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## **Interannual radial growth sensitivity to climatic variations and extreme events in mixed and pure stands of silver fir and beech in the Italian Peninsula**

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### **Abstract**

Climate change is increasingly favoring the occurrence of extreme weather events, affecting species distribution and tree growth. It has been proposed that mixed forests are more resistant to extreme drought and heat than corresponding monocultures. For this reason, we sampled tree cores in nine stands along a latitudinal gradient of the Italian Peninsula (Trentino - Alto Adige, Molise, Calabria), considering mixed forests and corresponding monocultures of silver fir and beech. The objectives of the study were to identify differences between mixed and pure stands of beech and silver fir to climatic patterns and extreme events. Pointer years, and correlation and response functions, were analysed to evaluate the climate-growth relationships between mixed and pure stands. Results showed a clinal variation in radial growth traits of beech and silver fir, in both mixture and monoculture. In particular, beech and silver fir in mixture were both positively affected by high summer water availability. In Trentino - Alto Adige and Molise, positive correlations were observed with winter temperatures, for silver fir; positive (Trentino - Alto Adige) and negative (Molise) correlations were detected with spring temperatures, for beech. Pointer years showed a clear grouping of climate variables in Trentino - Alto Adige and Calabria, which influenced both species, in mixture and monoculture. On the other hand, grouping was relatively vague in Molise, especially for silver fir in pure and mixed stands. Complementarity in resource uptake and use between beech and silver fir was not always advantageous for both species.

## 1. Introduction

Continuous climate change and extreme events have made many forests more vulnerable to drought globally (Allen et al., 2010). The occurrence of such events is altering species distribution and tree growth in many regions of Europe (Way and Oren, 2010), as they threaten structure and function of forest ecosystems (Castagneri et al., 2014). Certain functional traits (Greenwood et al., 2017), local site conditions (Lebourgeois et al., 2013) and particular climate types (Zhang et al., 2017) may determine species-specific growth responses (Gazol et al., 2017a, b) and influence the capacity of trees to resist and recover from drought spells and heat waves. Studies on a global and regional occurrence of extreme events have shown that the decrease in tree growth is linked to drought (Anderegg et al., 2015) and that these effects can last for several years (Camarero et al., 2015).

Mediterranean forests are particularly vulnerable to climate change (Scarascia-Mugnozza et al., 2000). Indeed, an increase in the frequency and severity of drought events, as predicted in the coming decades in the Mediterranean region (IPCC, 2013; IPCC, 2017), with an increase of 4-5 ° C temperatures in some Mediterranean regions (Hanewinkel et al., 2012), has dramatic implications for the future of Mediterranean forest ecosystems. Indeed, these drying trends have been more marked from winter to summer, potentially encompassing the whole growing season of major forest species, reducing the productivity of Mediterranean forests (Sitch et al., 2008). Species-specific responses of tree species to warming trends can be investigated in monoculture and mixture in order to envisage warning signals of mortality risk (Cailleret et al., 2016, 2017; Tognetti et al., 2019), as well as long-term variation in forest composition and dynamics in drought-prone regions (Gazol et al., 2018).

Many studies have shown that mixed forests have higher degree of resistance and resilience to disturbances (del Río et al., 2014; Merlin et al., 2015; Forrester et al., 2016) and provide also a wider range of ecosystem services (Gamfeld et al., 2013; Lu et al., 2016; Mina et al., 2018). Forest management has been proposed as an effective solution to cope with significant negative impacts of changes in disturbance regime associated with climate change, especially if tailored to reduce competition for resources amongst trees within a stand (Lindner et al., 2010; Zalloni et al., 2019). Thus, the release of competition for water after drought events can be compensated by improved growth performance of survived trees (Madrigal-González et al., 2017). Nevertheless, drought-induced tree decline may have diffused and erratic patterns, triggering forest disequilibrium and vegetation shifts (Anderegg et al., 2016). In this sense, annual growth rings document the dynamics of forests facing drought-driven productivity decline and the often nonlinear transitions of tree functional conditions, discerning interannual variability (Trotsiuk et al., 2018) and inferring management options (Cobb et al., 2017).

Allometric variation and hydraulic redistribution, together with species-specific shade tolerance, plant phenology, crown structure, and root depth (Lebourgeois et al., 2013; Conte et al., 2018), would imply more efficient uptake and use of resources within the stand (Pretzsch et al., 2015), involving positive responses to climatic variations, as well as higher productivity of mixed-species forests in comparison with pure stands (Merlin et al., 2015; Bosela et al., 2015; Forrester et al., 2016; Mina et al., 2018). Nevertheless, the effect of climate on the relationships between tree species diversity and forest stand productivity is still under debate (Jactel et al., 2018).

In this project we analyzed silver fir (*Abies alba* Mill.) and beech (*Fagus sylvatica* L.), two important late successional forest species, both sensitive to summer drought and spring frost (Carrer et al., 2010; Cailleret and Davi, 2011; Mérian and Lebourgeois, 2011; Lebourgeois et al., 2013), the first relying on sensitive stomatal closure in relation to drought (i.e., isohydric; Burkhardt et al., 2018) and the second showing a low capacity to maintain leaf water potential during drought events (i.e., anisohydric; Geßler et al., 2007). Admixing deep-rooting silver fir to beech was found to improve soil greenhouse gas balance (Rehshuh et al., 2019) and benefit soil water hydraulic redistribution under drought conditions (Magh et al., 2018; Pretzsch et al., 2013), while climate-growth relationships in mixed and pure stands of silver fir and beech can be differentially altered by changes in climate. For this reason, we sampled tree cores in nine stands (for a total of 525 tree) along a

latitudinal gradient of the Italian Peninsula (Trentino - Alto Adige, Molise, Calabria) considering both pure and mixed forests of silver fir and beech. Extending southeast from the Alps into the Mediterranean Sea, the Italian Peninsula has a variety of climatic conditions that may allow testing whether any clinal variation in growth-related features occurs under warming trends and drought gradients in mixed vs. pure stands of beech and silver fir. To understand how growth variations were linked to climate factors, climate-growth relationships were investigated using correlation and response functions. In addition, tree growth responses to extreme climatic conditions events were identified through the analysis of pointer years. We hypothesised that the change of the growth-climate relationship is similar along the latitudinal gradient, and that the mixture effect that maximally affects radial growth of beech and silver fir is stronger at the southern distribution limit of these species.

## 2. Materials and methods

### 2.1 Study area

This study was conducted in three mountains regions (Trentino - Alto Adige, Molise and Calabria) selected along a latitudinal transect in the Italian Peninsula. In particular, the following forest sites were sampled: i) Lavarone and Cembra (Trentino - Alto Adige), ii) “Abeti Soprani” (Molise) and iii) Sila National Park (“Sila Piccola”; Calabria) (Fig. 1).

Three plots were selected in each site: i) a pure plot of beech (Fp), ii) a pure plot of silver fir (Ap) and iii) a mixture of both species (M, with Fm for beech and Am for silver fir). The plots located in the three regions were indicated as: T for Trentino - Alto Adige, M for Molise, and C for Calabria.

Plots were selected based on the minimum number of individuals within each stand ( $\geq 50$  trees of investigated species per plot) and range of elevation (in each region, the difference in altitude between the plots was not greater than 250 m) (Table 1). Plots had an average size of 0.185 ha.

The three sites are uneven aged forest stands. In mixed plots, silver fir is the dominant species and beech is the sub-dominant one (Table 1). Considering the horizontal structure of the mixed plots, trees of the two species are highly mixed and randomly distributed in relation to their neighbours, except in the pure beech site in Calabria, where the horizontal structure consisted in the alternation of areas with different density of canopy trees (INFC 2004). Plots show similar slope, between  $19^\circ$  and  $28^\circ$ , except for ApC ( $37^\circ$ ), but differ for soil type and depth. Plots in Trentino - Alto Adige and Molise have mesic and humid soils (Lithosol and Rendzina), whereas soils of those in Calabria are dry (Distrupt). Soils differ in depth mainly in the pure beech plots, where they are relatively shallow and rocky in comparison with mixed-species and pure silver fir plots.

All sites have been unmanaged since 1979-80, except for the mixed-species plot in Trentino - Alto Adige, where selective logging was carried out in 2001-2002.

Other tree species were present, though with small coverage areas: in Trentino - Alto Adige, *Picea abies* L. and other tree species with an average of 15% and 3%, respectively; in Molise, *Ostrya carpinifolia* Scop. and *Acer pseudoplatanus* L. with an average of 8% for both species; in Calabria, *Acer opalus* Mill., *Tilia cordata* Mill., *Ostrya carpinifolia* Scop. and *Populus* spp. with an average of 12%, 4% and 14%, respectively.

### 2.2 Tree sampling and ring-width chronologies

All samples were collected in the summer 2017. The measurements were performed on all the trees with a diameter  $\geq 7$  cm, following the COST Action CA15226 Climate-Smart Forestry in Mountain Regions protocol. The structural and dendrometric parameters were recorded with Field-Map technology and software (<http://www.fieldmap.cz/>) in Calabria and Molise, and with Laser Technology Criterion 400 in Trentino - Alto Adige. Only dominant-codominant trees were sampled in each plot to avoid that climatic signals in tree rings of subdominant-suppressed trees were confounded by competition-related effects. Two cores per tree were collected at breast height (1.3 m) in opposite directions and perpendicular to the slope in order to avoid compression wood (for silver

fir) and tension wood (for beech). A total of 290 beech and 235 silver fir trees was sampled (Table 1). Cores were glued to grooved wooden supports and sanded with progressively finer grade abrasive paper up to an optimal surface resolution, thus allowing the reading of the annual rings. Ring-width series were measured with a LINTAB measuring table with an accuracy of 0.01 mm, equipped with a Leica MS5 stereoscope. The analysis was performed with the TSAP software package. All tree ring series were cross-dated using COFECHA to assess measurement and dating accuracy. Only cross-dated cores with a significant ( $p \leq 0.05$ ) “Gleichläufigkeit” were used for further analyses. In order to remove non-climatic trends due to tree age, size and stand dynamics, each single series was standardized using ARSTAN program with a cubic spline curve function with a 50% frequency cut-off. For all sites, a 32-years cubic smoothing spline was applied, except for ApC; in the latter case, a 20-years cubic smoothing spline was used, due to the younger age of trees. From the standardized average chronologies, the following descriptive statistics were used to compare chronologies: the mean chronology, being the average number of years for two cores per tree; the mean sensitivity (MS), which is the average difference between successive ring width values, ranging from 0-2 with 0 representing no difference between successive ring widths and 2 representing every second ring missing (Fritts, 1976); the first order autocorrelation (AC1) to detect the persistence retained before and after the standardization; the expressed population signal (EPS), indicating the reliability of a chronology by comparing the chronology with the theoretical chronology based on an infinite number of trees (ranging from 0 to 1, from no agreement to perfect agreement with the population chronology), with a threshold of 0.85 (Wigley et al., 1984); the mean RBAR, which is the average correlation coefficient calculated for a common time interval between the single series in a chronology (Table 2).

### 2.3 Meteorological data

The climatic data were obtained for each site by means of an interpolation function derived both from a spatial downscaling of European climate data and from the nearest meteorological stations. Grid was a reduced version of E-OBS in combination with WorldClim climatic surfaces; it was used to obtain a climate data set with a resolution of  $0.0083^\circ$  (about  $1 \times 1$  km) (Conte et al., 2018). In particular, the monthly minimum and maximum temperatures and total monthly precipitation, from 1951 to 2012, were considered. The grid was also compared with climate data of local meteorological stations of Faedo and Vezza (Trentino - Alto Adige), Capracotta (Molise), and Taverna (Calabria), where information related only to the last years was recorded. Furthermore, two interpolation functions were used to obtain the most representative chronologies of climatic conditions. The first was obtained through the use of R package, between the grid data ( $1 \times 1$  km) and the coordinates of each plot. This interpolation allowed to extrapolate both data of monthly maximum and minimum temperatures ( $T_{max}$ ,  $T_{min}$ ) and those of total monthly precipitation (P), from 1951 to 2012. The second interpolation was performed through the use of the software “Statistica”, between the grid data and the data of the nearest meteorological stations, in order to obtain climate data in recent years, using a general linear model. To obtain the linear regression equation, meteorological stations presenting data with a fairly long time period, were selected. This allowed to calculate, for each plot, the correlation coefficient  $R^2$ , [Trentino - Alto Adige ( $R^2 = 0.98$ ,  $R^2 = 0.97$ ,  $R^2 = 0.63$ , respectively, for  $T_{max}$ ,  $T_{min}$ , and P), Molise ( $R^2 = 0.94$ ,  $R^2 = 0.95$ ,  $R^2 = 0.57$ , respectively, for  $T_{max}$ ,  $T_{min}$ , and P), and Calabria ( $R^2 = 0.96$ ,  $R^2 = 0.97$ ,  $R^2 = 0.60$ , respectively, for  $T_{max}$ ,  $T_{min}$ , and P)], in order to evaluate the homogeneity of grid and station data. The exact equation was then used for the extrapolation of the climatic data (T and P) of each month in the last 5 years.

### 2.4 Identification of pointer years

Pointer years indicate those years in which conspicuously wide or narrow tree rings are created in response to extreme environmental conditions and/or climatic events (Schweingruber et al., 1990). To determine the pointer years, we used the method proposed by Becker (1989) and used by

Lebourgeois et al. (2010) and Lebourgeois et al. (2013). The residual series were used to calculate the radial growth variation (RGV%), through the following equation:

$$RGV\% = 100 \times \left( \frac{RW_n - RW_{n-1}}{RW_{n-1}} \right)$$

where  $RW_n$  is the ring width of the year  $n$ , and  $RW_{n-1}$  the ring width of the previous year.

RGV% indicates the extension of the ring of the current year compared to the previous one, with positive value, if the ring of the current year is wider, or with a negative value, if it is narrower.

A given year was considered as pointer year when the radial growth variation respect to previous year was at least 15%, and at least 80% of the cross-dated trees showed the same behaviour.

## 2.5 Statistical analysis

The climate-growth relationships between residual chronologies, for the period 1951-2016, were evaluated with a correlation function analysis calculated using maximum and minimum temperatures and monthly precipitation from April of the previous year to September of the current year, using the library *treeclim* (Zang and Biondi, 2015) of the R software.

Temporal changes in climate-growth relationships were analysed by calculating correlation functions from 1952 to 2016 in moving time windows of 20 years, in consecutive shifts of one year.

To detect the responses of mixed and pure stands to extreme climatic events, principal component analysis (PCA) was performed on pointer years. To construct the matrix, all the pointer years of the period 2016-1951 and 39 climatic variables (monthly summer and winter precipitation, and monthly minimum and maximum temperatures of the current and the previous year referred to pointer years) were used. PCA was calculated from variance matrix with descriptors of the same order of magnitude. PCA analyses were performed using the library *factoextra* (Kassambara and Mundt, 2017) of the R software.

## 3. Results

### 3.1 Tree-ring width chronologies

Table 2 reports the descriptive statistics of the 12 tree-ring chronologies. Tree-ring width ranged from 0.03 to 9.97 mm and had a mean time span that varied significantly among the investigated plots. Trees in Calabria were generally younger than those of the other populations [FpC ( $109 \pm 13.95$ ), AmC ( $108 \pm 15.47$ ) and ApC ( $82 \pm 7.88$ )]; ApT ( $208 \pm 35$ ) in Trentino - Alto Adige, the oldest population occurred.

Mean sensitivity (MS) ranged from 0.101 to 0.199, showing that beech, especially in pure plots, scored higher values [FpT (0.199), FpM (0.185), FpC (0.159)] than silver fir. The first order of autocorrelation (AC1), on the other hand, showed high values especially in beech in mixed plots (from 0.869 to 0.946). Ranges of RBAR (0.228-0.338) and EPS (0.92-0.97) indicated a likely common tree growth response to climatic variability and an excellent common variability in all the tree ring series.

### 3.2 Long-term climate influence on radial growth

Table 3 shows the results of the correlation and response functions in the three investigated sites.

$T_{max}$  of the winter months showed positive correlations on the radial growth of the silver fir in all the sites and a positive response, particularly in Trentino - Alto Adige.

Positive correlations and responses were found between summer precipitation of the previous year and radial growth of the mixed silver fir, in Trentino - Alto Adige; winter precipitation showed a negative correlation with radial growth of silver fir, in Molise. Radial growth of beech, on the other hand, was negatively influenced by  $T_{max}$  in summer months (July-August) of the previous year, in Trentino - Alto Adige and positively in FmM. A negative correlation and response of  $T_{max}$  in last

spring in the southern sites (FmM and FmC), while positive correlation in current spring in FmT was observed. Summer precipitation of the previous year had a positive influence on radial growth of FpT and FmT, while a negative impact was observed for FmM. In Molise, as for silver fir, also radial growth of beech was negatively correlated with the amount of winter precipitation.

### 3.3 Temporal variability in climate-growth relationships

Correlations between climatic variables (P and T) and radial growth of the investigated trees, during the period 1952-2016, are reported in Figure 2. Results confirmed the importance of climatic conditions in determining radial growth patterns (e.g., August precipitation in Trentino - Alto Adige) (Table 3). In addition, the graph highlighted a significant shift and the period in which these variables influenced the radial growth of the two species.

More specifically, in the first period of growth (1952-1975), in Trentino - Alto Adige, summer rainfall (positive) and temperature (negative) of the previous year had a major influence on the radial growth of silver fir; beech was mainly positively influenced by summer temperature of the current year. These correlations disappeared in the last decades. In Molise, radial growth of silver fir (but in some cases also of beech) was influenced negatively by winter precipitation of the current years in the first decades; whereas, in the second period (1976-2016), rainfall in summer of the previous year (positively) and summer  $T_{max}$  (negatively) of the current year were the two most important climatic factors influencing tree growth. In Calabria, on the other hand, silver fir showed negative correlation with winter  $T_{max}$ , except in February and March, and with  $T_{max}$  of the current summer; beech was influenced by summer precipitation of the current year (positively) and by winter temperature (negatively) in the first decades. In the second period, both species, especially in mixed stands, showed positive correlations with precipitation of last spring and current summer.

### 3.4 Pointer years

Residual tree ring chronologies showed an average of 10 pointer years (from 5 to 15 among the 9 plots) with positive pointer years more frequent than negative ones. The number of pointer years differed between mixed and pure plots of the two species. In detail, beech showed more numerous of pointer years in pure plots than in corresponding mixed plots with silver fir. Silver fir, instead, had less pointer years in pure plots. Beech showed high radial growth variation (RGV%), mainly in the pure plots of Trentino and Molise, and in the mixed stand of Calabria, compared to silver fir (Table 4 and Table S1). PCA (Fig. 3 and 4) performed on pointer years explained 52.2% of the variance expressed by the two variables highlighting the most explanatory variables. The first PCA axis explained the greatest variance (42.9%), discriminating temperatures (positive coordinates) from precipitation (negative coordinates). Summer precipitation in Trentino, and summer and winter temperatures in Calabria, especially of the previous year, had a positive influence (greater number of positive pointer years) on the radial growth of both species in mixed and pure plots (Fig. 3). In Molise, on the other hand, several climate variables influenced the response of the species. In detail, we noticed that both species in pure plots and beech in the mixed plot showed a positive response to summer precipitation of the previous year, while silver fir in the mixed plot showed a negative (greater number of negative pointer years) to current year temperatures (Fig. 4).

## 4 Discussion

The correlation and response functions, and the analysis of pointer years, showed different responses in stem radial growth of beech and silver fir, both at regional and plot levels (mixed vs. pure), to varying climatic conditions and extreme events. Differences in sensitivity to climate between mixed and pure stands may depend on species-specific adaptive capacities (Nicoll et al., 2006) and environmental requirements, for which each species responds to climate change independently (Sala et al., 2005). In mixed forests, higher tree species diversity may mitigate climate change impacts on forests (Hooper et al., 2005) and enhance resistance of forest stands to drought events only in certain environments and forest types (Grossiord et al., 2014). Interspecific differences in resource uptake by

roots and crowns may influence the vertical profile of water relations through contrasting root depth (Magh et al., 2018), water use (Forrester et al., 2010), and canopy traits (Pretzsch, 2014). Several studies indicated that the associations of different tree species living together in a defined habitat show some degree of interdependence and positive responses, in terms of productivity, even under difficult climatic conditions, probably due to the different water use strategies (e.g., Hisano et al., 2017; Toïgo et al., 2015). In our case, climate-growth relationships (Fig.2) showed that the availability of water from summer had a positive influence on the growth response of silver fir in all mixed stands. The high sensitivity of silver fir to summer drought has been already observed in several dendrochronological studies (e.g. Carrer et al., 2010), probably due to its drought-avoidance strategy and its lower water-use efficiency compared to other species (Guehl 1987, Peguero-Pina et al., 2007). Indeed, Linares (2001) and Sánchez-Salguero et al. (2017) highlighted that Circum-Mediterranean populations of *Abies* spp., currently subjected to warm and dry conditions, constitute an example of endangered forests and ecosystems highly vulnerable to climate warming.

In addition to water availability, the positive correlation of mild winters on tree growth was also observed, mainly in silver fir of mixed plots in Trentino – Alto Adige and Molise, suggesting that winter temperatures represent another important driver for the radial growth of this species in energy-limited environments. Indeed, high winter temperatures were found to play a fundamental and advantageous role in primary growth of silver fir (Pinto et al., 2008), especially for high-altitude populations (Lebourgeois et al., 2010). Our results agree with those found in mountain ranges of France (Lebourgeois et al., 2013) and Iberian Peninsula (Castagneri et al., 2014), where a significant positive response to high winter temperatures was observed for silver fir, mainly in relatively moist conditions. Warmer winter temperatures would probably promote an earlier start of cambial activity (Rossi et al., 2007) extending the vegetative period of silver fir, which might take advantage from increasing winter photosynthesis (Guehl, 1985) decreasing frost-induced embolism (Cruziat et al., 2002).

Yet, the greater frequency of positive pointer years in silver fir of mixed plots was related to the positive effects of water availability, for Trentino – Alto Adige, and mild winters, for Calabria, on the variation of radial growth. In Molise, silver fir in the mixed stand showed a strong marked sensitivity to summer temperatures as well, negatively affecting the radial growth in this species (negative pointer years). A negative effect of summer temperatures of the previous and current years has been generally observed in sites with dry summers (Babst et al., 2013). Cailleret and Davi (2011) found that the radial growth in silver fir was more sensitive to summer drought than in beech (Southwestern Alps), though the latter species was more impacted by extreme events (heat wave in summer 2003, late frost). On the contrary, our study showed that beech in admixture (in Trentino and in Molise) was more sensitive than silver fir to high summer temperatures, especially if these were accompanied by poor water supply. Similar results were found in mixed forests of the Dinaric Alps in Bosnia and Herzegovina (*Fagus-Abies-Picea*) and in Southern Italy (*Fagus-Abies*), where silver fir showed stable stem radial growth (Castagneri et al., 2014) and low sensitivity to summer drought (Rita et al., 2014) compared to beech. The greater sensitivity to the variation in climatic conditions and resource availability of beech than silver fir, in mixed forests, was confirmed also by the high values of MS and autocorrelation of the first order. In mixture, beech can show higher sensitivity than silver fir, probably due to complementary strategies of the two species in water extraction by roots and/or interception by canopies (Paluch and Gruba, 2012; Lebourgeois et al., 2013), and the isohydric behaviour of silver fir vs. the anisohydric behaviour of beech (Hartmann 2011).

Moreover, the low radial growth variation among pointer years indicated a negative correlation of poor soil water availability on beech in the mixed plot with respect to the corresponding pure plot (Table 2). This sensitivity to summer drought might significantly influence the radial growth and competitive capacity of beech (Geßler et al., 2007; Tognetti et al., 2019). Jucker et al. (2016) observed that facilitation processes might replace competition among species under increasing levels of stress, especially when water supply is a limiting factor. Therefore, greater water availability would lead to an increase in competition effects for nutrients and/or light, and consequently to greater

complementarity effects (Jactel et al., 2018). On the other hand, de Andrés et al. (2017, 2018) found that water supply might limit facilitation effects in beech admixed with other species, due to the release from stress.

Spring temperatures positively (Trentino – Alto Adige) and negatively (Molise) correlation the radial growth of beech in mixture. Spring frosts was found to decrease in radial growth (Dittmar et al., 2006), while warmer springs had positive influences on radial growth of this species (Di Filippo et al., 2007). Beech in the mixed plot of Calabria, instead, showed a positive response to winter temperatures, with a greater variability in radial growth than in the corresponding pure plot. A positive response to winter temperatures of the previous year was also observed in beech of Central and Eastern Europe (Dittmar et al., 2003).

## 5 Conclusion

Our analysis highlighted clinal patterns in species-specific responses of beech and silver fir to climatic variations and extreme events. Overall, climate-growth relationships showed that beech and silver fir in mixture were both affected by summer water availability, but with greater sensitivity in beech. Furthermore, in Trentino - Alto Adige and Molise, significant correlations were observed with winter temperatures, for silver fir, and spring temperatures, for beech. Winter temperatures played a major role in determining radial growth of silver fir. Whereas, summer drought predominantly influenced radial growth in beech. However, water availability and air temperature both affected radial growth variation, making it difficult to disentangle uncertainties of climate change patterns. Different patterns in resource uptake and use between co-existing silver fir and beech, showing unlike root systems and canopy traits, was not always advantageous for both species. Pointer years showed a clear latitudinal grouping of beech and silver fir in mixture and monoculture, emphasizing the responsiveness in radial growth of beech in Trentino - Alto Adige and Molise, following the occurrence of extreme events.

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## References

- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger T., Rigling A., Breshears D. D., Hogg E. H. T., Gonzalez P., Fensham R., Zhang Z., Castro J., Demidova N., Lim J. H., Allard G., Running S. W., Semerci A., & Cobb N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and management*, 259(4), 660-684.
- Anderegg, W. R. (2015). Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist*, 205(3), 1008-1014.
- Anderegg, W. R. L., Martinez-Vilalta, J., Cailleret, M., Camarero, J. J., Ewers, B., Galbraith, D., Gessler A., Grote R., Huang C., Levick S., Powell T. L., Rowland L., Sánchez-Salguero R.,

- & Trotsiuk V. (2016). When a tree dies in the forest: scaling climate-driven tree mortality to ecosystem water and carbon fluxes. *Ecosystems* 19, 1133–1147.
- Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer M., Grabner M, Tegel W., Levanic T., Panayotov M., Urbinati C., Bouriaud O., Ciais P., & Frank D. (2013). Site- and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography*, 22(6), 706-717.
- Becker, M. (1989). The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. *Canadian journal of forest research*, 19(9), 1110-1117.
- Bosela M., Tobin B., Šebeň V., Petráš R., & Larocque G.R. (2015). Different mixtures of Norway spruce, silver fir, and European beech modify competitive interactions in central European mature mixed forests. *Canadian Journal of Forest Research*, 45, 1577-1586. doi: 10.1139/cjfr-2015-0219
- Burkhardt J., Zinsmeister D., Grantz D. A., Vidic S., Sutton M. A., Hunsche M., & Pariyar S. (2018) Camouflaged as degraded wax: hygroscopic aerosols contribute to leaf desiccation, tree mortality, and forest decline. *Environmental Research Letters*, 13, 085001. <https://doi.org/10.1088/1748-9326/aad346>
- Cailleret M., & Davi H. (2011). Effects of climate on diameter growth of co-occurring *Fagus sylvatica* and *Abies alba* along an altitudinal gradient. *Trees*, 25, 265-276. doi:10.1007/s00468-010-0503-0
- Cailleret M., Bigler C., Bugmann H., Camarero J.J., Čufar K., Davi H., Mészáros I., Minunno F., Peltoniemi M., Robert E.M.R., Suarez M.L., Tognetti R., Martínez-Vilalta J. (2016) Towards a common methodology for developing logistic tree mortality models based on ring-width data. *Ecological Applications*, 26, 1827-1841.
- Cailleret M., Jansen S., Robert E.M.R., Desoto L., Aakala T., Antos J.A., Beikircher B., Bigler C., Bugmann H., Caccianiga M., Čada V., Camarero J.J., Cherubini P., Cochard H., Coyea M.R., Čufar K., Das A.J., Davi H., Delzon S., Dorman M., Gea-Izquierdo G., Gillner S., Haavik L.J., Hartmann H., Hereş A.-M., Hultine K.R., Janda P., Kane J.M., Kharuk V.I., Kitzberger T., Klein T., Kramer K., Lens F., Levanic T., Linares Calderon J.C., Lloret F., Lobo-Do-Vale R., Lombardi F., López Rodríguez R., Mäkinen H., Mayr S., Mészáros I., Metsaranta J.M., Minunno F., Oberhuber W., Papadopoulos A., Peltoniemi M., Petritan A.M., Rohner B., Sangüesa-Barreda G., Sarris D., Smith J.M., Stan A.B., Sterck F., Stojanović D.B., Suarez M.L., Svoboda M., Tognetti R., Torres-Ruiz J.M., Trotsiuk V., Villalba R., Vodde F., Westwood A.R., Wyckoff P.H., Zafirov N. & Martínez-Vilalta J. (2017) A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology*, 23, 1675-1690.
- Camarero, J. J., Gazol, A., Sangüesa-Barreda, G., Oliva, J., & Vicente-Serrano, S. M. (2015). To die or not to die: early warnings of tree dieback in response to a severe drought. *Journal of Ecology*, 103(1), 44-57.
- Carrer M., Nola P., Motta R., & Urbinati C. (2010). Contrasting tree-ring growth to climate responses of *Abies alba* toward the southern limit of its distribution area. *Oikos*, 119, 1515-1525. doi: 10.1111/j.1600-0706.2010.18293.x
- Castagneri, D., Nola, P., Motta, R., & Carrer, M. (2014). Summer climate variability over the last 250 years differently affected tree species radial growth in a mesic *Fagus–Abies–Picea* old-growth forest. *Forest Ecology and Management*, 320, 21-29.
- Cobb, R. C., Ruthrof, K. X., Breshears, D. D., Lloret, F., Aakala, T., Adams, H. D., Anderegg W. R. L., Ewers B. E., Galiano L., Grünzweig J. M., Hartmann H., Huang C., Klein T., Kunert N., Kitzberger T., Landhäusser S. M., Levick S., Preisler Y., Suarez M. L., Trotsiuk V., & Zepel M. J. B. (2017). Ecosystem dynamics and management after forest die-off: a global synthesis with conceptual state-and-transition models. *Ecosphere*, 8(12).
- Conte E., Lombardi F., Battipaglia G., Palombo C., Altieri S., La Porta N., Marchetti M., & Tognetti R. (2018). Growth dynamics, climate sensitivity and water use efficiency in pure vs. mixed

- pine and beech stands in Trentino (Italy). *Forest Ecology and Management*, 409, 707-718. <https://doi.org/10.1016/j.foreco.2017.12.011>
- Cruiziat, P., Cochard, H., Améglio, T. (2002). Hydraulic architecture of trees: main concepts and results. *Ann. For. Sci.* 59, 723–752.
- del Río, M., Condés, S., & Pretzsch, H. (2014). Analyzing size-symmetric vs. size-asymmetric and intra-vs. inter-specific competition in beech (*Fagus sylvatica* L.) mixed stands. *Forest Ecology and Management*, 325, 90-98.
- Di Filippo, A., Biondi, F., Čufar, K., De Luis, M., Grabner, M., Maugeri, M., Saba E.P., Schirone B., & Piovesan, G. (2007). Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: spatial and altitudinal climatic signals identified through a tree-ring network. *Journal of Biogeography*, 34(11), 1873-1892.
- Dittmar, C., Zech, W., & Elling, W. (2003). Growth variations of common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe—a dendroecological study. *Forest Ecology and Management*, 173(1-3), 63-78.
- Dittmar, C., Fricke, W., & Elling, W. (2006). Impact of late frost events on radial growth of common beech (*Fagus sylvatica* L.) in Southern Germany. *European Journal of Forest Research*, 125(3), 249-259.
- Forrester, D.I., Theiveyanathan, S., Collopy, J.J. & Marcar, N.E. (2010) Enhanced water use efficiency in a mixed *Eucalyptus globulus* and *Acacia mearnsii* plantation. *Forest Ecology and Management*, 259, 1761–1770.
- Forrester D.I., Bonal D., Dawud S., Gessler A., Granier A., Pollastrini M., & Grossiord C. (2016). Drought responses by individual tree species are not often correlated with tree species diversity in European forests. *Journal of Applied Ecology*, 53, 1725-1734. doi: 10.1111/1365-2664.12745
- Fritts, H.C., 1976. *Tree Rings and Climate*. Academic Press, New York.
- Gamfeldt L., Snäll T., Bagchi R., Jonsson M., Gustafsson L., Kjellander P., Riuz-Jaen M.C., Fröberg M., Stendahl J., Philipson C.D., Mikusiński G., Andersson E., Westerlund B., Andrén H., Moen J., & Bengtsson J. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, 4, 1340. doi: 10.1038/ncomms2328
- Gazol, A., Camarero, J. J., Anderegg, W. R. L., & Vicente-Serrano, S. M. (2017a). Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Global ecology and biogeography*, 26(2), 166-176.
- Gazol, A., Ribas, M., Gutiérrez, E., & Camarero, J. J. (2017b). Aleppo pine forests from across Spain show drought-induced growth decline and partial recovery. *Agricultural and forest meteorology*, 232, 186-194.
- Gazol A, Camarero JJ, Sangüesa-Barreda G and Vicente-Serrano SM (2018) Post-drought Resilience After Forest Die-Off: Shifts in Regeneration, Composition, Growth and Productivity. *Front. Plant Sci.* 9:1546.
- Geßler A., Keitel C., Kreuzwieser J., Matyssek R., Seiler W., & Rennenberg H. (2007). Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees*, 21, 1-11. doi: 10.1007/s00468-006-0107-x
- González de Andrés E., Camarero J.J., Blanco J. A., Imbert J.B., Lo Y.H., Sangüesa-Barreda G., & Castillo F.J. (2018). Tree-to-tree competition in mixed European beech–Scots pine forests has different impacts on growth and water-use efficiency depending on site conditions. *Journal of Ecology*, 106, 59-75. <https://doi.org/10.1111/1365-2745.12813>
- González de Andrés E., Seely B., Blanco J.A., Imbert J.B., Lo Y.H., & Castillo F.J. (2017). Increased complementarity in water-limited environments in Scots pine and European beech mixtures under climate change. *Ecohydrology*, 10, e1810. <https://doi.org/10.1002/eco.1810>
- Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., Fensham, R., Laughlin D.C., Kattge J., Bönisch G., Kraft N.J.B., & Jump A.S. (2017). Tree

mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters*, 20(4), 539-553.

- Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Checko, E., Forrester D. J., Dawud S. M., Finér L., Pollastrini M., Lorenzen M. S., Valladares F., Bonal D., & Gessler A. (2014). Tree diversity does not always improve resistance of forest ecosystems to drought. *Proceedings of the National Academy of Sciences of the United States of America PNAS*, 111(41), 14812-14815.
- Guehl, J.M., 1985. Etude comparée des potentialités hivernales d'assimilation carbonée de trois conifères de la zone tempérée (*Pseudotsuga menziesii* Mirb, *Abies alba* Mill et *Picea excelsa* Link). *Ann. For. Sci.* 42, 23–38.
- Guehl, J. M. 1987. Photosynthesis decrease and stomatal control of gas exchange in *Abies alba* Mill. in response to vapor pressure difference. – *Plant Physiol.* 83: 316–322.
- Hanewinkel, M., Cullmann, D. A., Schelhaas, M. J., Nabuurs, G. J., & Zimmermann, N. E. (2013). Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*, 3(3), 203.
- Hartmann, H. (2011) Will a 385 million year-struggle for light become a struggle for water and for carbon? – How trees may cope with more frequent climate change-type drought events. *Global Change Biology*, 17, 642–655.
- Hisano M., Searle E.B., & Chen H.Y. (2018). Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. *Biological Reviews*, 93, 439-456. doi: 10.1111/brv.12351
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs*, 75(1), 3-35.
- INFC (2004). *Inventario Nazionale delle Foreste e dei Serbatoi Forestali di Carbonio. Istruzioni per il rilievo degli attributi di seconda fase.* Ministero delle Politiche Agricole e Forestali, Ispettorato Generale - Corpo Forestale dello Stato. Istituto Sperimentale per l'Assestamento Forestale e per l'Apicoltura (ISAFa).
- IPCC (2017). "Meeting report of the intergovernmental panel on climate change expert meeting on mitigation, sustainability and climate stabilization scenarios," in IPCC Working Group III Technical Support Unit, eds P.R.J. Shukla, R. Skea, K. van Diemen, Ø. Calvin, F. Christophersen, J. Creutzig, et al. (London: Imperial College London).
- Jactel H., Gritti E.S., Drössler L., Forrester D.I., Mason W.L., Morin X., Pretzsch H., & Castagneyrol B. (2018). Positive biodiversity–productivity relationships in forests: climate matters. *Biology Letters*, 14, 20170747. <http://dx.doi.org/10.1098/rsbl.2017.0747>
- Jucker T., Avăcăriței D., Bărnoaiea I., Duduman G., Bouriaud O., & Coomes D.A. (2016). Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology*, 104, 388-398. doi: 10.1111/1365-2745.12522
- Kassambara, A., & Mundt, F. (2017). *Factoextra: extract and visualize the results of multivariate data analyses.* R package version 1.0. 4. 2017.
- Lebourgeois F., Gomez N., Pinto P., & Mérian P. (2013). Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *Forest Ecology and Management*, 303, 61-71. <http://dx.doi.org/10.1016/j.foreco.2013.04.003>
- Lebourgeois, F., Rathgeber, C. B., & Ulrich, E. (2010). Sensitivity of French temperate coniferous forests to climate variability and extreme events (*Abies alba*, *Picea abies* and *Pinus sylvestris*). *Journal of Vegetation Science*, 21(2), 364-376.
- Linares JC (2011) Biogeography and evolution of *Abies* (Pinaceae) in the Mediterranean Basin. The roles of long-term climatic changes and glacial refugia. *J Biogeogr* 38:619–630.
- Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl R., Delzon S., Corona P., Kolström M., Lexer M. J., & Marchetti M. (2010). Climate change

- impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest ecology and management*, 259(4), 698-709.
- Lu H., Mohren G.M., Ouden J.D., Goudiaby V., & Sterck F.J. (2016). Overyielding of temperate mixed forests occurs in evergreen–deciduous but not in deciduous–deciduous species mixtures over time in the Netherlands. *Forest Ecology and Management*, 376, 321-332. <http://dx.doi.org/10.1016/j.foreco.2016.06.032>
- Madrigal-González, J., Herrero, A., Ruiz-Benito, P., and Zavala, M. A. (2017). Resilience to drought in a dry forest: insights from demographic rates. *For. Ecol. Manag.* 389, 167–175.
- Magh, R.-K.; Grün, M.; Knothe, V.E.; Stubenazy, T.; Tejedor, J.; Dannenmann, M.; Rennenberg, H. (2018). Silver-fir (*Abies alba* MILL.) neighbors improve water relations of European beech (*Fagus sylvatica* L.), but do not affect N nutrition. *Trees* 2018, 32, 337–348.
- Mérian P., & Lebourgeois F. (2011). Size-mediated climate–growth relationships in temperate forests: a multi-species analysis. *Forest Ecology and Management*, 261, 1382-1391. doi: 10.1016/j.foreco.2011.01.019
- Merlin M., Perot T., Perret S., Korboulewsky N., & Vallet P. (2015). Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. *Forest Ecology and Management*, Elsevier, 339, pp.22-33. <10.1016/j.foreco.2014.11.032>. <hal-01140201>.
- Mina M., Huber M. O., Forrester D. I., Thürig E., & Rohner B. (2018). Multiple factors modulate tree growth complementarity in Central European mixed forests. *Journal of Ecology*, 106, 1106-1119. doi: 10.1111/1365-2745.12846
- Nicoll, B. C., Gardiner, B. A., Rayner, B., & Peace, A. J. (2006). Anchorage of coniferous trees in relation to species, soil type, and rooting depth. *Canadian Journal of Forest Research*, 36(7), 1871-1883.
- Paluch, J.G., Gruba, P. (2012). Effect of local species composition on topsoil properties in mixed stands with silver fir (*Abies alba* Mill.). *Forestry* 85, 413–425.
- Peguero-Pina, J. J., Camarero, J. J., Abadía, A., Martín, E., Gonzalez-Cascon, R., Morales, F., & Gil-Pelegrín, E. (2007). Physiological performance of silver-fir (*Abies alba* Mill.) populations under contrasting climates near the south-western distribution limit of the species. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 202(3), 226-236.
- Pinto, P.E., Gegout, J.C., Herve, J.C., Dhote, J.F. (2008). Respective importance of ecological conditions and stand composition on *Abies alba* Mill. dominant height growth. *For. Ecol. Manage.* 255, 619–629.
- Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management*, 327, 251–264.
- Pretzsch, H.; Schütze, G.; Uhl, E. (2013). Resistance of European tree species to drought stress in mixed versus pure forests: Evidence of stress release by inter-specific facilitation: Drought stress release by inter-specific facilitation. *Plant Biol.* 2013, 15, 483–495.
- Pretzsch H., del Río M., Ammer C., Avdagic A., Barbeito I., Bielak K., Brazaitis G., Coll L., Dirnberger G., Drössler L., Fabrika M., Forrester D.I., Godvod K., Heym M., Hurt V., Kurylyak V., Löf M., Lombardi F., Matović B., Mohren F., Motta R., Ouden J.D., M. Pach M., Ponette Q., Schütze G., Schweig J., Skrzyszewski J., Sramek V., Sterba H., Stojanović D., Svoboda M., Vanhellefont M., Verheyen K., Wellhausen K., Zlatanov T., & Bravo-Oviedo A. (2015). Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *European Journal of Forest Research*, 134, 927-947. doi: 10.1007/s10342-015-0900-4
- Rehschuh, S.; Fuchs, M.; Tejedor, J.; Schäfler-Schmid, A.; Magh, R.-K.; Burzlaff, T.; Rennenberg, H.; Dannenmann, M. (2019). Admixing Fir to European Beech Forests Improves the Soil Greenhouse Gas Balance. *Forests* 2019, 10, 213.

- Rita, A., Gentilesca, T., Ripullone, F., Todaro, L., & Borghetti, M. (2014). Differential climate–growth relationships in *Abies alba* Mill. and *Fagus sylvatica* L. in Mediterranean mountain forests. *Dendrochronologia*, 32(3), 220-229.
- Rossi, S., Deslauriers, A., Anfodillo, T., Carraro, V. (2007). Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia* 152, 1–12.
- Sala, O. E., van Vuuren, D., Pereira, H. M., Lodge, D., Alder, J., Cumming, G., Dobson, A., Wolters, V. & Xenopoulos, M. A. (2005). Biodiversity across scenarios. In *Ecosystems and Human Well-Being: Scenarios: Findings of the Scenarios Working Group (Volume 2, eds S. R. Carpenter, P. L. Pingali, E. M. Bennett and M. B. Zurek)*, pp. 375–408. Island Press, Washington.
- Sánchez-Salguero, R., Camarero, J. J., Carrer, M., Gutiérrez, E., Alla, A. Q., Andreu-Hayles, L., Hevia A., Koutavas A., Martínez-Sancho E., Nola P., Papadopoulos A., Pasho E., Toromani E., Carreira J. A., & Linares J. C. (2017). Climate extremes and predicted warming threaten Mediterranean Holocene firs forests refugia. *Proceedings of the National Academy of Sciences*, 114(47), E10142-E10150.
- Scarascia-Mugnozza, G., Oswald, H., Piussi, P., & Radoglou, K. (2000). Forests of the Mediterranean region: gaps in knowledge and research needs. *Forest Ecology and Management*, 132(1), 97-109.
- Schweingruber, F. H., Eckstein, D., Serre-Bachet, F., & Bräker, O. U. (1990). Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia*, 8, 9-38.
- Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C., Woodward, F.I. (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology*, 14(9), 2015-2039.
- Tognetti R., Lasserre B., Di Febbraro M. & Marchetti M. (2019) Modeling regional drought-stress indices for beech forests in Mediterranean mountains based on tree-ring data. *Agricultural and Forest Meteorology*, 265, 110-120.
- Toïgo M., Vallet P., Perot T., Bontemps J.D., Piedallu C., & Courbaud B. (2015). Overyielding in mixed forests decreases with site productivity. *Journal of Ecology*, 103, 502-512. doi: 10.1111/1365-2745.12353
- Trotsiuk, V., Pederson, N., Druckenbrod, D. L., Orwig, D. A., Bishop, D. A., Barker-Plotkin, A., Fraver S., & Martin-Benito, D. (2018). Testing the efficacy of tree-ring methods for detecting past disturbances. *Forest ecology and management*, 425, 59-67.
- Way, D. A., & Oren, R. A. M. (2010). Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiology*, 30(6), 669-688.
- Wigley T.M., Briffa K.R., & Jones P.D. (1984). On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, 23, 201-213.
- Zalloni, E., Battipaglia, G., Cherubini, P., Saurer, M., & De Micco, V. (2019). Wood growth in pure and mixed *Quercus ilex* L. forests: drought influence depends on site conditions. *Frontiers in Plant Science*, 10, 397.
- Zang C., & Biondi F. (2015). treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography*, 38, 431-436. doi: 10.1111/ecog.01335
- Zhang, Q., Shao, M. A., Jia, X., & Wei, X. (2017). Relationship of climatic and forest factors to drought-and heat-induced tree mortality. *PloS one*, 12(1), e0169770

Figure 1. Location of the study sites along the Italian Peninsula.

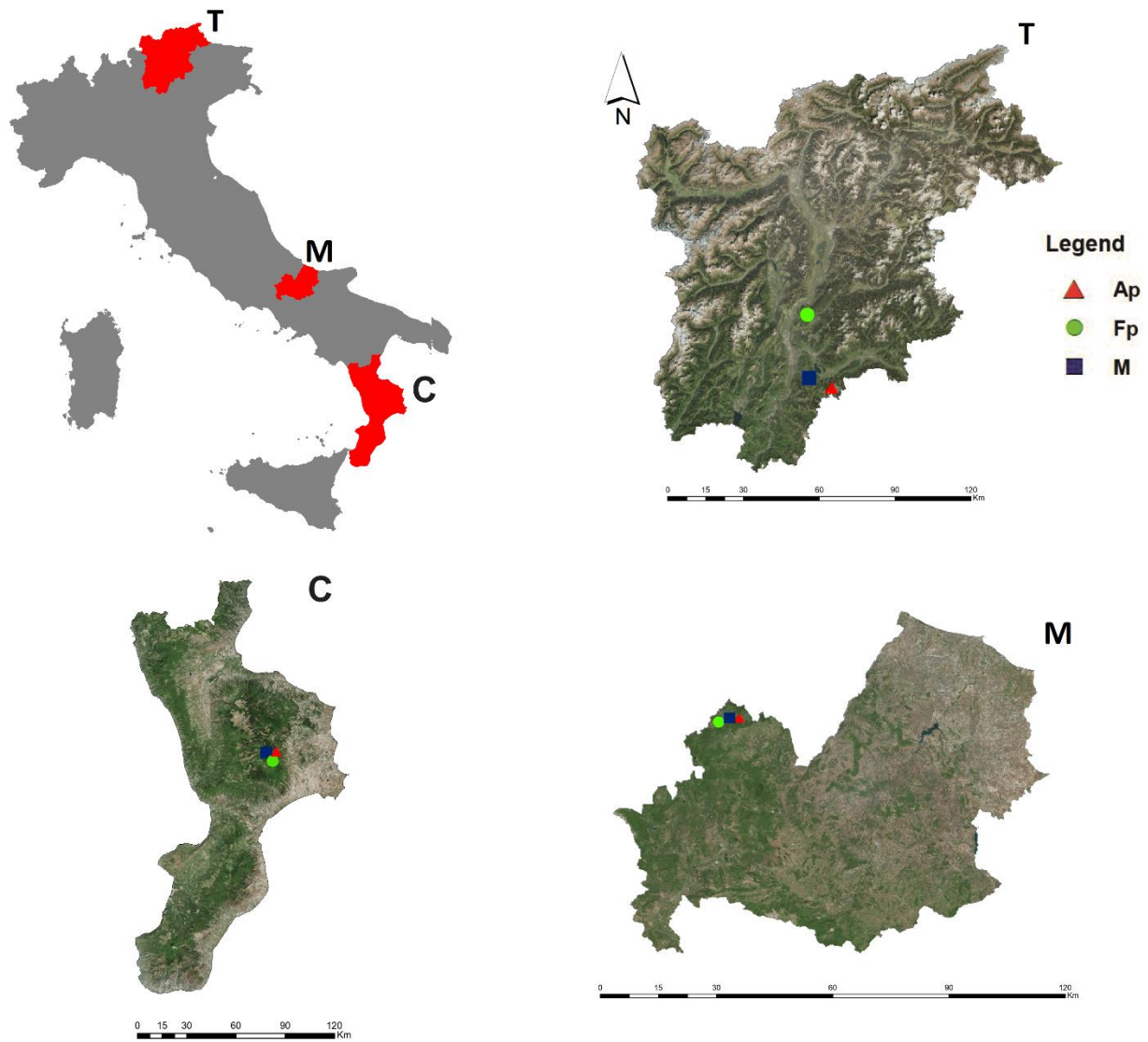


Table 1. Location of the study sites and forest structural parameters obtained for each triplet of pure and mixed-species. Exposure ( $^{\circ}$ ); altitude (m); slope ( $^{\circ}$ ); stand basal area, BA ( $\text{m}^2 \text{ha}^{-1}$ ); tree cover of the main species investigated (%); stand density (N. trees/ha); mean tree diameter at breast height, DBH (cm); mean tree height, H (m).

Sites	Plots	Latitude (N)	Longitude (E)	Exposure (°)	Altitude (m)	Slope (°)	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Main species (%)	Stand density (n. trees ha <sup>-1</sup> )	DBH (cm)	H (m)	Cores /trees (n)
Trentino - Alto Adige	pure_beech	46°12'6.12"	11°12'37.05"	91	1276	20	43.2	85%	1146	19	15	80/60
	pure_silver fir	45°56'57.18"	11°18'53.14"	123	1446	18	63.9	76%	693	27	18	100/60
	mixed_beech	45°57'43.72"	11°16'26.63"	164	1423	19	40.6	63%	937	13	12	54/36
	mixed_silver fir							26%		17	16	45/36
Molise	pure_beech	41°52'13.65"	14°16'37.85"	354	1182	21	33.6	87%	992	19	18	110/60
	pure_silver fir	41°52'11.02"	14°17'26.03"	317	1230	20	59.2	86%	533	35	19	86/44
	mixed_beech	41°52'14.35"	14°16'51.26"	327	1182	27	54.6	54%	446	25	18	47/31
	mixed_silver fir							34%		54	25	38/19
Calabria	pure_beech	39° 9'13.49"	16°39'53.05"	343	1289	24	59.8	79%	650	30	19	60/46
	pure_silver fir	39° 9'19.31"	16°41'2.30"	319	1220	37	61.5	78%	750	29	19	71/43
	mixed_beech	39° 9'7.96"	16°40'12.33"	307	1332	28	76.5	47%	628	28	18	42/25
	mixed_silver fir							47%		37	20	42/29

Table 2. The descriptive statistics of the mean ring width (MRW) with the standard deviation (SD) calculated on the series of raw annular amplitudes used in the analysis. Mean tree diameter at breast height (DBH) of sampled trees; mean sensitivity (MS), correlation of mean intersections (R<sub>BAR</sub>); expressed population signal (EPS) calculated on the accretion series of indexed rings and first-order autocorrelation (AC1).

Sites	Plots	Time span (n. of years)	Maximum Age	Minimum Age	DBH (cm)	MRW ± SD (mm)	MS	r <sub>bar</sub>	EPS	AC1
Trentino - Alto Adige	pure_beech	1888-2016 (129)	129	55	23	1.43±1.26	0.199	0.287	0.95	0.874
	pure_silver fir	1809-2016 (208)	208	50	39	1.79±0.60	0.114	0.323	0.94	0.913
	mixed_beech	1922-2016 (95)	95	50	25	1.26±0.43	0.157	0.262	0.93	0.914
	mixed_silver fir	1849-2016 (168)	168	53	32	1.63±1.46	0.101	0.267	0.95	0.772
Molise	pure_beech	1877-2016 (140)	140	50	24	1.05±0.36	0.185	0.311	0.97	0.381
	pure_silver fir	1846-2016 (171)	171	57	42	1.31±0.44	0.122	0.303	0.96	0.837
	mixed_beech	1898-2016 (119)	119	50	39	1.82±0.77	0.184	0.25	0.94	0.869
	mixed_silver fir	1856-2016 (161)	161	76	40	1.92±0.54	0.132	0.338	0.92	0.755
Calabria	pure_beech	1908-2016 (109)	109	50	34	2.19±0.81	0.159	0.25	0.94	0.844
	pure_silver fir	1935-2016 (82)	82	39	36	2.80±0.94	0.153	0.228	0.95	0.782
	mixed_beech	1889-2016 (128)	128	53	43	2.00±0.73	0.149	0.235	0.93	0.946
	mixed_silver fir	1909-2016 (108)	108	51	45	2.96±0.90	0.114	0.284	0.94	0.896

		FpT		ApT		FmT		AmT		FpM		ApM		FmM		AmM		FpC		ApC		FmC		AmC					
		cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r	cc	r				
Precipitation	Apr prev.	0.22				-0.23												0.34 0.27											
	Jul prev.											-0.22 -0.24																	
	Aug prev.			0.32 0.31		0.27		0.24																					
	Oct prev.																			0.25 0.22									
	Nov prev.																					-0.24 0.27							
	Jan corr.											-0.24 -0.25				-0.23													
	Feb corr.																							0.18					
	Jul corr.	-0.27																						0.13					
	Sept corr.											0.18																	
Temperature max	Apr prev.													-0.31 -0.26				0.27											
	May prev.													-0.29 -0.29								-0.29							
	Jul prev.													0.22 0.23															
	Aug prev.	-0.31				-0.28 -0.23																							
	Sept prev.									-0.22																			
	Oct prev.													-0.25 -0.24															
	Nov prev.																			-0.21									
	Dic prev.											0.24																	
	Jan corr.							0.33																					
	Feb corr.			0.30 0.25				0.42 0.32						0.22												0.21			
	Mar corr.							0.28																					
	Apr corr.	-0.29																											
	May corr.	0.28				0.28																							
	Jun corr.							-0.22						-0.25															
	Jul corr.					0.30 0.27																							
Aug corr.																													
Sept corr.																	-0.22 0.23				0.22								

Table 3. Significant correlation coefficient (cc) and response function (r) ( $p < 0.05$ ) between the residual chronologies of tree rings and monthly climatic variables ( $T_{max}$  and P).

Table 4. Summarized pointer years of beech and silver fir in the 9 stands over the period 1951-2016. RGV%: relative growth variation (%); N. tot: total number of pointer years; identification of negative and positive pointer years.

Sites	Plot	Total n. of pointer years	Negative pointer years		Positive pointer years	
			N.	RGV%	N.	RGV%
Trentino – Alto Adige	pure_beech	8	3	-38	5	77
	pure_silver fir	5	1	-28	4	35
	mixed_beech	5	1	-16	4	53
	mixed_silver fir	6	2	-28	4	40
Molise	pure_beech	11	3	-41	8	96
	pure_silver fir	9	4	-32	5	36
	mixed_beech	7	2	-29	5	44
	mixed_silver fir	15	6	-31	9	44
Calabria	pure_beech	12	4	-26	8	34
	pure_silver fir	5	2	-27	3	35
	mixed_beech	10	4	-26	6	60
	mixed_silver fir	6	2	-24	4	33

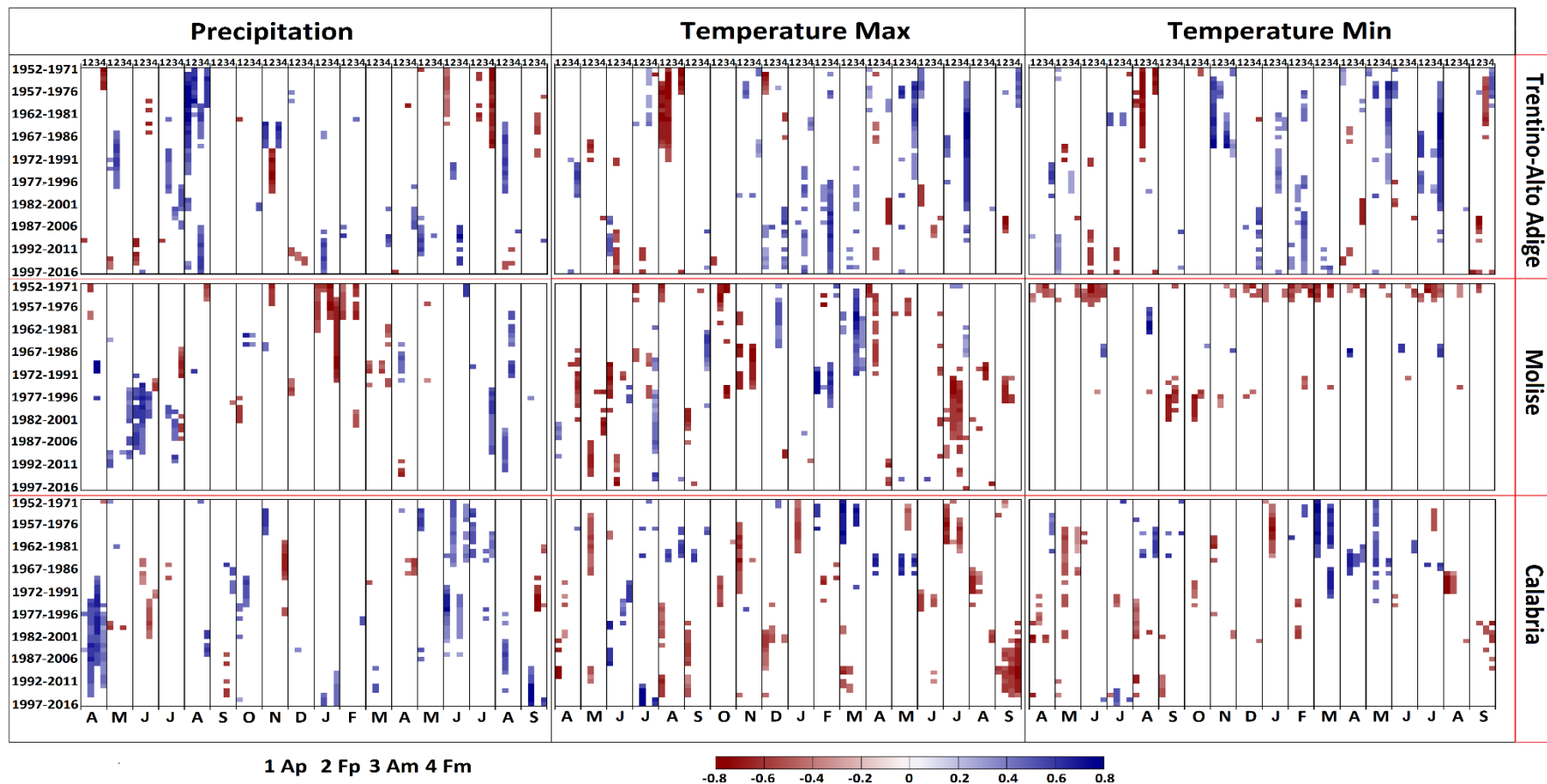


Figure 2. Climate-growth relationships between residual chronologies of the growth rings and monthly climatic variables ( $T_{\max}$ ,  $T_{\min}$  and  $P$ ), calculated using moving windows. Coefficients are represented, for each time window, in ten periods on the y axis. White cells indicate non-significant correlations, while cells with red (negative) and blue (positive) marks are significant ( $p < 0.05$ ). Numbers above indicate the plots in the three regions of Italy: 1 and 2 indicate the pure plots, while, 3 and 4 indicate the mixed plots.



Figure 4. Scatter plots of PCA (axes 1 and 2) performed on all the pointer years and grouped at the plots level. Each pointer years was indicated with the plus sign (positive pointer years) and with the minus sign (negative pointer years). Plots are represented by colors in the legend.