain even when only trees older than 90 years are compared (Fig. 6b). In Gariglione, scPSDI index and BAI of beech followed a similar oscillation since 1970s with an overall decreasing trend in both age classes (Fig. 6a, b) while growth trends of fir are more complex. After an initial drop in growth rate in the 1970s, fir trees older than 90 yr, increased growth rate, reaching a maximum around the year 2000, while the <90 yr cohort (trees established after forest cutting) maintained increased growth until about 2010 (Fig. 6b). The positive response of fir to March temperatures (Fig. S4 in Supplementary Material 2) could help to explain the increasing BAI until the 2000s when drier summers became the main limiting factor for both species (Fig. 6a).

Low mountain and hilly elevation show respectively a stable or increasing long-term trend following the oscillations of PDSI variations, but not its long-term decreasing trend (Table 3), while high-mountain sites seem not to be affected by summer drought (Fig. 6c).

3.4. Tree growth behavior among canopy trees in relation to diameter and age

Negative Growth Dominance (GDC) indicates a general greater proportional contribution of smaller/younger trees to the canopy productivity compared to larger/older ones (inversely asymmetric GDC) (Fig. 7; Fig. S5 in Supplementary Material 2). Considering GDC as a function of tree dimension (Fig. 7a), beech in Gariglione is characterized by the proportional contribution of both large and small trees to the overall productivity (neutral dominance; see also Fig. S5 in Supplementary Material 2). GDC analysis computed on tree ages revealed more negative values in agreement with a marked negative effect of age on tree production (Fig. 7b).

Most of the sites are characterized by a positive trend of GDC series towards 0, indicating an increasing contribution of larger/older trees to BAI in recent times (Fig. 7; Table 3). However, beech in the low mountain elevation belt shows an oscillating behavior with a decreasing GDC in recent years that resembles scPDSI variations (Fig. 7). Correlation functional analysis performed on prewhitened PC1 scores of GDC series revealed no relevant climatic signals linked to drought variations (Fig. S6 in Supplementary Material 2). Size-based GDC scores (PC1) are not correlated with age-based GDC scores (PC1) pointing out the need of both tree size and age in the study of growth dynamics (Fig. S7a in Supplementary Material 2). Indeed, GDC scores are not significant correlated to PC1 BAI scores (Fig. S7b in Supplementary Material 2).



(caption on next page)

Fig. 3. Growth release over time in the Gariglione Forest. a) Raw ring width chronologies of *Fagus sylvatica* (FASY) and *Abies alba* (ABAL). A 30-year filter cubic smoothing spline was applied. Shaded areas indicate the standard error. b) Average percent of growth change (%GC) of FASY and ABAL in the Gariglione Forest calculated after Nowacki and Abrams (1997). The blue horizontal line indicates %GC between 50 and 100 % (moderate release). The red horizontal line indicates % GC above 100 % (major release). Years of growth release peaks are shown. c) Focus on FASY individuals. The bar chart (on the left) displays the % of FASY individuals with moderate (blue) and major (red) releases. The grey line indicates the number of FASY trees participating in the calculation. The line chart (on the right) shows %GC variations per each FASY individual. Values represent the highest individual peaks extending beyond the scale. d) Focus on ABAL individuals. The bar chart (on the left) displays the % of ABAL individuals with moderate (blue) and major (red) releases. The grey line indicates the number of ABAL trees used in the calculation. The line chart (on the right) shows %GC variations per each ABAL individual. Values represent the highest individual peaks extending beyond the scale.

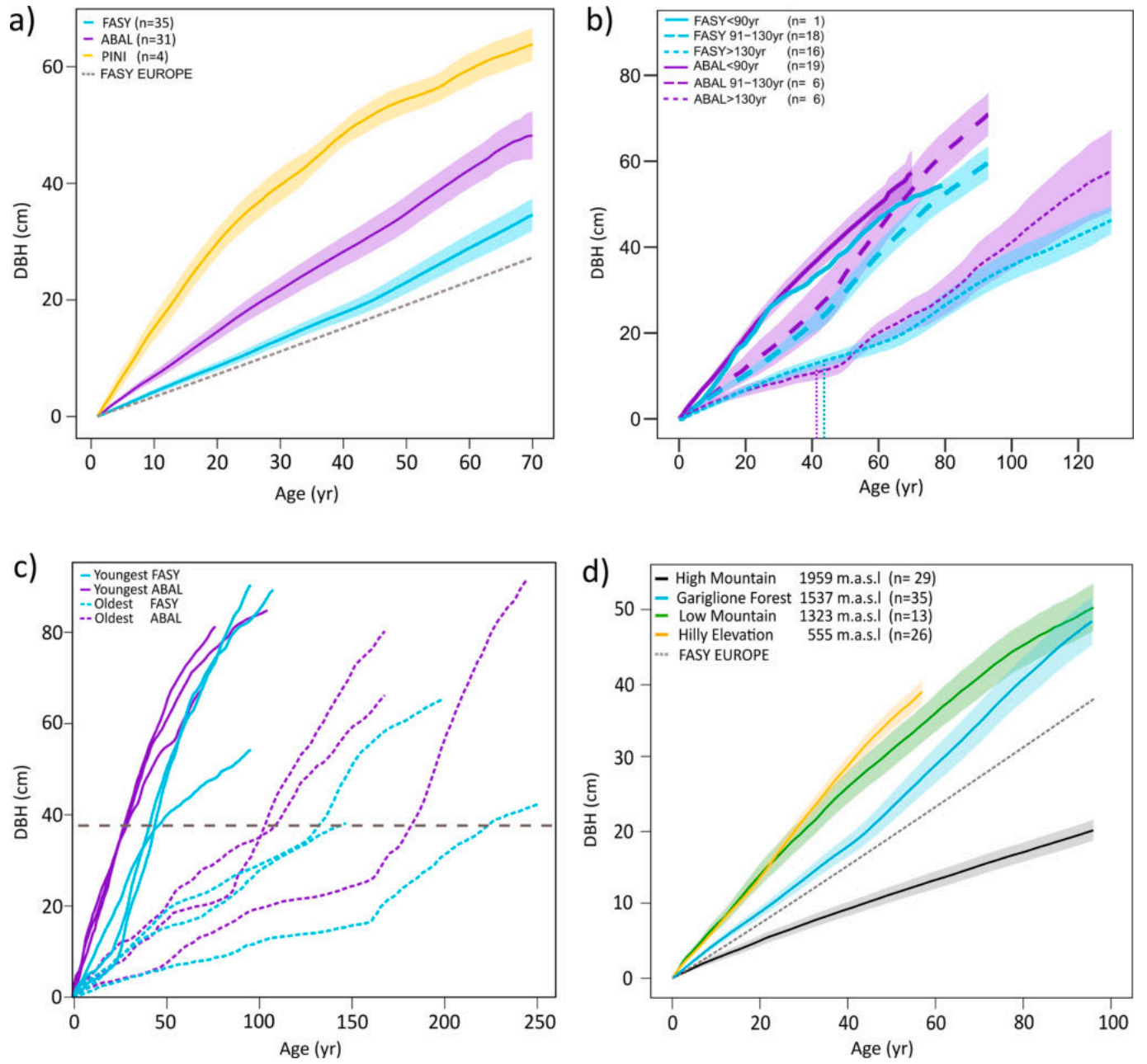


Fig. 4. DBH growth histories. a) DBH growth histories in FASY (beech, *Fagus sylvatica*), ABAL (fir, *Abies alba*) and PINI (black pine, *Pinus nigra* subsp. *laricio*) in the Gariglione Forest. The DBH growth history for FASY in Europe from (Pretzsch et al., 2021) is included (dashed black line). b) Gariglione DBH growth histories grouped into age groups. Dashed vertical lines indicate the mean age of the >130 years group in 1930. c) Gariglione DBH growth histories of the three oldest and the three youngest FASY and ABAL trees. The dashed horizontal line indicates the DBH threshold of 37.5 cm (i.e., canopy accession, Di Filippo et al., 2017). d) Multi-site comparison of FASY growth histories. Only trees with pith centered or partially centered were included.

4. Discussion

The mechanism of ecosystem resilience and canopy productivity following extensive cutting of a primary forest were reconstructed by means of dendroecological methods thus providing scientific knowledge on ecological restoration processes of old-growth forests. The comparison with beech forests distributed along an altitudinal gradient in the same region, including primary and secondary old-growth forest,

Table 2
Selected chronological indicators for forest functional naturalness compared to ranges of primary and secondary old-growth forests. AI: age indicators; GHI: growth history indicators. MEAN: mean age (years); RANGE3: difference between the mean of the 3 oldest ages and the 3 youngest (years); AGE3: mean age of the 3 oldest trees (years); MAX: age of the oldest tree. TrajRANGE3: difference between the mean of the 3 oldest ages and the 3 youngest at DBH = 37.5 cm (canopy accession) (years); TrajSLOW3: mean of the 3 oldest ages at DBH = 37.5 cm (years).[a]

	Metric	Hilly	Low mountain	Mountain (Gariglione)		High mountain
		(Beech)	(Beech)	(Beech)	(Fir)	(Beech)
AI	MEAN	88*	117*	134*	100	314**
	RANGE3	58*	102*	137*	129*	503**
	AGE3	116*	161*	215*	194*	578**
	MAX	117*	174*	252*	245*	624**
GHI	TrajRANGE3	31*	56	121*	106*	295**
	TrajSLOW3	70*	96*	166*	132*	388**

[a] Metrics falling into the ranges proposed by Di Filippo et al. (2017, Tab. 4) are indicated with single asterisk (secondary old-growth) and double asterisk (primary old-growth).

allowed us to frame the response to the cuts in terms of tree growth histories and trends in regional climate.

4.1. Resilience growth trajectories of the perturbed primary forest

4.1.1. Canopy recovery

The reconstructed response of the Gariglione Forest supports the disturbance response model proposed by Oliver and Larson (1996) in a human perturbed primary forest. Tree-ring dating revealed that the actual forest canopy is composed of two main cohorts:

1. Remnant trees: the retained trees and advanced regeneration (saplings) of the primary forest that survived forest cutting;
2. New trees: seedlings/post-harvesting regeneration.

The surviving overstory has a key function in forest development after severe disturbances (Guevara et al., 1986; Piovesan et al., 2022; Plotkin et al., 2013) or in periodically human perturbed ecosystems such as uneven-aged silvicultural systems (Danyagri et al., 2017). In the Gariglione Forest, pre-existing remnant trees and saplings of beech and fir were the pillars of a resilient response that produced a late-successional ecosystem with high biomass levels (Di Matteo et al., 2023). The few scattered remnant fir trees – some of which are now 200–250 years old – generated a vigorous post-cutting regeneration wave thanks to wind-dispersed (anemochorous) seeds and the fast growth rate of the new generation. These new trees showed a markedly higher growth rate in respect to trees of the primary forest, underscoring the high functional plasticity of this southern Italian provenance since it is able to regenerate in both primary and perturbed forest (Palli et al., 2022). The absence of pollution, fires, harvesting, overabundance of wild ungulates and livestock has favored the fir expansion. Indeed, still today fir is spreading in the understory in many areas of the tall Gariglione Forest thanks to the widespread presence of big trees. Our results suggests that major canopy disturbances may temporally enhance the fir abundance in mixed beech forests (Martin-Benito et al., 2022).

4.1.2. Growth responses and functional recovery towards the old-growth stage

The comparison between growth histories of the Gariglione Forest and the beech forests at other Calabrian sites highlighted the strong growth responses to the cuts of the 1930s–1950s. Growth releases were widespread and intense (major), as expected in mountain fertile soils at the southern distribution of the distribution range, where vegetative periods are longer (Ziaco et al., 2012).

Beginning in the 1960s, there was a twenty-year period with no growth releases, but continued growth increase. In beech, the average BAI culminated in the 1970s, approximately 40 years after cutting, consistent with the maximum wood increment indicated in regional yield table of even-aged beech stands (Castellani, 1982) and other studies on stand growth dynamics (Binkley, 2023; Pommerening et al., 2023; Pretzsch, 2021). Overall, BAI patterns agree with Net Primary Production (NPP) dynamics of temperate forests after stand-replacing disturbance, reaching a maximum after around 50 years (Birdsey et al., 2023; Tang et al., 2014). However, older fir trees, after a short-term decline in the 1970s, marked an important recovery of growth which led to an absolute maximum in the 2000s.

Since the 1980s the resumption of growth releases can be linked to the opening of gaps in the forest canopy generated by the reactivation of natural mortality processes of large trees. This study demonstrated an interesting performance of growth-averaging and boundary-lines methods in describing stand dynamics towards the old-growth stage (see also Carter et al., 2021 for managed stands). A low intensity natural disturbance regime is now driving the transition from mature to old-growth stage creating a horizontal and vertical structural diversification.

4.2. Rewilding towards old-growth stage: factors influencing growth trajectories

Dendroecological investigations revealed the complex factors influencing the growth trajectory of single trees in a rewilding forest ecosystem. Site, species, tree size, and climate variations are all confirmed to be relevant factors for BAI (Anderson-Teixeira et al., 2022; Vospernik, 2021). Moreover, our results stress the relevance of the tree age in studies on tree productivity of complex forest ecosystems (Ozdemir, 2021; Paluch and Jastrzębski, 2022; Piovesan et al., 2005) such as managed uneven-aged forests and old-growth stands. Overall, this study highlights the ability of old-growth forests to respond to human disturbances encouraging large-scale conservation and restoration projects of forest ecosystems as the best natural solution to global changes (Colangelo et al., 2021; Mikoláš et al., 2023) contributing to the urgent need to protect and restore tall forest (Huang et al., 2023).

4.2.1. The role of age and dimension on tree growth

We found that tree age is a relevant factor to explain stand growth dynamics in forest ecosystems affected by heavy cutting in the past. This study revealed that the oldest trees are not necessarily the largest in harvested primary forest coming back to the old-growth stage (Piovesan and Biondi, 2021). Old trees are characterized by significantly slower long-term growth trends (Piovesan et al., 2019; Piovesan and Biondi, 2021) and growth histories of beech and fir in Gariglione confirm this ecological rule (Fig. 4). In the case of beech, the comparison between diameter of the youngest and oldest trees in 2022 versus 1930 showed that younger trees become significantly larger despite starting from a smaller median diameter (Table S3 in Supplementary Material 1). The greater recovery of wood productivity of the hilly sites in the 2000s in coincidence with a wetter period can thus be explained by the significant younger age and smaller size of these trees compared to those growing in the old-growth forests. The age factor is often overlooked in ecology and evolutionary biology studies.

Negative GDC values are a common functional feature of canopy trees indicating a relative growth rate that decreases as the diameter or age increases (inverse asymmetric competition) (Binkley et al., 2006; Pommerening et al., 2016) and suggesting a decreasing resource use efficiency among larger/older trees in all the studied beech forests (Fernández-Tschieder and Binkley, 2018).

The negative GDC values presented in this study, agree with their high level of naturalness as reported in a few old-growth studies (Binkley et al., 2006; Pommerening et al., 2016). However, the GDC values of the primary beech forest of the high mountains do not appear distinctive given the high naturalness levels. Negative values of GDC characterize

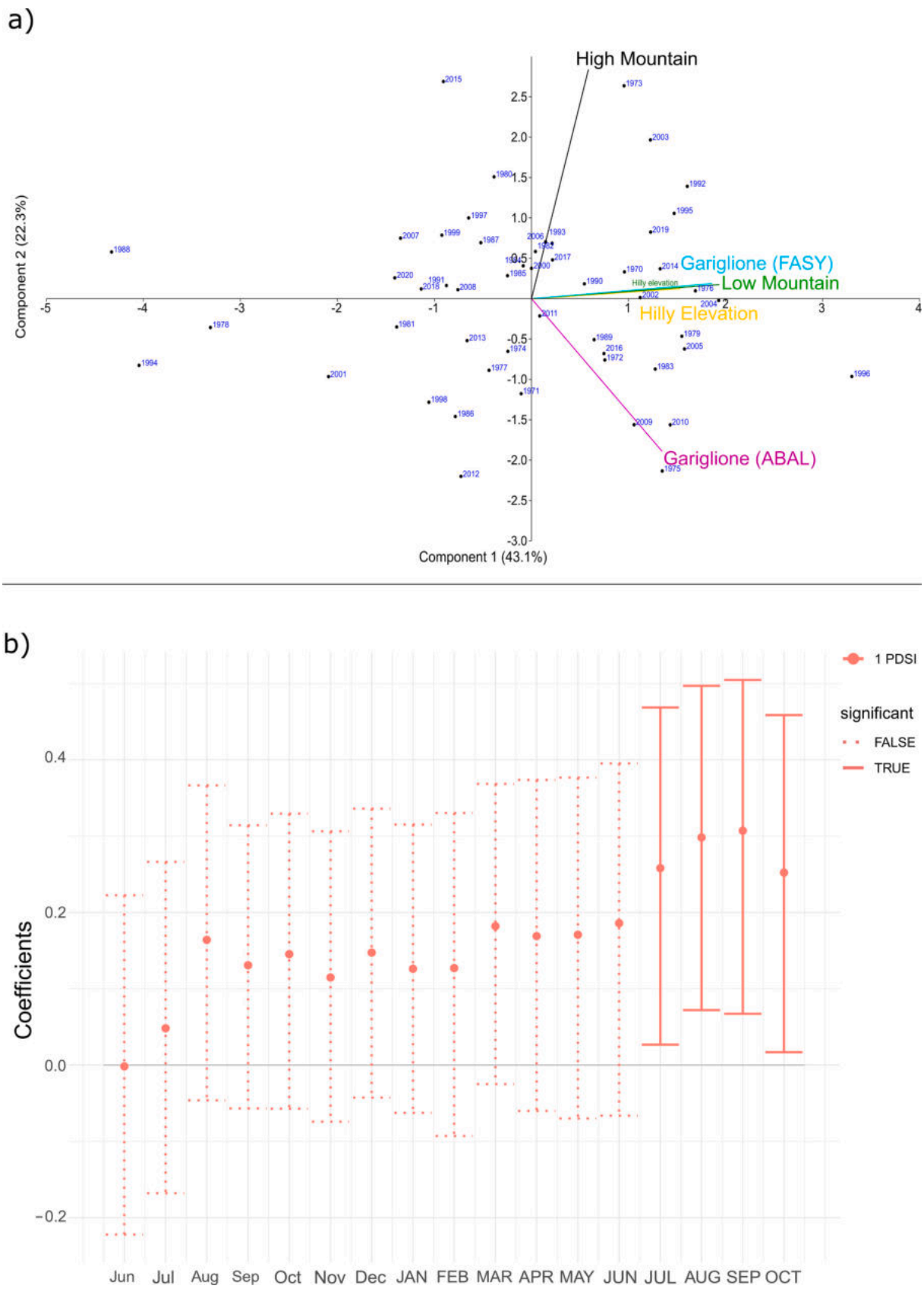


Fig. 5. Multivariate analysis and growth-climate correlations. a) PCA between prewithened yearly BAI site chronologies over the 1950–2020 period. b) Bootstrapped correlation functions calculated for the period 1950–2020 between PC1 scores and the scPDSI index (Harris et al., 2020) spanning a 17-month window, from June of the previous year to October of the current growth year (solid lines indicate $p < 0.05$).

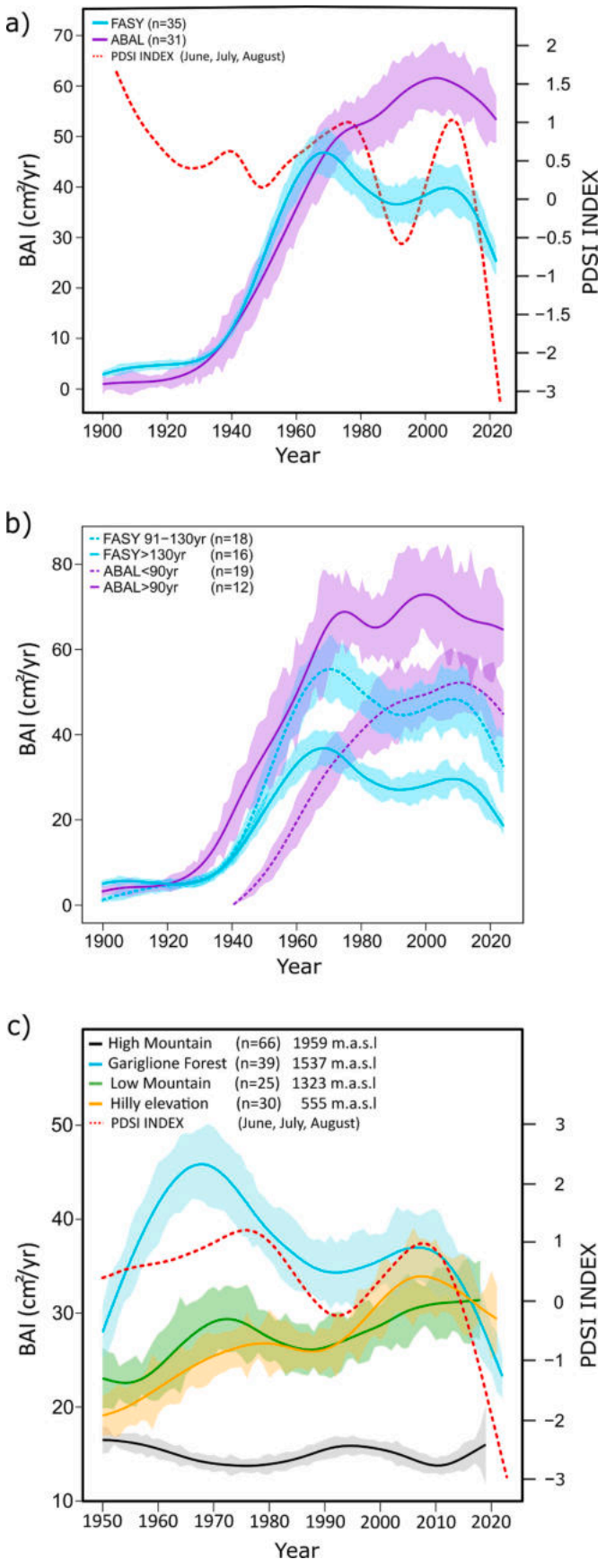


Fig. 6. Basal Area Increment (BAI) chronologies smoothed by 30 yr cubic spline filters. a) BAI chronologies of *Fagus sylvatica* (FASY) and *Abies alba* (ABAL) in the Gariglione Forest compared to site-specific summer scPDSI Index (red dashed line) smoothed by 30 yr cubic spline filters. b) BAI chronologies of FASY and ABAL in the Gariglione Forest grouped into age groups. c) Multi-site comparison of FASY BAI chronologies. The 30 yr smooth cubic spline of regional summer scPDSI index (June–August) is included (red dashed line).

also the distributed character of growth among trees within managed uneven-aged stands (Jull and Griesbauer, 2023; Lemire et al., 2020) for which further investigations in relation to stand dynamics, bioclimate and soil type are necessary to understand the possibility of using GDC as a functional indicator of stand naturalness.

4.2.2. Impact of warming climate on beech canopy along an elevational gradient

Our results demonstrate that in a rewilding stand, canopy tree growth may change because of structural dynamics and climatic variations.

After a large-scale disturbance, stand growth is expected to reach a plateau at a relatively young age and then decline due to changes in stand structure and the resource-use efficiencies of individual trees (Binkley, 2023). In Gariglione the return to a lower level of growth is coherent with the mountain bioclimatic position of the forest, which is located between the high mountain and the hilly elevation belts (Piovesan et al., 2008). The decline of BAI in beech is synchronized with an increasing drought severity since 1970 (Bennett et al., 2015; Bose et al., 2022; Pretzsch et al., 2018). As expected under Mediterranean climate, correlation functions revealed that growth is limited by summer drought stress (e.g., Peñuelas et al., 2008; Piovesan et al., 2008; Walder et al., 2021) with a non-linear bioclimatic pattern centered around the mountain belt (Piovesan et al., 2005). However, the high synchronization of high-frequency BAI curves between Gariglione and the low mountain site (Fig. S2 in Supplementary Material 2) is not reflected in the long-term BAI trends, indicating complex interactions of the environmental and land use factors in determining drought-driven growth trends (Bowman et al., 2013).

In the last 50 years, the growth trajectories of the beech canopy in the Gariglione were characterized by an overall negative directional BAI trend interrupted by a period of relevant growth increase during favorable climatic conditions (wetter phase) suggesting a plastic growth behavior of the rewilding tall secondary old-growth forests. Indeed, Gariglione has seen a marked drop in growth in consequence of natural stand dynamics conditioned by climate warming/drying (Ionita and Nagavciuc, 2021). On the contrary, the primary stand in the high mountain elevation belt showed a remarkably stable-low oscillating growth trend. This relatively stable tree growth may be due to the primary status of the forest (Chazdon et al., 2016; Piovesan et al., 2019; Ralhan et al., 2023), but also to its bioclimatic position at the altitudinal limit of the beech distribution, where growth rates are very low and drought is less limiting (Piovesan et al., 2019). At the opposite end of the elevational gradient, the lack of decreasing long-term BAI trends in trees growing in the low mountain and the hilly elevation belts is likely due to the complex forested terrain and different ecosystem legacies which reflect a less perturbed management history. At such low elevation sites at the range edge distribution, beech can grow vigorously because these stands are probably located in a climatic refugia that buffers the negative impact of increasing drought in the Mediterranean region (Doxa et al., 2022).

Surprisingly, the falling trend of BAI reported for most beech forests in Europe (Martinez del Castillo et al., 2022) and in other Mediterranean old-growth forests (Piovesan et al., 2008) is not present either in the high mountain belt (which is a primary old-growth forest) or in the low mountain (secondary old-growth) and hilly belt (mature stands). Water stress is reasonably less relevant in the high mountain belt (Piovesan et al., 2022), while the lack of negative BAI trends in the low mountain

Table 3
Mann-Kendall trend test computed for the 1970–2020 period. The values of the Test Statistic (S) are reported with the *Z*-score values in parentheses. Bold values identify significant trends.

	BAI	GDC_DBH	GDC_AGE	scPDSI
High mountain (beech)	123 (1.0205)	**450** (3.9907)	**378** (3.3508)	**−265** (−2.1443)
Gariglione (fir)	71 (0.5685)	**475** (3.8499)	**599** (4.8571)	−139 (−1.1209)
Gariglione (beech)	**−421** (−3.4113)	−19 (−0.1462)	**615** (4.9870)	−139 (−1.1209)
Low mountain (beech)	86 (0.7326)	171 (1.4220)	72 (0.61201)	**−278** (−2.2499)
Hilly elevation (beech)	**379** (0.3702)	**627** (5.0845)	15 (0.11371)	**−277** (−2.2417)

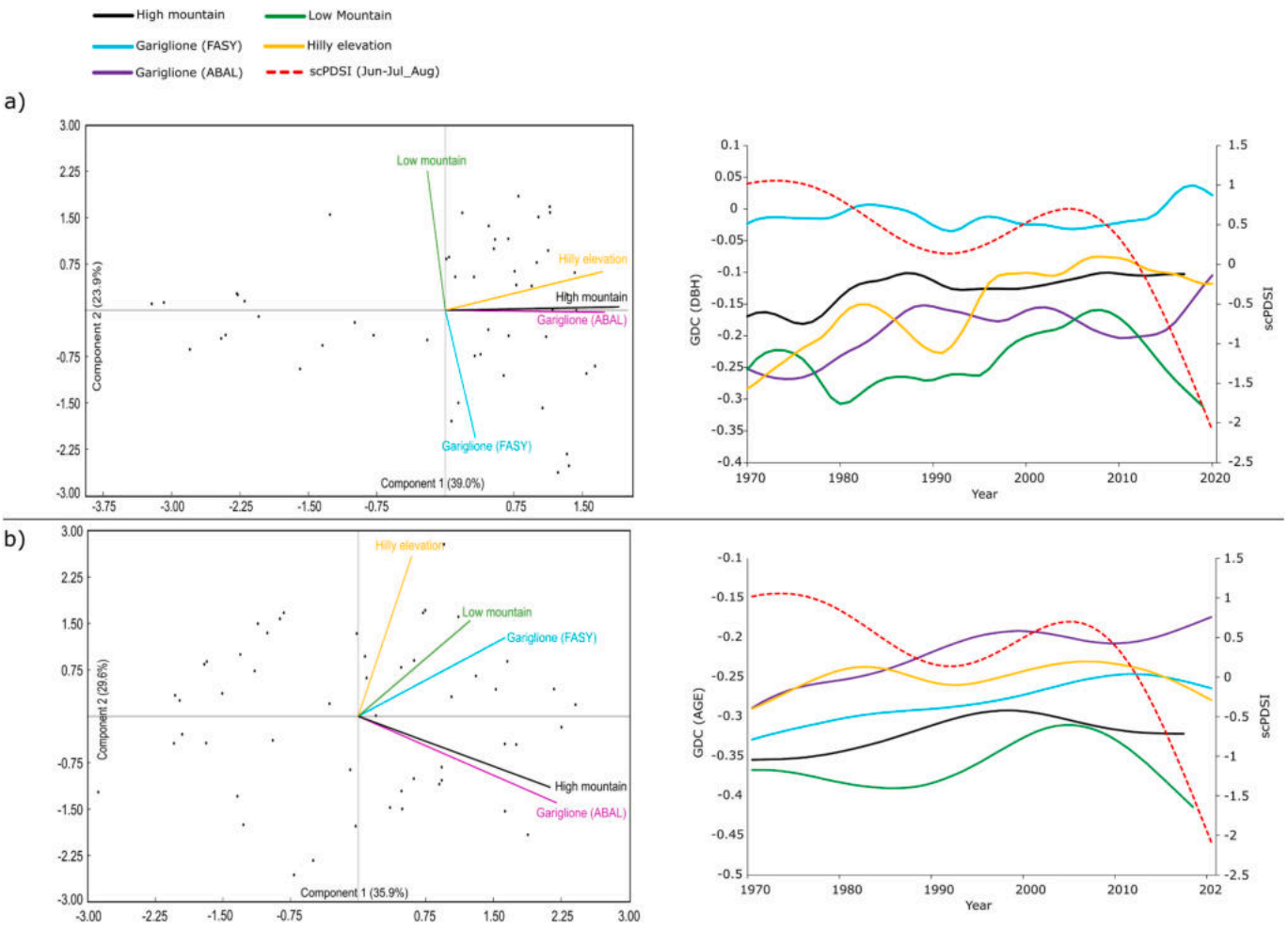


Fig. 7. Yearly growth Dominance Coefficient (GDC) time series calculated as function of tree diameter (a) and age (b). Left plots: PCA between site GDC time series over the 1970–2020 period. Right plots: site GDC series smoothed by 30 yr cubic spline filters.

and hilly belt is remarkable and stresses the need for greater sampling effort to understand the growth trajectories of this beech forest located at the range edge in the transition zone to the evergreen holly oak forest.

Another unexpected result was the positive or stable GDC trends in our sites despite an increasing long-term drought trend since the 1970s (Table 3). Drier climate conditions should impact large trees more than small trees (Vinod et al., 2023) leading to a more intense inverse asymmetric competition (negative GDC values; Au et al., 2022; Bose et al., 2022; Pretzsch et al., 2018). In this study the largest trees along the elevational and naturalness beech forest gradient do not signal a greater impact of drought in respect to smaller trees of the canopy confirming the drought resistance of old-growth forest (Colangelo et al., 2021; Wolf et al., 2023). The beech forest located at the lower elevational and latitudinal limit showed a remarkable increasing GDC trend in function of diameter, similar to fir in the Gariglione Forest where in recent years beech highlighted a tendency towards asymmetric growth dominance.

These results are very surprising because the growth history of large trees in the canopy is characterized by a vigorous growth spurt in consequence of heavy cuts, with BAI values among the highest reported for temperate deciduous forests (Anderson-Teixeira et al., 2022; Verschuren et al., 2023; Vospernik, 2021). Because of the ecological memory, this growth legacy should result in a reduction in their present resistance to drought stress with a simultaneous increase in mortality (Bennett et al., 2015; Socha et al., 2023). Instead, in rewilding Mediterranean mountain forests along a wide elevational gradient, even large and older trees are currently resisting climate warming (Au et al., 2022; Colangelo et al., 2021). Future in-depth studies are needed to understand age-dependent mechanisms underlying functional plasticity in a changing forest environment (e.g., epigenetic acclimation to a warmer climate) with particular reference to the ecological role of the oldest trees, for example in transgenerational fitness (adaptive vs maladaptive

transgenerational effects; Cannon et al., 2022). In conclusion, this study underscores the need of further research on stand dynamics in relation to the evolutionary ecology, regional environment, acclimation, height-driven constraints and compensations on tree vulnerability to drought (Fernández-de-Uña et al., 2023).

4.2.3. Species

In the last decades, fir trees had a higher growth performance than beech confirming the results of previous studies (e.g., Pretzsch et al., 2020) even though the Gariglione Forest lies in a Mediterranean mountain environmental context at the southernmost edge of the species range. This study also confirms the role of geographical adaptation in functional growth dynamics in southern peripheral populations (Dorado-Liñán et al., 2019) emphasizing a key role of refuge areas in conservation biology.

In the absence of adverse factors such as pollution, fires and intense grazing by wild ungulates and livestock (Bosela et al., 2018), silver fir showed the greatest long-term incremental response to wood harvesting (Martin-Benito et al., 2022). Such marked difference in respect to beech growth characterize the rewilding stage across warming climate. Life history traits – such as the less dense wood and evergreen phenology – and the genetic structure of the Calabrian refugia (Piotti et al., 2017; subsp. *apennina*, Palli et al., 2022) can explain such an extraordinary functional plasticity of fir in response to major disturbances and climate change. Moreover, in fir, the lower values of GDC indicate a greater shade tolerance compared to beech (Pommerening et al., 2016). Fir ability to survive under shaded conditions (Čater and Levanič, 2019) is also suggested by live branches distributed much lower in the canopy than beech and is in accordance with the lower dependence of fir regeneration on stand density (Trifković et al., 2023).

Interestingly, in Gariglione the oldest fir cohorts recovered BAI in the 1990s (see Bosela et al., 2018) while in beech, growth resumed a decade later, in phase with scPDSI variations, revealing a functional asynchrony of beech and fir growth that conferred community stability (Zhou et al., 2023). Such a relevant asynchrony between the medium-term growth trends of the two species may be a consequence of the different phenology (deciduous vs evergreen), reproduction ecology (mast seeding is synchronized by summer weather in beech, Piovesan and Adams, 2001) and ecophysiology (anisohydric beech compared with isohydric spruce, Ulrich and Grossiord, 2023). For example, fir can take advantage of the warmer winter and spring season in the Apennines (Colangelo et al., 2021; Condés et al., 2022; Rita et al., 2014). However, the very negative PDSI characterizing recent years may explain the growth reduction in fir in agreement with Europe-wide studies (Bosela et al., 2018; Büntgen et al., 2014).

The key role of silver fir in the resilient response to disturbances should be considered in nature conservation and ecological restoration programs of the mountain forests in the Mediterranean basin exploring further its function in stabilization in response to drought (Gottschall et al., 2023).

4.3. Limitations and caveats

The main limitations and caveats of the study are:

Bias in BAI as in indicator of wood production in tall forest. Declining BAI trend in the canopy of Gariglione forest may also be the consequence of its peculiar canopy structure composed of very tall trees, exposing them to extreme drought (Socha et al., 2023; Xu et al., 2022). Furthermore, the changing competition environment can also affect diameter increments along the stems (Donfack et al., 2023; Kramer et al., 2020) modifying the trunk form towards a cylindrical shape. For these reasons, and not only, a certain diameter should produce less BAI as tree canopy expands decade after decade. However, despite these limitations, BAI remain a good proxy of the tree volume growth with a special focus on climatic trends (Bowman et al., 2013; Latte et al., 2016).

Trade-off in growth-reproduction. BAI variations in time could be also a consequence of changing reproductive output in consequence of the ontogenetic cycle or reproductive ecology affected by climate variations (Selås et al., 2002).

Primary forest. The lack of primary forests in the mountain and hilly belts has not allowed us to verify the impact of climate change on an intact ecosystem; for the same reason it was not possible to verify whether there is an ongoing decrease in the differences between the growth patterns among elevation zones as recently found in the same region for primeval pine trees (Piovesan et al., 2023). A recent study showed that growth patterns in beech among elevation zones are less different since 1950 pointing to a key role of stand admixture in stimulating beech growth in the mountain belt (Pretzsch et al., 2021).

Future studies are needed to disentangle mechanisms of tree growth dynamics and turnover in a rewilding old-growth forest ahead of climate changes, with a special focus at the lower limit of distribution at the range edge.

5. Conclusion

Today, 70–90 years after the widespread and intensive forest cutting, the Gariglione Forest has renewed a tall forest structure with secondary old-growth age attributes and functional naturalness (Table 2). In Gariglione, a set of favorable environmental and land-use factors have allowed a prompt restoration of a functional forest ecosystem that in recent decades has entered the secondary old-growth stage. This occurred because of the following factors:

1. *The environment.* The primeval status of the perturbed ecosystem is located in a fertile site that permitted vigorous growth responses - evidenced by the high reconstructed BAI values.
2. *Silvicultural criteria.* The adoption of silvicultural practices has buffered the impacts of the extensive biomass removal on stand recovery. The presence of saplings and scattered remnant mature seed-bearing trees left during cutting permitted a widespread canopy recovery. Fir had a key role in the resilient response both in terms of stand regeneration and canopy growth.
3. *Land management.* After the end of the cutting period (1950s), the forest was managed by the State Forest Service through uneven-aged silviculture up to the beginning of the 1970s, when the forest became a biogenetic reserve - managed mostly as a strict reserve - thus laying the foundations for the rewilding towards old-growth status.

The Gariglione forest is an effective example of restoration of forest integrity in the Mediterranean mountains achieving a win-win integration of environmental and social systems. Thus, the Gariglione Forest demonstrates the effectiveness of active management followed by passive rewilding for restoring habitat integrity of degraded forest under the international environmental initiatives, a living lab for studying the complex dynamics that have led to a tall forest of high naturalness and carbon stocks. The results of this study can be used to plan and implement appropriate adaptation and mitigation strategies for the long-term recovery of nature in the Mediterranean mountains under the umbrella of the EU Nature Restoration Law. Although subsequent studies are necessary to disentangle the impact of global warming on productivity in rewilding forests, the Gariglione Forest demonstrate that the restoration of complex tall forest may require less than a century in Mediterranean mountains. Today more than ever it is strategic to guarantee strict protection to the secondary old-growth forest of Gariglione; we thus propose its inclusion in the World Heritage serial site “Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe” for providing a unique example in a Mediterranean mountain environment of the exceptional resilience of tall old-growth forests to human and global change disturbances despite being located at the extreme southern edge of the distribution of beech, fir and other temperate tree species.

Overall, natural forests where large, ancient trees integrate with new

generations have proven very resistant to global changes. A complex canopy layer dominated by late-successional species, the widespread presence of both small, medium and large trees, the ecological role of old trees, and the functional asynchrony of beech and fir growth are conferring community stability. Monitoring the effective conservation of old-growth forest areas and their restoration in rewilding landscapes should be considered key pillars in environmental policies towards sustainability.

CRediT authorship contribution statement

Michele Baliva: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Investigation, Formal analysis, Data curation. **Jordan Palli:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Investigation, Formal analysis, Data curation. **Federica Perri:** Writing – review & editing, Investigation, Data curation. **Francesco Iovino:** Writing – review & editing, Writing – original draft, Validation, Project administration, Investigation, Funding acquisition, Conceptualization. **Giuseppe Luzzi:** Writing – review & editing, Project administration, Investigation. **Gianluca Piovesan:** Writing – review & editing, Writing – original draft, Validation, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: All authors reports financial support was provided by Sila National Park Agency. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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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.2024.175806.

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