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Impacts of climate changes and disturbances on *Fagus sylvatica* L. and *Pinus mugo* Turra subsp. *mugo* in Majella National Park, Central Apennine

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“Whenever you want turn on a dream and let it burn you” William Shakespeare

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Short ABSTRACT:

Impacts of climate changes and disturbances on *Fagus sylvatica* L. and *Pinus mugo* Turra subsp. *mugo* in Majella National Park, Central Apennine

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The two main activities of the PhD thesis project were described. The first study focuses on the analysis of vegetation dynamics of *Pinus mugo* Turra subsp. *mugo* and *Fagus sylvatica* (L.) at the subalpine ecotone level of the Majella Massif. We were interested in investigating the upward movement of mountain pine treeline into abandoned pastureland and downward into areas potentially suitable for beech, and the concurrent beech encroachment upward. Vegetation shifts in these ecotonal zones may cause a negative impact on the spatial distribution and survival of rare or endemic species, thus influencing the appearance, structure and productivity of the subalpine ecotone of the Majella National Park. Growth dynamics and canopy cover of beech closed forest and mountain pine *krummholz* were analyzed in relation to disturbances at four different sites. Spring and summer temperatures and summer precipitation affected stem radial growth of both species. In details, spring and summer temperatures negatively affected Tree Ring Width (TRW) of beech, except for the highest site; whereas, spring temperatures affected positively and summer temperatures negatively TRW of mountain pine. Forest dynamics show the expansion of mountain pine upward, encroaching on formerly grazed pastures and harvested areas, especially where the soil is shallow and rocky; downward expansion is also occurring following progressive abandonment of forest management practices. At the same time, beech recruitment is growing upward, interspersed within mountain pine *krummholz*, taking advantage from canopy shadowing and higher temperatures. The structure and function of these secondary forests reflect the successional changes induced by a complex mix of

natural disturbances and anthropogenic pressures, with challenges to the implementation of adaptive management strategies.

In the second study, we investigated tree ring widths and xylem vessel characteristics in *Fagus sylvatica* L. to evaluate the plasticity of hydraulic functionality of xylem and radial growth of stem under different environmental conditions. To assess how beech adapts to past forest management and climate change in last decades, dendrochronology was combined to wood anatomy to disentangle the structural responses of tree species. The stem growth dynamics of beech were defined at two altitudes (1200 vs. 2000 m a.s.l.) in the Majella National Park (Central Italy). Correlations between climate variables and anatomical traits were assessed in the present environmental conditions. Vessel traits, hydraulic properties and stem radial increments of beech in this Mediterranean mountain context differed between plots, following an altitudinal cline. Hydraulic architecture was affected by climate and altitude, through a reduction in hydraulic diameter (DH), with increasing altitude and adjustment in radial growth and anatomical traits in particular mean cell size per ring (MCA), mean value of cell (vessel) density (CD), accumulated potential hydraulic conductance (KH), xylem-specific potential hydraulic conductivity (KS), vessel grouping index (RVGI), mean percentage of conductive area (RCTA). At higher elevation, in stand with low density, forest stands showed high sensitivity to environmental variability and trees showed phenotypic plasticity adapting their anatomical traits to limiting conditions. At lower elevation, trees had higher hydraulic efficiency and growth rates, though at higher risk of increased vulnerability to cavitation. Temperature influenced DH at the beginning and at the end of the growing season, while a negative influence of summer temperatures, especially in August and September were shown in all sites except for the highest one. Precipitation was a limiting factor for stem radial growth and xylem vessel functionality in beech on the Majella massif and, probably, in other southern sites with a similar Mediterranean setting.

Keywords: Subalpine ecotone, mountain pine, beech, dendrochronology, climate-growth relationship, wood anatomy

Extended ABSTRACT:

I. Introduction

The PhD thesis reports the results of the activities directed to:

A1) to perform dendroclimatological analysis to study climatic factors influencing tree-ring structure at a macroscopic and microscopic level and studying the correlations of tree growth with climate data providing information about recent modifications related to climate changes and the legacy of past forest management;

A2) to investigate anatomical features of longer timescales and to correlate the time dimension of xylem plasticity with the investigated environmental trends. The anatomical method allows to explore the mechanisms that characterize the tree growth in order to study how environmental factors influence tree growth;

A3) to understand the relationships between tree-rings and anatomical parameters to implement the knowledge of trees as dendroclimatic proxies.

The tree growth dynamics at the subalpine ecotone and forest stands levels highlight the effects of climate and land use changes on the forest cover evolution in the mountain and subalpine ecotones, and, consequently, the governance implications within the Majella National Park that could be assessed by policy makers. The combination of climate and land use changes has a strong impact on the tree growth and forest area expansion, that may affect the final set of benefits for local communities, particularly in the case of more recent abandonment of agro-forestry activities (mainly grazing) and of the reduction of associated goods (livestock productions, wood and non-wood forest products, etc.). The study results suggest that managing forests and related changes can help defining an adaptive and ecosystem-based approach, as well as the “resilience thinking” in the forest management. The study aimed to investigate: (i) the development of a resilient configuration of landscape mosaic in fragile and threatened mountain forest environments, considering climate and land use driving forces; and (ii) the inclusion of local knowledge and tree growth analysis into decision-making processes at different institutional levels.

II. Materials and Methods

Sites description of subalpine ecotone

Temporal and spatial evolution of mountain pine *krummholz* and beech closed forest was studied in four different sites from 1954 to 2017, mapping sites in Geographic Information System (GIS). The sites mapping selected the most representative areas of the transition zone between the two communities in three years: 1954, 1996 and 2017. The four study sites were located at different altitudes and exposures at the subalpine ecotone and they represent stands with different age structures and without visible recent human practices. The site Pescofalcone (PE) is located on the northeastern slope of Monte Pescofalcone, in the Oriented Natural Reserve of Orfento Valley, at 2127 m a.s.l.; the site Ugni (UG) is situated on the northern slope of Monte Ugni, in the Oriented Natural Reserve of Feudo Ugni, at 1935 m a.s.l.; the site Piana Grande (PG), is located on the southwestern slope of the uplands of “Majelletta”, in the Oriented Natural Reserve of Orfento Valley at 1895 m a.s.l.; the site Blockhaus (BK) is located along the southeastern slope of the large pastures of “Majelletta” at 1770 m a.s.l.

Description of the elevational gradients of beech forest stands

Beech forest stands in two elevational gradients in the Orfento valley and Mount Ugni were considered. The all areas of Orfento Valley and Mount Ugni were established as Natural State Reserves in 1971 and 1981, respectively. In the Orfento valley were defined two plots (O1 at 1226 m a.s.l.; O2 at 2127 m a.s.l.), located on the northeastern slope of Monte Pescofalcone. In the Mount Ugni two plots (U1 at 1212 m a.s.l.; U2 at 1935 m a.s.l.) were located on the northern slope of Monte Ugni. The plots at the highest altitude represent the beech altitudinal limit in the transition zone between *Pinus mugo* and *Fagus sylvatica*. The stands were subjected to different managements in the past, i.e. old coppice with standards in U1, U2 and O1, the most common management practices for beech in Italy. Any kind of forest management was performed for the plot O2, due to the altitude and the distance of this plot from the nearest village. In all these areas no thinning has been carried out at least in the last 30 years (Calderaro et al., 2018 submitted). In the period 1901-2016, mean annual temperature was 13.3 °C and mean total annual precipitation was 733.3 mm.

Tree rings analysis

Dendrometric and dendrochronological surveys were performed in four different circular areas, with a 40 m diameter. Dendrometric data, diameter at breast height (DBH) and tree height, were measured and woody cores were collected. Tree cores were prepared following standard dendrochronological procedures (Schweingruber, 1988). Tree-ring widths (TRW) were measured with a 0.01-mm resolution with LINTAB measurement equipment, coupled to a stereomicroscope (60x magnification; Leica, Germany) and time series analysis program TSAP Win. Raw chronologies, were obtained both for beech and for mountain pine. The individual chronologies were standardized in R environment (R Foundation for Statistical Computing, Vienna, Austria), producing tree-growth index (TRI) chronologies of each tree species in each study site. Mean standardized chronologies were used to analyze climate–growth relationships. Descriptive statistics defined key properties of each chronology in each study site.

Wood anatomical analysis

Tree cores of 5 trees from each plot of beech stands along the elevational gradients were sampled for the wood anatomy analysis. The protocol for the analysis of wood anatomy, developed by TESAF Department, University of Padua and WSL of Birmensdorf (Switzerland), was implemented (von Arx et al., 2016). Images were captured from different slides representing parts of the same core were stitched together through the software PTGui. Image analysis was performed with the software "ROXAS" (von Arx et al., 2016; Prendin et al. 2017). Among all the wood anatomical data output of ROXAS, we used hydraulic diameter (DH), mean cell size per ring (MCA), cell density (CD), accumulated potential hydraulic conductance (KH), xylem-specific potential hydraulic conductivity (KS), vessel grouping index (RVGI), mean percentage of conductive area (RCTA). Tree ring widths raw series obtained with ROXAS were processed in the same way as the raw series obtained with the LINTAB measurements, and compared to the mean series of each plot.

Climate data analysis

Climatic data derived from the CRU TS 3.1 gridded data set with 0.5° spatial resolution (Mitchell & Jones, 2005) were used in the dendroclimatological analysis for the study of subalpine ecotone. Significant correlation coefficients were obtained by the interpolation of monthly observations from

the CRU data set and monthly climatic data recorded by the three local meteorological stations of the study area (Pescocostanzo, Sant'Eufemia a Majella and Caramanico)(Palombo et al., 2014). The averaged climatic data from the four grid points closest to the research area were selected. For the period 1901–2013 for the first study, maximum and minimum monthly temperature and total monthly precipitation were downloaded from gridded data set. Climate-growth relationships were defined using the *treeclim* package (Zang& Biondi, 2013) in the R environment.

For wood anatomical analysis, monthly temperature, precipitation and Standardised Precipitation-Evapotranspiration Index (SPEI), (Vicente-Serrano, Begueira and López-Moreno 2010) of the area was gathered to identify significant correlations with ring width and anatomical parameters. Temperature data derived from the CRU TS 4.01 gridded data set (Harris et al., 2014) with 0.5° spatial resolution was used for the period for the period 1901–2016. Precipitation data was available from monthly precipitation data recorded by the three local meteorological stations in the study area.

III. Results and Discussion

Land-cover changes

The land cover (%) in 1954, 1996, and 2017 was extracted in the four sampling sites of subalpine ecotone. In PE, the highest site evaluated, mountain pine formed a dense *krummholz*, with adult trees limiting beech expansion. Beech trees grew above their altitudinal limit (2127 m a.s.l.), within the mountain pine stand. In UG, land cover remained relatively constant from 1954 to 2017; beech took advantage from the sheltering canopy of mountain pine and expanded towards higher elevation. PG is characterized by an abundant recolonization of mountain pine, especially in those clearings where grazing was once practiced. Mountain pine and beech stands are distant from each other. Young beech trees established within mountain pine *krummholz*. The open area is characterized by beech recruitment and abundant mountain pine seedlings, especially on rocky and sunny soils. In BL, in the 1950s, mountain pine was completely cut to produce charcoal. Here, abundant mountain pine recruitment is present in abandoned grazing areas. Beech expanded upwards, but only to a certain extent.

Variation in disturbance regime and land cover, related to climate (summer became increasingly drier in the period 1954–2013, in the study area) and land-use changes (human pressure decreased in the

same period), impacted the ecotonal boundaries, creating favorable conditions for the establishment of beech at higher altitude and of mountain pine at lower altitude. Seed production and dispersal agents (wind vs. vertebrates) and interactions with slope aspect and disturbance legacy may explain the spatial and temporal variability in species-specific establishment across sites.

Land cover in the mid of the twentieth century showed a closed mountain pine mat and beech forest stand with scattered vegetation. The upward shifts of mountain pine *krummholz* above the current treeline appear to be driven by both climate and land-use changes (Palombo et al., 2013), whereas introgression of mountain pine downwards into the beech closed forest can be mainly related to the progressive abandonment of traditional forest management. Indeed, the effect of land-use changes was more important in the zone of transition between beech closed forest and mountain pine *krummholz* than in the upper treeline ecotone (e.g., Treml et al., 2016). Nowadays, the upward shifts in recruitment of beech, in contact with mountain pine, take advantage from canopy shadowing, natural disease of mountain pine and high temperatures. In the MNP, since 1975, beech forest cover has expanded into abandoned farm lands and subalpine pastures at a rate of 1.2% per year-1 (van Gils et al., 2008), from the contiguous, mid-altitudinal beech stands. Transient forest expansion, due to the process of natural succession causing tree encroachment into abandoned farmland, represents a major land-use change with tremendous impacts on the mountain landscape.

Tree growth response to climate

Climatic variables affected the growth of mountain pine and beech at the transitional ecotone between closed forest and *krummholz* of Majella Massif.

At the subalpine ecotone, TRW was negatively correlated with maximum temperatures in beech, although being positively correlated with maximum temperatures in September and November of the previous year and October of the current year, at the highest elevation in PE. In PE, anthropic disturbance was less relevant than climatic constraint. Precipitation influenced tree growth in beech at the beginning of the growing season (May) and in July, in the last 30 years. The positive correlation observed at the beginning of the growing season can be related to the high altitude of this site, where the species grows at 2127 m of altitude in extreme life conditions. Beech has European-wide natural area, yet, ecophysiological and dendroecological studies revealed that populations at the southern margin of its distribution are sensitive to drought (Tognetti et al., 1995; Peñuelas et al., 2008; Piovesan et al., 2008; Fotelli et al., 2009; Tognetti et al., 2014; Bolte et al., 2016; Coccozza et al.,

2016). Direct evidence of the impact of summer drought on beech growth was here provided by the positive correlation between TRW and precipitation in July, even at high elevation. Beech in BK suffered from anthropogenic disturbance, especially during the 1950s, when the forest was completely harvested. In addition to the relevance of the start of dry season on beech growth (Maselli et al., 2014), increasing damage from late spring frost in recent years may control inter-annual productivity variation on the Majella Massif (e.g., Bascietto et al., 2018).

Precipitation did not affect tree growth of mountain pine in the last decades. High temperatures and significant climate-growth relationships may explain amelioration of growing conditions of mountain pine over the current climatic conditions of the subalpine ecotone, contributing to an increase in the range distribution of this conifer species. Mountain pine is expanding towards higher and lower altitude, re-colonizing large areas formerly grazed and cut, especially where the soil is shallow and rocky. Mountain pine is a pioneer species of avalanche chutes and abandoned pasturelands, threatening endemic herbaceous species and influencing local resource management (Dai et al., 2017). The response of forest communities and ecotonal vegetation to global change can, therefore, be influenced by interactions of single climatic and land-use components with tree species. On the other hand, ecotone evolution and vegetation shift in different elevations may modify the status of biodiversity refugia at high elevation on the Apennines (Stanisci et al., 2005).

Wood anatomy

Vessel traits, hydraulic properties and stem radial increments of beech in this Mediterranean mountain context were related to plot-specific environmental conditions and management legacy, which also affected structural features and stand dynamics of beech both at the lower elevation and at the subalpine ecotone. Hydraulic architecture was affected by climate and altitude, through a reduction in hydraulic diameter (DH), with increasing altitude and adjustment in radial growth and anatomical traits in particular mean cell size per ring (MCA), mean value of cell (vessel) density (CD), accumulated potential hydraulic conductance (KH), xylem-specific potential hydraulic conductivity (KS), vessel grouping index (RVGI), mean percentage of conductive area (RCTA). Trees showed phenotypic plasticity adapting their anatomical traits to limiting conditions. At higher elevation (O2 and U2 plots), forest stands showed high sensitivity to environmental variability through a lower DBH and hydraulic diameter. At lower elevation (O1 and U1 plots), trees showed high proportions of conducting area in the stem and higher mean DH values. This higher hydraulic efficiency and growth rates, caused a higher risk of increased vulnerability to cavitation. Temperature influenced

DH at the beginning and at the end of the growing season, while a negative influence of summer temperatures, especially in August and September were shown in all sites except for the highest one. Yet, precipitation was a limiting factor for stem radial growth and xylem vessel functionality in beech on the Majella massif and, probably, in other southern sites with a similar Mediterranean setting.

1. Introduction

1.1 Factors influencing trees limit distribution

Climate change scenarios predict an increase of the mean global temperature in the range of 0.3–4.8 °C in 2100 compared to mean values in 1985–2005 (IPCC, 2013; Greenwood and Jump, 2014) resulting in a forest line shifts anticipated in the coming decades. During the 20th century, many mountain areas experienced agricultural land abandonment, which usually led to enhanced seedling survival and decreased mortality from grazing (Speed et al., 2010). Therefore, in Mediterranean mountains, the forest lines are heavily influenced by land-use change (Tognetti and Palombo, 2013). Past land-use and management strongly reduced the resilience of forest ecosystem (e.g., to wildfires and persistent drought) (Reyer et al., 2015). The impact of land-use changes on altitudinal ecotone dynamics is particularly important in areas with a long history of intense anthropogenic influence, such as the European mountains (Batllori et al., 2010; Ametzegui et al., 2016).

Subalpine ecotones, bounded by the treeline at their upper margin, are the forest zone influenced primarily by abiotic controls, including persistent snowpack, desiccating winds, acute and chronic extreme temperatures, soil moisture and evapotranspirative stresses in both summer and winter, and short growing seasons (Millar and Rundel, 2016). The transition zone between the upper limit of the closed forest and the uppermost individuals of tree species is called timberline (Körner, 2007, Fig. 1). The subalpine ecotones are considered an indicator of landscape response to climate change (Harsch et al., 2009; Gottfried et al., 2012). Whereas, the treeline is the upper altitudinal or latitudinal limit in which upright trees or krummholz patches reach either two or three meters in height (Harsch et al., 2009), where harsh environmental conditions inhibit the establishment, growth and survival of trees (Tranquillini, 1979).

Although the mechanisms of the alpine treeline are still under debate, the upper altitudinal limit of tree establishment occurs at elevation where the mean temperature of the growing season is about 6.4 °C (Körner and Hoch, 2006, Compostella and Caccianiga, 2016). Abiotic (e.g., temperature, drought, water logging or soil nutrients) and biotic factors (e.g., insect outbreaks, pathogens), as well as anthropogenic (e.g., fire, timber harvesting, logging, pastoralism) disturbances affect the dynamics of these transitional zones (Palombo et al., 2014a). Climatic variables and plant factors, as well as biomass loss and seedling mortality (Trembl et al., 2016), shape these ecotonal zone during early stages of tree growth (Gamanche and Payette, 2005) and in seed formation (Holtmeier, 2009). Temperature

in the growing season broadly drives the position of tree and forest lines (Jobbágy and Jackson, 2000; Körner and Paulsen, 2004). Harsch et al. (2009) found evidence for the global treeline advance at 52% of study sites, whereas in cases where no actual advance was documented, treeline generally responds to climate through changes in growth form or tree density (Greenwood and Jump, 2014). However, our understanding on how climate and land cover changes influence vegetation shift of the altitudinal ecotone from closed forest to *krummholz* zone in Mediterranean mountains is still poor. Dendrochronological techniques were used to develop time series of disturbance legacy, climatic variation, and tree recruitment across the ecotone between the closed forest and the *krummholz* zone in central Apennines (Italy).

Treelines dominated by *krummholz* patches of mountain pine (*Pinus mugo* Turra ssp. *mugo*) exist in the Alps, the Dinaric Alps, Carpathian Mountains, Japan, Sikhote Alin Mountains, Sachalin and Kamchatka (Holtmeier, 2009). Treelines are common at mid-latitude (30°-45°) above 2500 m a.s.l. in Eurasia (Dai et al., 2017). In the Alps, the treeline is covered by a *krummholz* mat, a transitional zone to high-altitude meadows. Whereas, in the Apennines, where the peaks are lower than 3000 m a.s.l., the treeline overlaps with the limit of deciduous forests dominated by European beech (*Fagus sylvatica* L.) (Pezzi et al., 2007). In the Apennines, the beech timberline has a compact frame due to anthropogenic origin (e.g., grazing, burning, logging) (Fig. 2-3).

1.2 Tree limit distribution in Majella National Park

The *krummholz* belt dominated by mountain pine is an exception in the Apennines. In the Majella Massif (central Apennines), mountain pine reaches the southern edge of its latitudinal distribution range, therefore, it acts as a sensitive species to land-use and climate changes in the Mediterranean region (Palombo et al., 2013; Dai et al., 2017). The light demanding mountain pine is the most tolerant species to cold climates and to bedrock lithology between the European pines (Ballian et al., 2016). The tree growth of mountain pine in Majella National Park is particularly affected by temperature at the start and end of the growing season, but also by summer precipitation (Palombo et al., 2014b). Nevertheless, the *krummholz* dynamics are influenced by the summer pastoralism and the seed dispersion of mountain pine rather than climate factors (Dai et al., 2017). As a result of the cessation of grazing activities and forestry practices in the Majella Massif, mountain pine is expanding toward both high and low altitudes in areas potentially suitable for the development of beech forests. Pine species are considered invasive and may contribute to the instability of forest-grassland ecotones (Richardson et al., 1994; Mast et al., 1998).

European beech is one of the most widespread indigenous and economically important broadleaved tree species in Europe (Ellenberg and Leuschner 2010) and it is considered a sensitive indicator of environmental changes through dendroclimatic signals (Di Filippo et al., 2012; Tognetti et al., 2014). Climate change scenarios predict that beech forest areas across Europe will decrease in the next century (Sabate et al. 2002, Geßler et al. 2007, Zimmermann et al. 2015). Beech is particularly susceptible to climate extremes for its relatively low physiological acclimation capacity (Grime and Mackey 2002, Valladares et al. 2002, Stojnić et al. 2018), and the high sensitivity of stem growth in response to drought in comparison with other temperate broad-leaved trees (Leuschner et al. 2001, Zimmermann et al. 2015). Nevertheless, this is not a universal response and high trait plasticity of beech trees after disturbance may allow this species to withstand decreasing water availability to a certain degree (Kahle 2006, van der Werf et al. 2007).

In particular, high summer temperatures favour radial growth of beech at the expense of vertical growth, suggesting a positive effect of increasing summer temperature at higher latitudes or altitudes on cambial activity of this species (Bosela et al. 2018). This means that the current warming trend may accelerate cambial growth of beech at the latitudinal and altitudinal extremes of this species distribution. However, southern European beech populations are increasingly suffering from summer drought (Linares and Camarero 2012, Piovesan et al. 2008), which may trigger induce tree mortality (Bolte et al. 2016, Coccozza et al. 2016). The capacity of beech to cope with drought is strictly related to hydraulic efficiency, e.g., changing the lumen of sapwood area ratio, vessel diameter and conductivity (Hajek et al. 2016). Variation in the precipitation regime may trigger intra-specific hydraulic differences (e.g., conduit size, distribution, and density) (Chenlemuge et al. 2015, Schreiber et al. 2015), as consequence of genetic variability or phenotypic plasticity (Schuldt et al. 2015). Trade-offs between water transport capacity and relative drought resistance may shape the adaptation of beech populations to changes in climate (Hajek et al. 2014, Hoeber et al. 2014, Kotowska et al. 2015).

Water availability and air temperature affect xylem formation that varies between sites and years (Sass and Eckstein 1995). Moreover, changes in vessel features are species-specific. Therefore, beech is able to adjust stem hydraulic architecture mainly by changing water conduit number, xylem vessel size, and tree growth rate (Giagli et al. 2016). In Alpine environments, secondary growth (e.g., cambium differentiation and xylem formation) of beech has been found to vary with temperature (Prislan et al. 2013), with radial growth at different altitude depending mainly on precipitation and temperature in June–July (Di Filippo et al. 2007). Therefore, joint studies on quantitative wood

anatomy and tree ring width of beech along environmental gradients may help clarify the relationships between climate change and radial growth (Fonti et al. 2010). In particular, altitudinal variation can provide insight into the role of increasing temperature in xylem formation (Kraus et al. 2016, Martinez del Castillo et al. 2016, Prislan et al. 2018). As a general rule, low temperature in summer at higher elevations and longer drought periods in summer at lower elevations should affected radial growth in beech in mountain environments (Neuwirth 2013). In particular hydraulic properties a of beech in are also related to environmental conditions and management legacy, which also affected structural features and stand dynamics of the species both at the lower elevation and at the subalpine ecotone.

1.3 Beech forest management in Italy

In Italy, beech covers 1,0 M ha (National Forest Inventory, INFC 2005), corresponding to 9.4% of the total national forested area (Nocentini 2009). In the Alps, beech generally forms pure stands above 1000 m altitude in areas with relatively low rainfall, while it grows at around 600-700 m in more humid areas. In the Apennines, beech usually grows above 900-1000 m. Beech forests are widespread on the northern slopes and where rain and fog maintain moist air conditions. On the sunnier and warmer southern slopes, the distribution limit of beech tends to shift upward (Nocentini et al. 2009). In the Italian Peninsula, beech stands have shown a well-defined bioclimatic organization of dendroclimatic signals and the existence of altitudinal gradients in tree growth (Di Filippo et al. 2012, Chiesi et al. 2014, Tognetti et al. 2014).

Forest management practices have significantly modified the distribution, composition and structure of beech forests in the Apennines (Nocentini 2009), where they are the most common sources of wood (Scarascia-Mugnozza et al. 2000). However, after the II World War, the progressive depopulation of mountain areas due to socio-economic changes (Fig. 4) has led to the abandonment of coppice-with-standards used for the production of firewood and charcoal (Hahn and Fanta 2001, Brunet et al. 2010). Conversion of beech coppices to high forest implies different stand traits (such as tree density, stand basal area, canopy cover), leading to variation in stand structure and environmental conditions, in particular soil moisture and temperature (cf. Aussenac 2000).

1.4 Objectives and Hypothesis

The vegetation dynamics of mountain pine (*krummholz*) and beech (closed forest) at the subalpine ecotone level of the Majella Massif were analysed. In this study we examined the sensitivity of mountain pine and beech to disturbance regimes (fire, drought, grazing, harvesting) at the subalpine ecotone and identified the pattern of tree growth and the establishment period of trees as indicators of the effects of climate change in Mediterranean mountains.

1) Tree growth of mountain pine and beech was assessed at the transition zone between the beech closed forest and the mountain pine *krummholz* in the Majella Massif. Ecotone development was determined in four different sites through aerial photographs from 1954 to 2017. The relationships between climate change and radial growth is still a matter of controversy, and joint studies on quantitative wood anatomy and tree ring width along environmental gradients may help clarify patterns and processes. Thus, dendroclimatological analysis was used: to define the influence of temperature and precipitation on tree growth of mountain pine and beech during the vegetation season. We hypothesized that climate change, adding to land-use change, is differently impacting on spatial dynamics of mountain pine *krummholz* and beech forest stands, thus affecting the resilience of the ecotone.

2) To describe the radial growth dynamics, xylem vessel plasticity and forest stand structure at two altitudes (1200 vs. 2000 m a.s.l.) in the Majella National Park, the relationships and trade-offs between radial growth dynamics and hydraulic efficiency (linked to trade-offs between wood anatomical traits and mechanical strength) within beech were investigated hypothesizing that: (i) tree growth (in particular xylem formation) is influenced by increasing temperature and also by altitudinal gradient (ii) variation in xylem vessel plasticity (in response to altitude) is related to anatomical traits and structure (in detail cell density, mean cell size per ring), and (iii) high hydraulic efficiency (differences in hydraulic diameter, and hydraulic conductivity) leads to high growth rates at the cost of xylem safety.

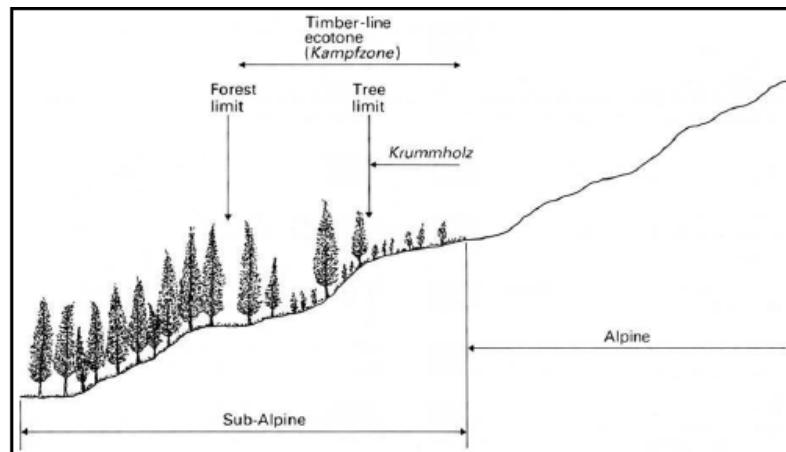


Figure 1. Representation of Forest Limit, Timberline and Treeline at the Sub-Alpine ecotone.



Figure 2. Subalpine ecotone with mountain pine and beech in Piana Grande della Majelletta (on the left) and Mount Ugni (on the right) (Picture by C. Calderaro).



Figure 3. Aerial photograph of dry-stone walls and agricultural land terracing on the mountain ridge between the communities of Roccamorice and Passo Lanciano (Picture by C. Calderaro).

2. Materials and Methods

2.1 Studied species:

2.1.1 Mountain pine, *Pinus mugo* Turra

The mountain pine (*Pinus mugo* Turra) (Fig. 4) is an evergreen conifer with a generally shrubby prostrate habit with branches ascending towards the apex and height of 2-5 m. The biological form is P rept - Creeping fanerophytes. It consists of an erect main trunk and a series of secondary trunks, more or less prostrate. The gray-brown bark with aging becomes scaly. The mountain pine is a plant very resistant to cold climate, rooted on the rocks and grows on the slopes and/or on partially

consolidated debris. It grows between 1200 ÷ 2700 m a.s.l., reaching 1500 ÷ 2300 m on the subalpine belt, which represents its optimum. The mountain pine has a slow growth, it is heliophilous and plays an important role for soils, especially on the mountains with limestone and dolomitic formation. It grows in closed formations that hold the snow, thus preventing the formation of avalanches. As far as the chorological type is concerned, the species can be classified as “Southern European orophyte” (occupies the mountain ranges of southern Europe, from the Iberian Peninsula, the Alps, the Balkans and Caucasus and Anatolia) and as Orophyte of the mountains range of Europe and Asia. Mountain pine is distributed in Italy in the Eastern Alps and the Apennines, in Europe in the Carpathians, up to Bulgaria and the Pyrenees.

Pinus mugo Turra subsp. *mugo* which has instead discontinuous range from the central Alps in particular to the Eastern Alps with separated populations on the Balkans and Apennines: on the Apennines of Parma (M. Nero and M. Maggiorasca), in Abruzzo on the Majella NP and Camosciara area (National Park of Lazio, Abruzzo and Molise). The species is mainly distributed in the subalpine belt but in the eastern Alps it can descend on coniferous landslides and torrential riverbeds even at low altitudes.



Figure 4. Particular of mountain pine close to Blockhaus site in Majella NP (Pictures by C. Calderaro).

2.1.2 Beech, *Fagus sylvatica* (L.)

Its biological form is “Arboreal fanerophytes”. It is a short-lived species (200-300 years old) and it has a straight and slender trunk. In good edafic conditions, the species can join 40 m of height but in general, in mature beech woods, plants join 30-35 m in height and a trunk diameters from 80-100 cm. The bark is thin in youth age, while at maturity it accumulates mineral crystals that make it more

resistant. The fruit is a walnut with a leathery pericarp and a brown maturity (September-October) (Fig. 5). The beechnuts are very rich in calories and are consumed by the marsican bear (*Ursus arctos marsicanus*), wild boar (*Sus scrofa*) and deer (*Cervus elaphus*) to accumulate fat reserves before winter. The reproductive maturity takes place in the forest, very late at 60-80 years, while in the isolated specimens in half the time, the fruiting is inconstant but every 4-5 years becomes abundant (mast period). The wood has a diffuse porosity with tree rings and parenchymatic rays of different width, they are clearly visible in the tangential section of the tree. Beech is a mesophilous and shadow lover species that prefers fertile, fresh, medium-textured and well-drained soils, but also adapts to less fertile and stony soils as long as there is abundant atmospheric moisture especially in spring.

The root system is initially fictitious but soon expands in width: the expansion of the root system does not normally exceed the projection of the crown. Beech wood is rich in amylaceous substances that are very nutritious, in fact in the forests the wood on the ground is quickly attacked by lignivorous mushrooms and insects that degraded it in a short time. The wood is hard and heavy but easy to work with appropriate treatments; it is used for furniture and it is also an excellent fuel to produce a refined coal. As a chorological type it is classified: Centroeurop. - Europe tempered from France to Ukraine and European area. In Italy beech is widespread in mountainous areas in all the eastern Mediterranean regions.

It is important to highlight that since men used forests for economic purposes, they often selected the forest composition according to their needs, favoring beech or preferring a woody composition of more requested species, thus altering the natural associations. In Central and Northern Europe beech is a species of lowlands, while in the Southern it is mainly a mountain species.

In northern Italy on the slopes of the Alps, Pre-Alps and Northern Apennines, beech is associated or should naturally be associated with white fir (*Abies alba*), a species of more microtermic type climate, and numerous other accompanying species as: yew (*Taxus baccata*), Maples trees (*Acer pseudoplatanus*, *Acer platanoides*), Greater ash (*Fraxinus excelsior*), Mountain elm (*Ulmus glabra*), Rowanberry (*Sorbus aucuparia*), Linden (*Tilia sp.*), Cherry wild (*Prunus avium*) and Poplar (*Populus sp.*). These species are referred to the association Abieti-Fagetum, in inland Alps the species meets more microthermal associations, referable to Abieti-Piceo-Fagetum, where in different proportions beech is also associated with Spruce (*Picea abies*). On sunny and well drained southern slopes and more xeric environment beech resists to the warm season thanks to the daily orographic storms. It is also associated with white Carpinus (*Carpinus betulus*) and black Carpinus (*Ostrya carpinifolia*) in the Ostryo-Fagetum type associations on the Majella massif. Along the Apennine ridge, in the

deciduous mountain forests, beech is certainly the emblematic and the most important and spread forest species. In the northern Apennines, it grows mainly on acid or sub-acidic soils, while on the southern ones it predominates on soils with a basic reaction carbonate matrix. Pignatti (1982) describes the vegetational optimum of beech, in the Alps between 600 and 1300 m a.s.l. and in Italian peninsula between 1000 and 1700 m a.s.l., surely the atmospheric moisture modifies locally the altitudinal ranges reported (www.actaplantarum.it).



Figure 5. On the left side particular of beech forest (in grey) at Mount Ugni, on the right side a particular of beechnuts.

2.2 Sampling sites for photointerpretation and dendrochronological analysis at the subalpine ecotone

Temporal and spatial evolution of mountain pine *krummholz* and beech closed forest was studied in four different sites from 1954 to 2017, mapping sites in Geographic Information System (GIS) (Fig. 6-7). The sites represented the transition zone between the two communities in three years: 1954 by aerial images of the “Volo Base IGM 1954/56”, Geographical Military Institute (Italy); 1996 by aerial images of “Volo Parco Scientifico e Tecnologico d'Abruzzo 1996”, available on Geoportal of Abruzzo region); and 2017 by web platform at international level (Google Earth).

A broader observation based primarily on the analysis of the shape and size of the two different surfaces with the two species, beech and mountain pine was assessed by the contrasts with the surrounding surfaces, the shades of gray and the spatial arrangement of the different elements of the landscape (structure and texture). The Land cover (%) in 1954, 1996, and 2017 was extracted in the four sampling sites (Table 1). In each site, an area of 200 m in diameter (Fig. 10) was marked, considering the shifting of 3 m year⁻¹ of mountain pine (as found by Palombo et al., 2013) and the

time span between 1954 and 2017 in order to include the ecotone in the area of photointerpretation. Thus the four study sites were located at different altitudes and exposures at the subalpine ecotone and they represent stands with different age structures and without visible recent human practices (Table 1, Table 2). The beech stands in PE, PG and BK include uneven aged and unthinned forests, as defined by the National Park since 1991. In UG there is an even aged forest and clear structure of old coppices, confirmed by a high number of stumps (31) and trees (247) per ha. Low numbers of stumps (5) and trees (8) per ha are in PG (Table 2). The mean height of the beech ranged between 11.5 and 14.5 m in UG, PG and BK, whereas it reached 4 m in PE, where extreme climatic conditions were for the species growth (Table 2).

Site	Altitude	Slope	Geographical coordinates
PE (Pescafolcone)	2127 m a.s.l.	NE	E 14° 04' 45.34''; N 42° 07' 26.85''
UG (Ugni)	1935 m a.s.l.	N	E 14° 9' 35.02''; N 42° 09' 10.46''
PG (Piana Grande)	1895 m a.s.l.	SW	E 14° 06' 17.71'' N 42° 08' 49.53''
BL (Blockhaus)	1770 m a.s.l.	SE	14° 07' 34.25''; N 42° 09' 10.46''

Table 1. Sites descriptions at the subalpine ecotone with the main features: altitude, slope and geographical coordinates.

Site	PE	UG	PG	BK
N. of stumps	17	31	8	16
Number of stems/individual	1.23	4	5	6
N. trees/ha	135	247	64	127
Max diameter (cm)	13	34	32	31
Mean diameter $\pm$ SD (cm)	8.5 $\pm$ 1.7	15.4 $\pm$ 5.2	15.3 $\pm$ 6.1	17.3 $\pm$ 6.1
Average height (m)	4	14.25	11.5	12.5

Table 2. Principal structural traits referred to beech stands in four sites.

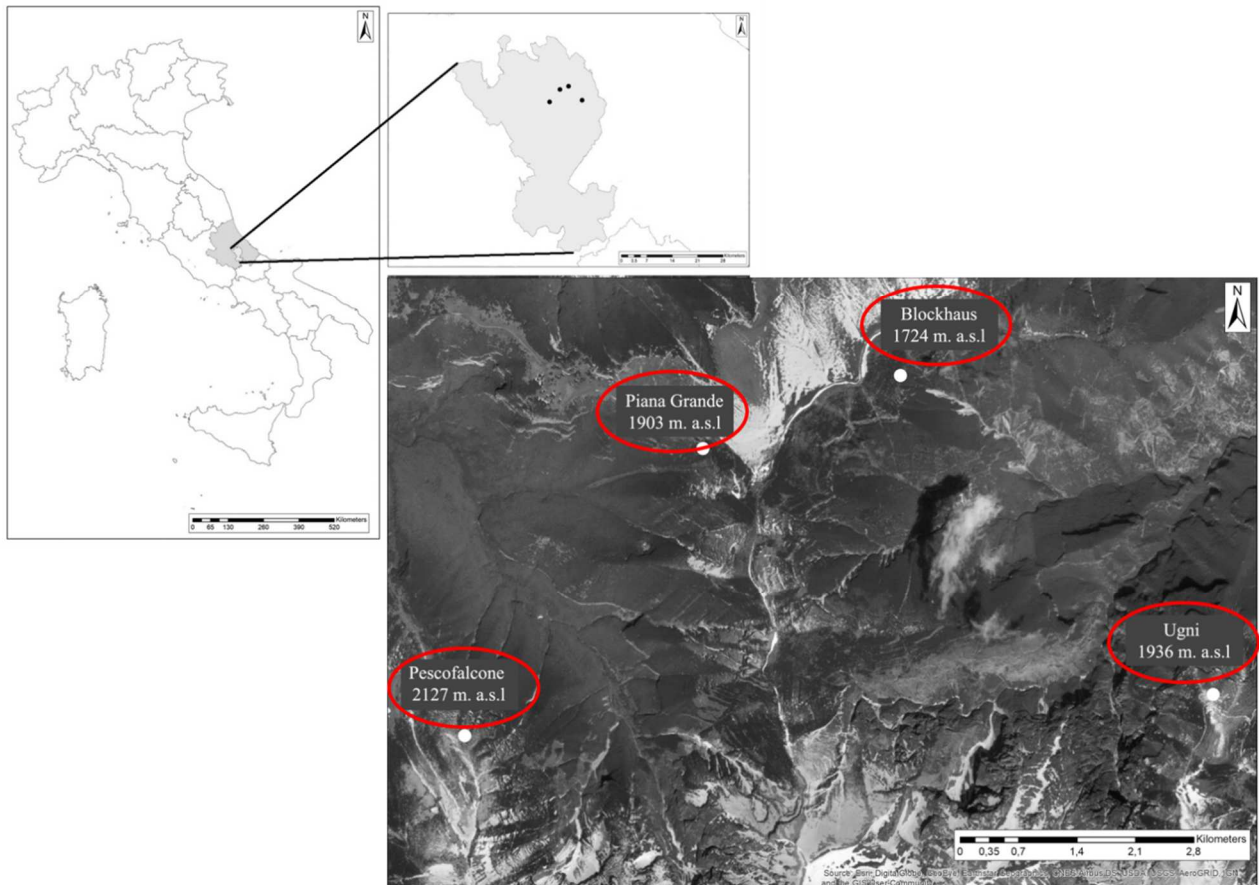


Figure 6. Location and altitude of four study sites (Pescofalcone, Ugni, Pianagrande, Blockhaus – white dots) in the MNP.



Figure 7. One of the studied sampling plots close to M. Blockhaus in Majella National Park the subalpine ecotone with beech and mountain pine is evidenced (Picture by C. Calderaro).

2.2.1 Tree-ring analysis

The age classes of trees were determined through dendrochronological analysis both at the subalpine ecotone and at the elevational gradients.

From August 2013 to July 2014 dendrometric and dendrochronological surveys were performed at the subalpine ecotone in four different circular areas (PE, UG, PG, BL), with a 40 m diameter and the geometric center established on the transition zone between beech closed forest and mountain pine krummholz. In each site, trees were selected to maximize the temporal and spatial extent of the time series and georeferenced in GIS environment. The four sampling plots were selected to show vegetation shift and temporal evolution of the two forest types. Two woody cores of 20 co-dominant or dominant trees of each species were collected at 120° from each other, (15 cores for dendrochronological analysis and 5 cores for wood anatomical analysis) using a 0.5-cm diameter increment borer. The prostrate habit of mountain pine results in a dense and impenetrable cover over the whole area; the main difficulty was to distinguish individual stems from the branches. Mountain pine trees were cored close to the base of the trunk and on the cross-slope side of the trunk to avoid sampling on branches and compression wood (Palombo et al., 2018). Beech trees were sampled at breast height (1.3 m). Dendrometric data, diameter at breast height (DBH) and tree height, were measured only for beech trees with a DBH 9 cm (Table 2).

For the elevational gradient of beech forest stands, dendrometric measurements and tree cores were collected and georeferenced in four plot along the elevational gradient (O1, O2, U1, U2) in a circular sampling area of 40 m diameter. Tree cores were collected from large trees in 20 individuals per plot (15 cores for dendrochronological analysis and 5 cores for wood anatomical analysis) with a 0.5-cm diameter increment borer, and average height was measured for each plot. Trees were sampled at breast height and cores were collected avoiding eccentricity and tension wood due to slope inclination.

Tree cores were mounted on woody supports, dried in fresh-air and sanded, following standard dendrochronological procedures (Schweingruber, 1988). Tree-ring widths (TRW) were measured with a 0.01-mm resolution with LINTAB measurement equipment, coupled to a stereomicroscope (60x magnification; Leica, Germany) and time series analysis program TSAP Win (Frank Rinn, Heidelberg, Germany). Raw chronologies, for each site, were obtained both for beech and for mountain pine. Raw TRW chronologies of each dated tree were cross-dated firstly visually and then

statistically using the COFECHA program (Holmes, 1983; Grissino-Mayer, 2001) to calculate cross-correlations between individual series and reference mean chronology. The individual chronologies were standardized in R environment (R Foundation for Statistical Computing, Vienna, Austria), producing tree-growth index (TRI) chronologies of each tree species in each study area.

In order to remove age related trends in TRW and non-climatic noise in TRW raw series and to underline the high frequency signal amplifying the climatic signal, individual-based detrending model, using a spline function with a 30% frequency variability cut-off at 15 years, was applied to all trees of both species, producing standardized chronologies. Mean standardized chronologies were used to analyze climate–growth relationships. The quality of the obtained chronologies was evaluated for the investigated period and were computed to compare and describe the chronologies using dendrochronological statistics (Briffa and Cook 1995). Descriptive statistics defined key properties of each chronology in each study site: mean ring width (MRW), medium-frequency growth variability was defined by standard deviation (SD); mean sensitivity (MS), which is an indicator of the mean relative change between consecutive ring widths (Fritts 1976) and is calculated as the absolute difference between consecutive indices divided by their mean value. Higher values of MS and higher SD are indicative of climatic effects on the chronologies (Fritts, 1976). Mean inter-series correlation ($\bar{r}$) defined pairings of tree ring series in a common time interval (Briffa, 1995); first order serial autocorrelation (AC) quantified the temporal persistence in growth among consecutive years, measuring the persistence retained before and after standardization; expressed population signal (EPS) estimated the signal strength, such as the amount of climatic information included in the developed chronologies (Wigley et al., 1984). The EPS quantifies the degree to which a particular sample chronology portrays a hypothetically perfect chronology and, considering the inter-series correlation and the sample size, estimates how well a finite number of samples represents the theoretical population mean. An $\text{EPS} > 0.85$ is considered a generally acceptable threshold for statistically reliable chronologies (Wigley et al., 1984).

2.2.3 Climate variables and relationships with tree growth

For the subalpine ecotone, climatic data (maximum and minimum monthly temperature and total monthly precipitation) of the period 1901–2013 were derived from the CRU TS 3.1 gridded data set with 0.5° spatial resolution (Mitchell & Jones, 2005) and used for comparison with tree-ring records. Significant correlation coefficients were obtained between monthly observations of the CRU data set and monthly climatic data recorded by the three local meteorological stations in the study area

(Pescocostanzo, Sant'Eufemia a Majella and Palena) (Palombo et al., 2014b). Averaged climatic data from the four grid points in the study area were selected. Climate-growth relationships were assessed using the treeclim package (Zang and Biondi, 2013) in the R environment (R Foundation for Statistical Computing, Vienna, Austria). A linear model was fitted to seasonal temperature and summer precipitation. The climate-growth relationships (tree-ring chronologies and monthly climatic data) were examined using correlation function (CF) analysis (Fritts, 1976) and moving CF (MCF) analysis was performed to detect the stationarity and consistency of CFs over time. The CFs were separately calculated in each month, from March of the previous year to October of the current year, in the period 1901-2013. Climate data from March of the previous year ($t-1$) to October of the current year (t) were used as independent variables, whereas the standard mean tree-ring chronologies in the four sampling sites were used as dependent variables. The MCF analysis was repeatedly performed for consecutive time windows of chronologies to investigate the temporal stability of their main climatic signals. Treeclim assessed the statistical significance of the correlation coefficients through a bootstrap process (Guiot, 1991).

2.3 Sampling sites for wood anatomical analysis at the elevational gradients of beech stands

The wood anatomy analysis was conducted in beech forest stands at two elevations in the Orfento Valley and Mount Ugni, areas established as Natural State Reserves in 1971 and 1981, respectively (Fig. 8). Microcores were sampled in four sampling plots from May 2013 to September 2014 (Fig. 10). The Orfento area included two plots located on the northeastern slope of Monte Pescofalcone in the Oriented Natural Reserve of Orfento Valley (Table 2). The Mount Ugni area included two plots located on the northern slope of Mount Ugni, in the Oriented Natural Reserve of Feudo Ugni (Table 3). The highest considered plots (the subalpine ecotone) represent the beech altitudinal limit in the transition zone between mountain pine (*Pinus mugo* Turra spp. *mugo*) and beech. Informations about stand management were obtained from the Italian State Forestry Corps “Carabinieri Forestali” and from aerial photographs (Calderaro et al. 2018 submitted). The stands were subjected to different management practices, before the establishment of the reserve, i.e., old coppice with standards in U1, U2 and O1, the most common management practice for beech in Italy (Table 3). Any kind of forest management for the plot O2 due to the altitude and the distance from the nearest village. In all these areas, no thinning was carried out in the last 30 years (Calderaro et al. 2018 submitted).

Site	Altitude	Slope	Geographical coordinates
O1	1226 m a.s.l.	NE	E 14° 5' 23.27", N 42° 7' 56.79"
O2	2127 m a.s.l.	NE	E 14° 04' 45.34", N 42° 07' 26.85"
U1	1212 m a.s.l.	N	E 14° 10' 24.91"; N 42° 8' 27.22"
U2	1935 m a.s.l.	N	E 14° 9'35.02; N 42° 09' 10.46"

Table 3. Sites descriptions at the elevational gradient with the main features: altitude, slope and geographical coordinates.

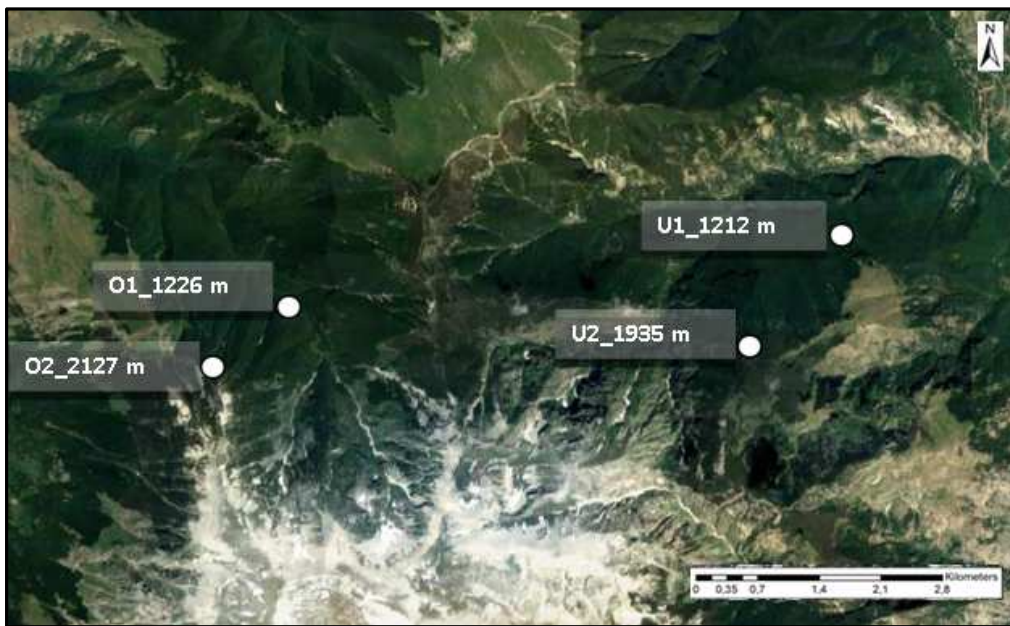


Figure 8. Location and altitude of four study sites of the two altitudinal transect (O1, O2, U1, U2 – white dots) in the North East side of MNP.

2.3.1 Wood anatomical analysis

Tree cores ($n = 5$ trees per plot) from elevational gradients plots were used for wood anatomical analysis to produce microslides (Fig. 11). The protocol for the analysis of wood anatomy, developed by TESAF Departement, University of Padua (Italy) and WSL of Birmensdorf (Switzerland), was implemented (von Arx et al. 2016). Core samples were split in 4-5 cm long pieces, and heartwood was boiled in a water-paraffine solution before fine transversal sections (15-20 μm thick) were cut with a rotary microtome (Fig. 9). Microsections were stained with a solution of safranin (1% in distilled water), astrablue (0.5% in distilled water and acetic acid) to identify lignified tissue and non-

lignified tissue. Samples were treated with ethyl alcohol at different concentrations for the processes of cleaning and dehydration, they were fixed with EUKITT, to obtain permanent slides. High-resolution digital images were captured with a camera mounted on an optical microscope. Images from different parts of the same core were stitched together through the software PTGui. Image analysis was performed with the software "ROXAS" (von Arx et al. 2016, Prendin et al. 2017). Ring borders were manually identified and a manual fine-editing was performed to remove wrongly identified or broken cells. Among all the wood anatomical data output of ROXAS, we used hydraulic diameter (DH), mean cell size per ring (MCA), mean value of cell (vessel) density (CD), accumulated potential hydraulic conductance (KH), Xylem-specific potential hydraulic conductivity (KS), vessel grouping index (RVGI), mean percentage of conductive area (RCTA). Raw TRW series obtained with ROXAS were processed in the same way as the raw series obtained with the LINTAB measurements, and compared to the mean series of each plot.

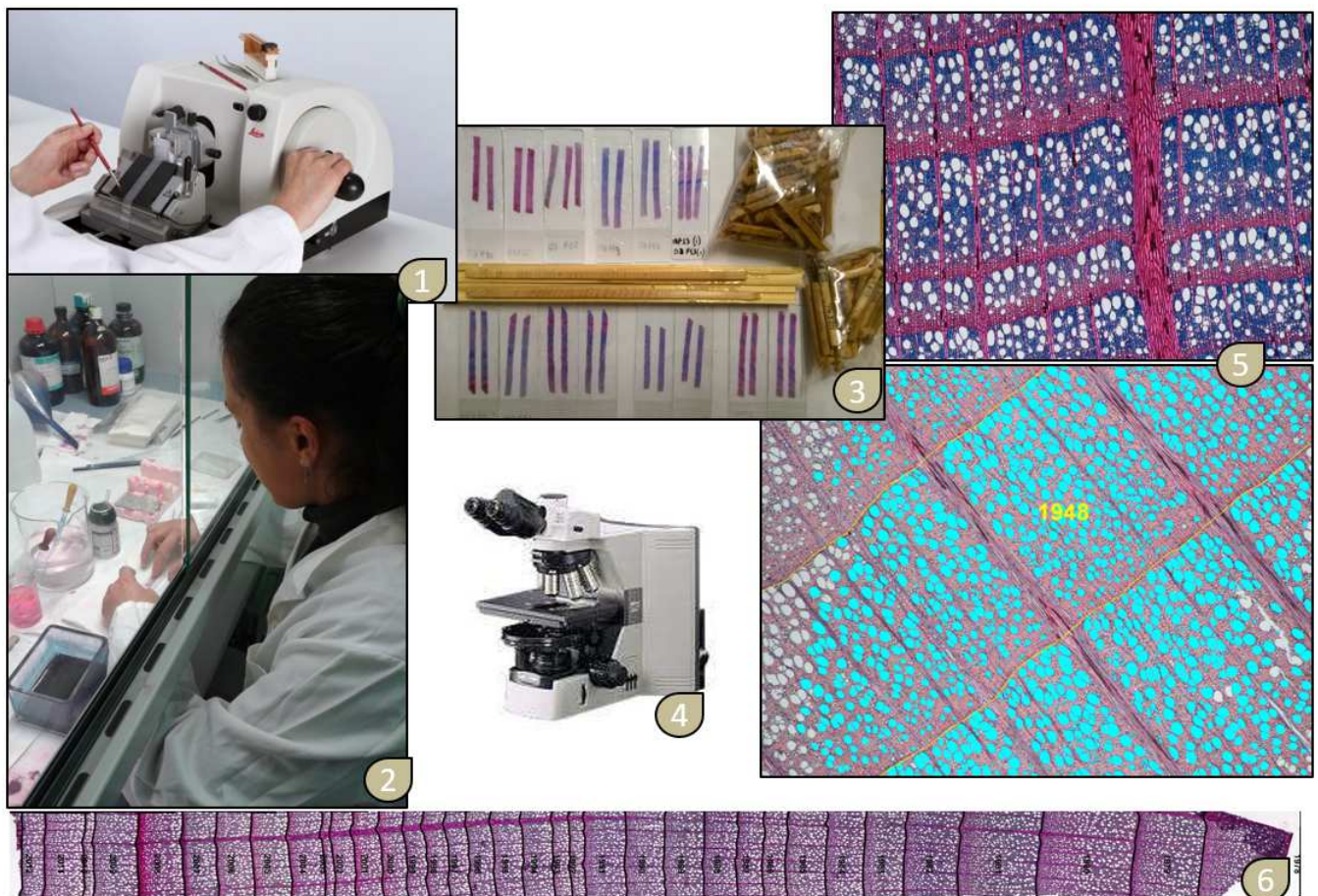


Figure 9. Protocol of the wood anatomy process and analysis. (1) Cutting phase with a rotary microtome; (2) staining cleaning and dehydration processes; (3) fixation pahse with EUKITT, to obtain permanent slides; (4) High-resolution digital images captured with a camera mounted on an optical microscope and images stitched together with PTGui; (5-6) Automatical image analysis performed with ROXAS for the entire core.

2.3.2 Climate and tree growth relationships

For the elevational gradients monthly temperature, precipitation and Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al. 2010) of the area were gathered to identify significant correlations with ring widths and anatomical parameters. Temperature data derived from the CRU TS 4.01 gridded data set (Harris et al. 2014) with 0.5° spatial resolution was used. Precipitation data was available from monthly precipitation data recorded by the three local meteorological stations in the study area (Pescocostanzo, Sant'Eufemia a Majella, and Caramanico) (Palombo et al. 2014b). The SPEI values were downloaded online (<http://spei.csic.es/index.html>). Statistical analysis was performed using R version 3.4.3 (R Core team 2017). Relationships between local weather parameters (temperature and precipitation), tree-ring widths and wood anatomical traits (DH, KH, CD, RVGI, RCTA) were established using the treeclim package (Zang and Biondi 2013) to evaluate the monthly and seasonal degree of correspondence between factors. The significance of correlations was evaluated with a 95% confidence interval from nonparametric test based on bootstrapping. Treeclim assessed the statistical significance of the correlation coefficients through a bootstrap process (Guiot 1991). The climate-growth relationships (between DH and monthly climatic data) were examined using correlation function (CF) analysis (Fritts 1976). The CFs were separately calculated in each month, from March of the previous year to October of the current year, in the period 1901-2015. Climate data from March of the previous year ($t-1$) to October of the current year (t) were used as independent variables, whereas the DH in the four sampling sites were used as dependent variables.

Kruskal-Wallis test was used to compare means between anatomical traits among locations. Differences between locations were analyzed with Dunn post-hoc tests.

3. Results

3.1 Results at the subalpine ecotone:

3.1.1 Land-cover changes

In PE, the highest site evaluated, the land cover varied from 2% to 13% for beech and between 98% and 87% for mountain pine, between 1954 and 2017 (Table 4, Fig. 10). Mountain pine formed a dense

krummholz, with adult trees limiting beech expansion. Beech trees grew above their altitudinal limit (2127 m a.s.l.), within the mountain pine stand. In UG, land cover remained relatively constant from 1954 to 2017, with a percentage of about 40% for beech and 60% for mountain pine (Table 4, Fig. 10). Beech took advantage from the sheltering canopy of mountain pine and expanded towards higher elevation. PG is characterized by an abundant recolonization of mountain pine, especially in those clearings where grazing was once practiced. Mountain pine and beech stands are distant from each other. Young beech trees established within mountain pine krummholz; land cover varied from 37% to 49% for beech and between 26% and 41% for mountain pine (1954-2017) (Table 4, Fig. 10). The open area is characterized by beech recruitment and abundant mountain pine seedlings, especially on rocky and sunny soils. In BL, abundant mountain pine recruitment is present in abandoned grazing areas. Beech expanded upwards, but only to a certain extent; land cover varied from 26% to 32% for beech and between 74% and 68% for mountain pine (1954-2017).

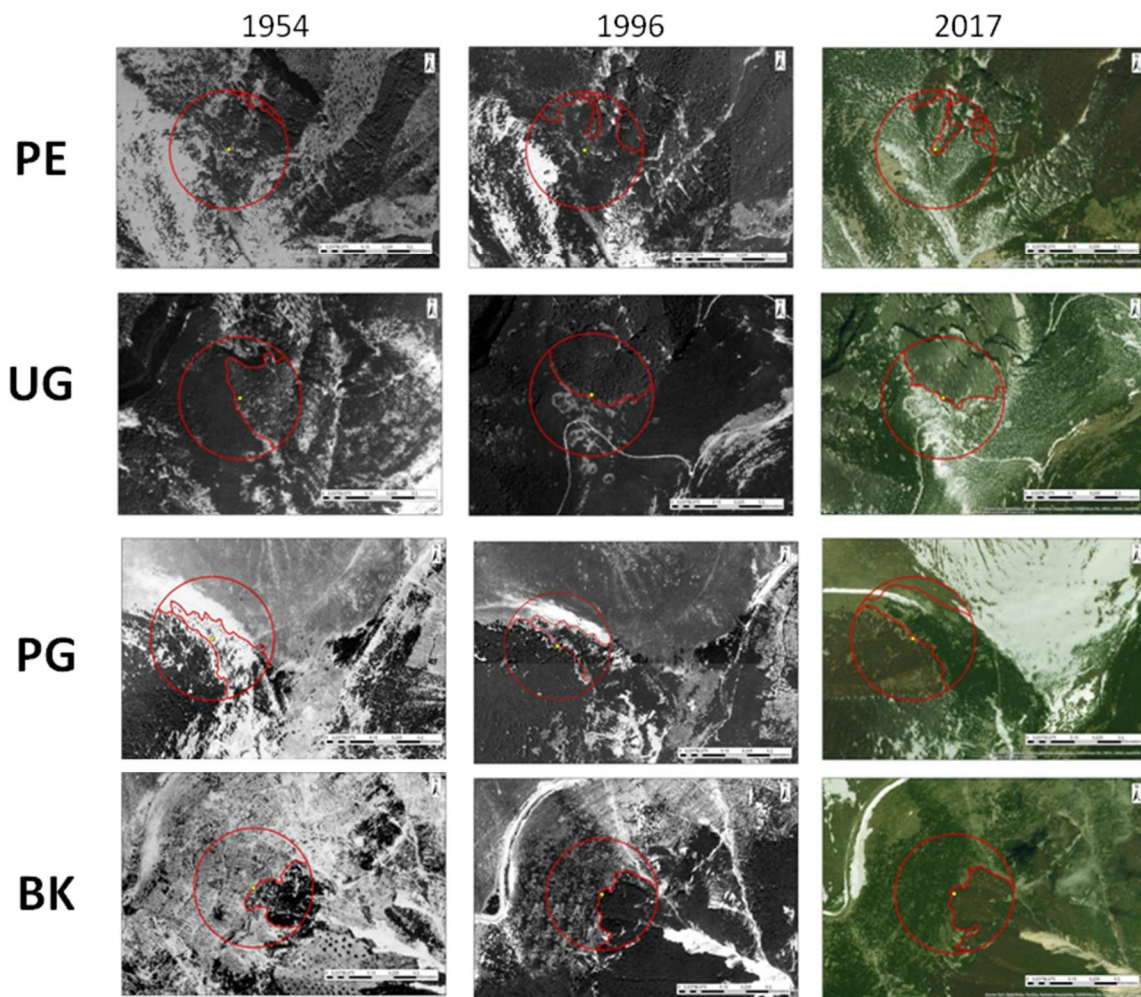


Fig. 10. Diachronical analysis on aerial photos carried out in 1954, 1996, and 2017. originated from aerial images of the “Volo Base IGM 1954/56”, Geographical Military Institute (Italy), aerial images of “Volo Parco Scientifico e Tecnologico d'Abruzzo 1996” and 2017 available from WEB platforms at international level (Google Earth).

Site	Species	Year	Year	Year
		1954	1996	2017
PE	<i>F. sylvatica</i>	2%	15%	13%
	<i>P. mugo</i>	98%	85%	87%
UG	<i>F. sylvatica</i>	40%	44%	40%
	<i>P. mugo</i>	60%	56%	60%
PG	<i>F. sylvatica</i>	37%	50%	49%
	<i>P. mugo</i>	26%	23%	41%
BK	<i>F. sylvatica</i>	26%	34%	32%
	<i>P. mugo</i>	74%	66%	68%

Table 4. Geoportal of Abruzzo region and orthophotos of 2017 available on WEB platforms at international level (Google Earth). Land cover (%) in 1954, 1996, and 2017 in PE-Pescofalcone, UG-Ugni, PG-Piana Grande, BK-Blockhaus.

3.1.2 Tree-ring chronologies and age structure

Raw mean chronologies of beech showed an exponential negative trend, the typical biological growth development. The maximum age of beech was 95, 102, 118 and 92 years in PE, UG, PG, and BK, respectively (Table 5). All the standardized mean chronologies for beech showed an increasing trend of growth, except for PE, where decreasing TRW were found. Beech showed values of mean TRW of 1.274, 1.228, and 1.072 in BK, UG and PG, respectively; whereas, mean TRW was 0.468 in PE, the site at the highest altitude. Beech showed mean inter-series correlations of standardized chronologies with $r = 0.454$ (PE), $r = 0.487$ (UG), $r = 0.558$ (PG) and $r = 0.497$ (BK). The statistical

cross-dating between standard chronologies showed significant EPS values (> 0.85) in each site (Table 4). The highest value of MS in beech was found in PE and BK (0.400 and 0.385, respectively), underlying wider mean tree-ring width.

Raw mean chronologies of mountain pine also showed an exponential negative trend. Some cores presented missing rings or density fluctuations. Mountain pine showed the longest chronologies in PE and UG (100 and 98 years) (Table 5), since 1914 and 1916, respectively; the shortest chronologies were in PG and BK (83 and 75 years), since 1931 and 1940, respectively. TRW series spanned from 0.621 mm year⁻¹, the minimum values, in PE to 0.820 mm year⁻¹, the maximum value, in PG with common trends. The cross-dating of standard chronologies led to 5% discard of the total cores, due to the measuring difficulties; EPS values close to the threshold value of 0.85, except for UG, were obtained (Table 6). Mountain pine exhibited significant mean correlation coefficients ($P < 0.001$) in all plots and mean inter-series correlations with $r = 0.394$ (PE), $r = 0.270$ (UG), $r = 0.633$ (PG) and $r = 0.419$ (BK) in standardized chronologies (Table 6). The MS in mountain pine varied less than in beech, from 0.304 (UG) to 0.365 (PG). The MS of mountain pine showed the minimum values of 0.274 in UG, and 0.304 in PE (Table 6).

Mean standardized chronologies showed similarities and synchronization between the growth trend curves in both species (Fig. 11). TRW of beech reached a mean value greater than 1 mm year⁻¹; while TRW of mountain pine a mean value of 0.5 mm year⁻¹. In PE, beech trees showed an average age similar to BK, with a mean TRW of 0.5 mm year⁻¹ and a maximum DBH of only 8 cm.

Site	PE	UG	PG	BL
Medium age beech (years)	72	84	71	68
Maximum age beech (years)	95	102	118	92
Time span (beech)	1918 – 2012	1911 – 2012	1896 – 2013	1921 – 2012
Medium age pine (years)	69	68	50	54
Maximum age pine (years)	100	98	83	75
Time span (pine)	1914 – 2013	1916 - 2013	1931 - 2013	1940 - 2014

Table 5. Age structure (including medium and maximum age of both species) and time span in PE, UG, PG, BK.

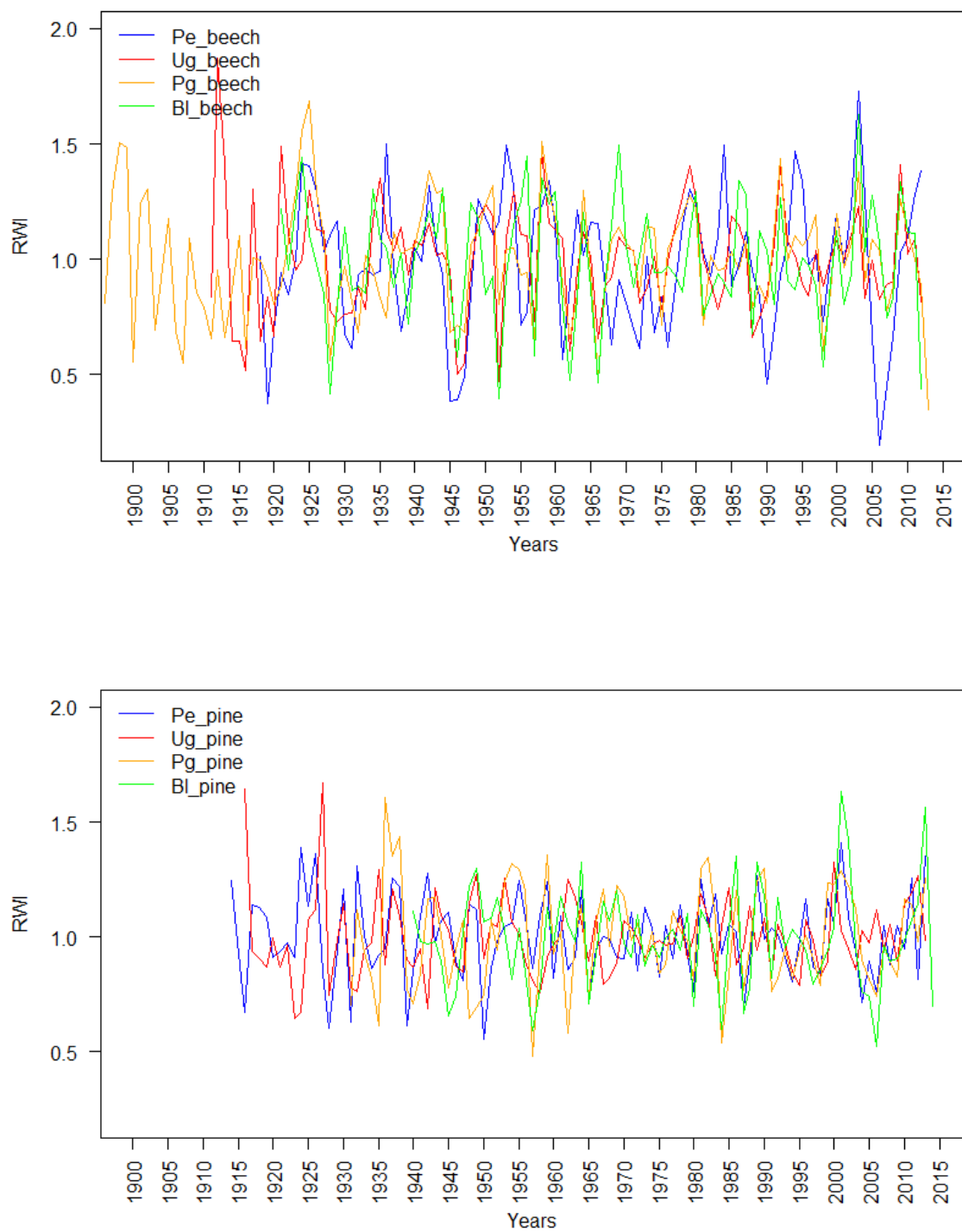


Fig. 11. Mean standardized chronologies of beech and mountain pine in four study sites. Chronologies were built using the 30 years splined data.

Descriptive statistics	Total years		MRW-mm		AC		Rbar		EPS		SD		MS	
Species	<i>F. sylvatica</i>	<i>P. mugo</i>	<i>F. sylvatica</i>	<i>P. mugo</i>	<i>F. sylvatica</i>	<i>P. mugo</i>	<i>F. sylvatica</i>	<i>P. mugo</i>	<i>F. sylvatica</i>	<i>P. mugo</i>	<i>F. sylvatica</i>	<i>P. mugo</i>	<i>F. sylvatica</i>	<i>P. mugo</i>
PE	95	100	0.468	0.621	0.617	0.598	0.454	0.394	0.847	0.856	0.246	0.180	0.400	0.304
UG	102	98	1.228	0.645	0.568	0.700	0.487	0.270	0.912	0.535	0.211	0.176	0.274	0.323
PG	118	83	1.072	0.820	0.523	0.458	0.558	0.633	0.918	0.757	0.222	0.249	0.312	0.341
BK	92	75	1.274	0.725	0.450	0.612	0.497	0.419	0.930	0.730	0.180	0.212	0.385	0.365

Table 6. Descriptive statistics of tree-ring width for beech (*Fagus sylvatica*) and mountain pine (*Pinus mugo* Turra ssp. *mugo*) in the four sampling sites. Chronology time span (total years), MRW mean ring width and SD standard deviation, first-order serial autocorrelation (AC), mean inter-series correlation (*rbar*), mean sensitivity (MS), standard deviation (SD), mean expressed population signal (EPS) (number of years > 0.85). MRW and SD were computed on the raw tree ring series; MS, AC, *rbar* and EPS were computed on the indexed tree ring series. (EPS = obtained for 30 years with 15 years overlapping; (mean) = average of all values ≥ 0.85)

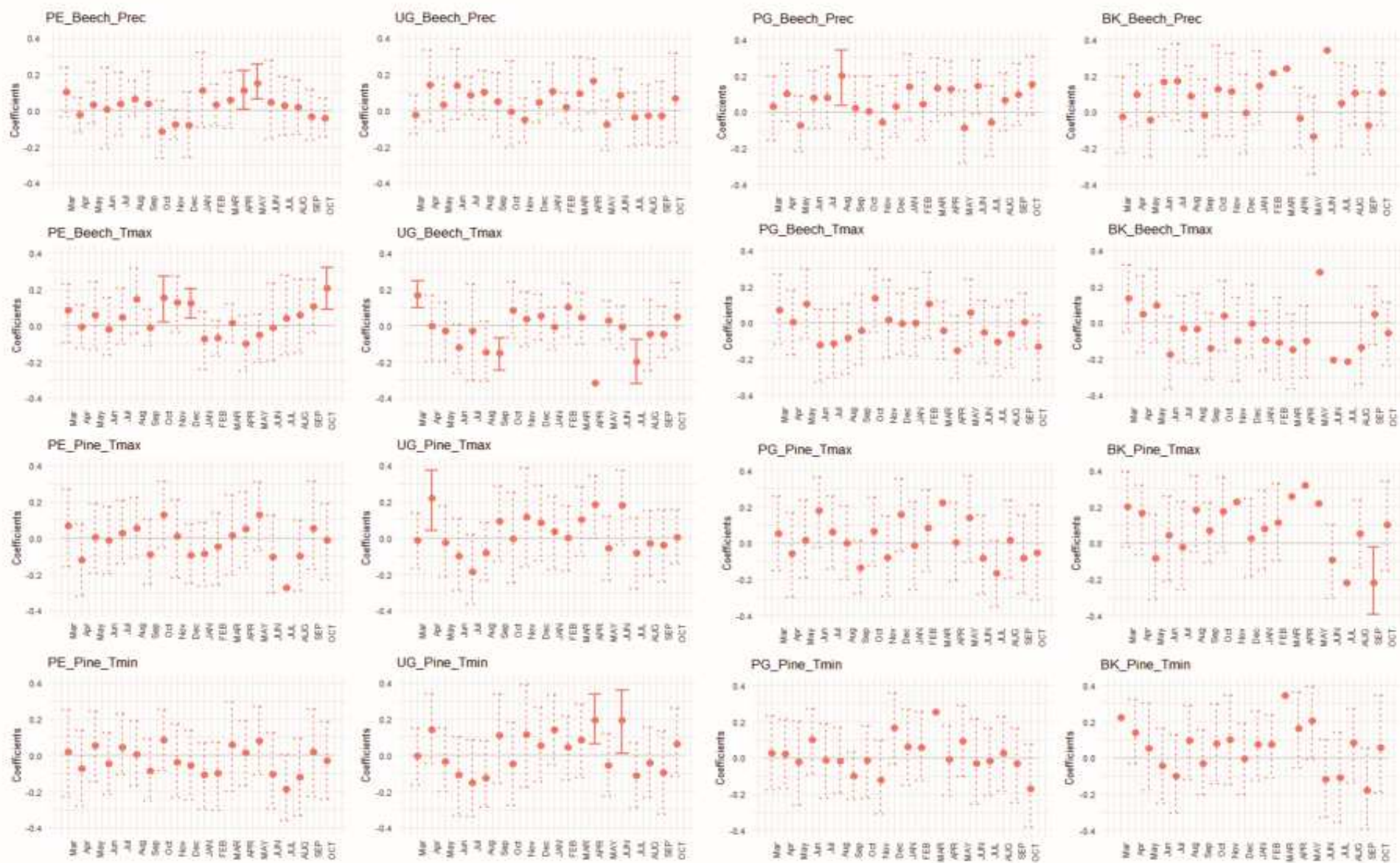
3.1.3 Tree growth response to climate

Climate influenced tree growth in both species (Fig. 12). Correlation functions at the subalpine ecotone showed positive correlations between TRW of beech and precipitation in April and May of the current year in PE and August of the previous year in PG (Fig. 12). TRW of beech was negatively correlated with maximum temperatures in September and July of the previous and current year and July of the current year, respectively, in UG, whereas it was positively correlated with March of the previous year. Tree growth of beech was positively influenced by maximum temperatures in PE at the end of the growing season (October of the previous and current year) (Fig. 12).

Moving correlation functions of beech confirmed the effect of precipitation on tree growth (Fig. 13). In the last 30 years, the precipitation in July of current year positively influenced tree growth in UG, and the precipitation in July of previous year influenced TRW in PE. Tree-ring growth of beech was positively correlated with maximum temperatures in May of the current year in UG, PG and BK, not in PE, between 1988 and 2013 (Fig. 13). The moving correlation functions also showed positive correlation between the minimum temperature of August in PE and UG in the last 30 years (graphs not showed).

Tree growth of mountain pine positively correlated with maximum temperatures in April of the previous year in UG, and negatively with maximum temperatures in September of current year in BK (Fig. 12). Tree growth of pine was positively correlated with minimum temperatures in April and June of current year in UG (Fig. 12). Moving correlation functions between TRW and precipitation in mountain pine did not show positive correlations between TRW and precipitation of the current year in recent decades, except in August of the previous year in PG (Fig. 13). Moving correlation functions showed positive correlations between TRW and maximum temperature in March of the current year (from 1984 until 2013) and of the previous year in BK (Fig. 13).

Figure 12. Plot of bootstrapped response function analysis relating tree-ring growth of beech to precipitation (top-left) and maximum temperature (top-right) from previous March to current October, and bootstrapped response function analysis relating tree-ring growth of mountain pine to maximum temperature (down-left) and minimum temperature (down-right) in the period 1901-2013. Months of the previous-year are reported in lowercase letters, months of the current year n uppercase letters.



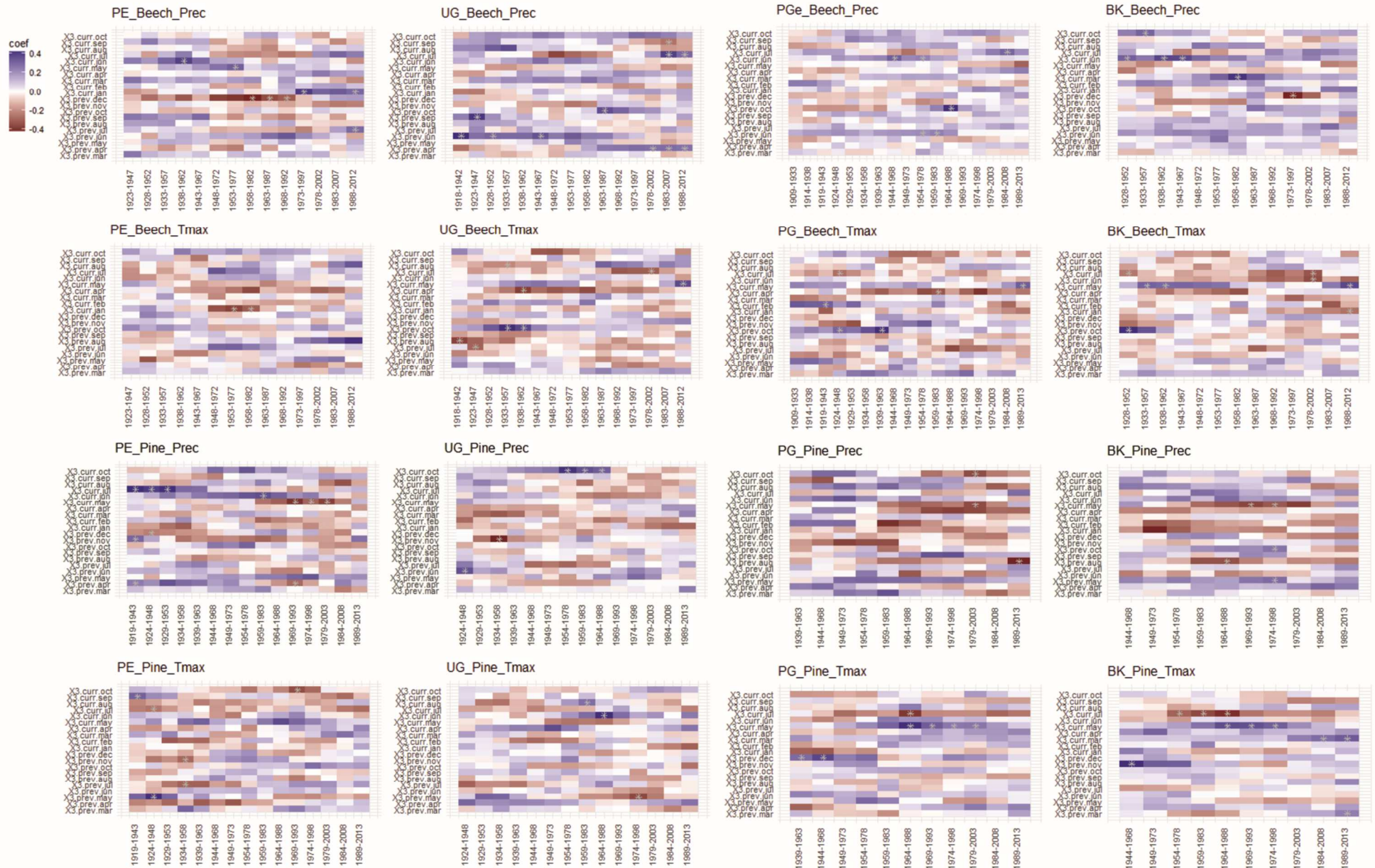


Figure 13. Moving correlation functions relating tree-ring growth with precipitation and maximum temperatures from current March to current October of beech and mountain pine at the subalpine ecotone in Majella National Park. The moving correlation is carried out in windows of 35 years, offset by 5 years. Significant correlations are denoted by asterisks. The naming scheme, i.e., abbreviated year (current or previous) and month. It is evident that the majority of coefficients displays temporal fluctuations. The asterisks in the plot indicate windows with significant correlations, positive or negative, for the given variable.

3.2 Results at the elevational gradient:

3.2.1 Stand description and tree rings

From our results the variability of structural features of beech stands in Orfento and Ugni along the elevational gradients distinguished the effects of forest management practices in the forest stands and from those at higher altitudes, at the subalpine ecotone. Beech stands in O1 and U1 and O2, U2, included coppiced, uneven aged and unthinned forests. At higher altitudes, with steep slope, shallow soil, and intense wind (O2, U2), stand structure was that of an aged coppice, particularly in U2. Tree distribution was irregular and sparse. The spatial pattern determined gaps in the forest canopy allowing tree regeneration in U2 and O2. U2 showed the highest diameter at breast height (DBH), and did not show establishment of new seedlings, growing in the sampling area.

The long distance from the nearest village and the low productivity of the forest stand limited the forest use in O2, at high elevation, with consequences on its structure and tree size (trees showed a mean DBH of only 8 cm compared to other plots). Conversely, at lower altitude, the effect of relatively recent coppicing was evident in O1, with high proportion of stems aggregated in stumps. Sprouts, densely clustered in clumps, had small DBH, with a mean DBH of 8 cm and maximum of 36 cm (O1). O1 showed peaks in the first two diameter classes (5-15 cm, data not shown), with presence of natural abundant regeneration, colonizing open canopy gaps, interspersed between several big trees. This was confirmed by the highest number of stumps and trees (Table 5). In U1, at lower altitude, the slope steepness decreased, soil thickness increased, and wind was less intense. Therefore, U1 showed a lower number of sprouts compared to O1; here, the structure was that of an old coppice stand, in which all diameter and age classes were well represented (data not shown). This plot also showed the highest maximum DBH (54.5 cm).

Trees diameter of each plot was different (Table 5). Significant differences between plots were found in the number of trees per ha, average DBH, and average height (Table 5). Mean height ranged between 19.5 m in O1 and only 4 m in O2, showing the same value (14 m) in U1 and U2. Maximum

tree age was found in O1 and U1, where trees reached a maximum age of 112, and 118 years, respectively (Table 5). Mean TRW was higher in O1 and U1, reaching mean values of 1.458 and 1.751 mm, respectively; whereas, the lowest values of TRW was recorded in O2 (0.518 mm) (Table 6). The mean chronologies showed an increasing trend of growth, except for O2, where TRW decreased (data not shown). TRW reached a mean value greater than 1 mm per year in all plots, except for O2, in which TRW reached 0.5 mm per year and maximum DBH of 8 cm. Mean inter-series correlations of standardized chronologies, as well as EPS values (> 0.85), statistically verified the visual crossdating (Table 6). MS value was high in O2 and U1 (0.423 and 0.336, respectively).

Plots	O1	O2	U1	U2
N. of stumps	210	34	81	31
Maximum diameter (cm)	36.5	13	54.5	34
Mean diameter $\pm$ SD (cm)	8.1 $\pm$ 1.5	8.5 $\pm$ 1.7	12.4 $\pm$ 3.3	15.4 $\pm$ 5.2
Average height (m)	19.5	4	14.7	14.25
Average age of cored trees (years)	81	72	83	84
Maximum age (years)	112	95	118	102
Time span	1901 - 2012	1918 – 2012	1895 - 2012	1911 – 2012
Forest Management	Coppice	None	Coppice	Coppice

Table 7. Structural traits, tree age and time span of beech stands (O1, O2, U1 and U2).

Descriptive statistics	TRW (mm)	AC	rbar	EPS	MS
O1	1.219	0.521	0.293	0.828	0.307
O2	0.518	0.544	0.410	0.872	0.423
U1	1.700	0.585	0.453	0.885	0.336
U2	1.376	0.605	0.433	0.924	0.277

Table 8. Descriptive statistics of tree-ring width for beech in the four sampling plots. Mean TRW, first-order serial autocorrelation (AC), mean inter-series correlation (rbar), mean expressed population signal (EPS) (number of years > 0.85), mean sensitivity (MS). Mean TRW was computed on the raw tree ring series; AC, rbar, EPS and MS were computed on the indexed tree ring series (EPS = obtained for 30 years with 15 years overlapping; mean = average of all values ≥ 0.85).

3.2.2 Anatomical traits

Wood anatomy showed low DH in O2. Cell density (CD) increased from earlywood to latewood conduits in all plots. Significant linear relationships (Table 9) between hydraulic functional traits (in each ring) and plot characteristics related to differences in altitudes were observed (Table 9, Fig. 14). Mean CD was higher in U2 and O2 (Fig. 14), ranging between 200 and 250 mm⁻¹, than in O1 and U1. Mean cell size per ring (MCA) was the lowest in O2, reaching a minimum value of 14000 μm^2 . Values of KH, KS and DH were also the lowest in O2. TRW was negatively correlated with CD in O2 (Table 7), while, a positive correlation was found in all other plots. RVGI did not show differences between plots; whereas, a positive correlation was observed between KH and TRW (Table 9). RCTA was negatively correlated with TRW in O1 and O2, and this was not the case in U1 and U2 (Table 9). All plots showed a significant correlation between RCTA and Ks. The correlation between KS and DH was higher in U1 and O1 than U2 and O2 (Table 9). Precipitation and SPEI were positively correlated in all plots, while, temperature and SPEI were negatively correlated.

3.2.3 Relationships between local weather conditions and tree ring traits

Correlations between tree ring traits and conventional monthly weather data highlighted the influences of climatic drivers on TRW and DH (Table 9, Fig. 15). Precipitation influenced positively tree growth at the beginning of the growing season (April) in O1 and U2, in May in O2; whereas, the relationship between precipitation and tree growth was negative in U1. Temperature negatively influenced TRW in July in O1 and U2, in September in O2; while, temperature had a positive influence on TRW in October (data not shown).

Relationship between DH and temperature in November of previous year was positive, and negative in May of previous year and in October of current year in O1; it was negative in March of current year in O2. In O1, DH was positively correlated with precipitation in July of previous year and in May of current year; whereas, in O2, DH was negatively correlated with precipitation in December of previous year (Fig. 15). In O2 and O1, DH and SPEI in May and September of previous year,

respectively, were positively correlated; whereas, in O1, DH and SPEI in September of current year were positively correlated. In O2, the relationship between DH and SPEI in March of previous year was negative (Fig. 15).

In U1, DH and temperature in June of current year were positively correlated, while DH and temperature in August of previous year, and in August and September of the current year, were negatively correlated (Fig. 15). In U2, temperature and DH were not correlated. Positive correlations between DH and precipitation in June and August of previous year and in May of current year were found; whereas, in U1, a negative correlation was observed between DH and precipitation in November of previous year. In U2, DH was positively correlated with precipitation in June of the current year (Fig. 15). DH and SPEI in September of current year in U1 and DH and SPEI in July of current year in U2 were positively correlated; whereas, the relationship was negative between DH and SPEI in October of previous year in U1 (Fig. 15).

Correlations between precipitation and anatomical traits were significant for KH and DH in U1 (Table 7).

	temp		prec		SPEI		TRW		RCTA		KH		KS		RVGI		DH	
	O1	O2	O1	O2	O1	O2	O1	O2	O1	O2	O1	O2	O1	O2	O1	O2	O1	O2
Temp	1	1																
Prec	-0.22*	-0.26*	1	1														
SPEI	-0.19	-0.2	0.95*	0.96*	1	1												
TRW	-0.18	0.02	0.17	0.16	0.18	0.23*	1	1										
RCTA	0.09	-0.18	-0.01	-0.06	0	-0.06	-0.45*	-0.34*	1	1								
KH	-0.07	-0.12	0.17	0.08	0.19	0.14	0.59*	0.62*	0.27*	0.37*	1	1						
KS	0.05	-0.17	0.02	-0.02	0.03	0	-0.32*	0.03	0.90*	0.85*	0.42*	0.69*	1	1				
RVGI	0.11	-0.08	-0.02	-0.03	-0.04	-0.02	-0.43*	-0.41*	0.72*	0.75*	0.12	0.04	0.61*	0.49*	1	1		
DH	-0.03	0	0.13	0.01	0.11	0.06	0.02	0.49*	0.59*	0.24*	0.57*	0.75*	0.76*	0.68*	0.34*	-0.02	1	1

	temp		prec		SPEI		TRW		RCTA		KH		KS		RVGI		DH	
	U1	U2	U1	U2	U1	U2	U1	U2	U1	U2	U1	U2	U1	U2	U1	U2	U1	U2
temp	1	1																
	-																	
prec	0.25*	-0.25*	1	1														
SPEI	-0.19	-0.19	0.96*	0.96*	1	1												
TRW	0.03	0.03	0.01	0.18	0.03	0.14	1	1										
RCTA	-0.02	0.14	0.17	0.06	0.13	0.08	-0.18	-0.06	1	1								
KH	0.04	0.18	0.14	0.12	0.12	0.13	0.56*	0.56*	0.41*	0.46*	1	1						
KS	-0.09	0.13	0.23*	0.12	0.2	0.14	-0.17	0.15	0.92*	0.92*	0.52*	0.67*	1	1				
							-	-										
RVGI	0.07	0.12	0.08	-0.03	0.04	0.02	0.53*	0.31*	0.59*	0.70*	-0.09	0.23*	0.45*	0.59*	1	1		
DH	-0.16	0.02	0.22*	0.15	0.21	0.17	-0.04	0.57*	0.76*	0.36*	0.55*	0.83*	0.91*	0.65*	0.21	0.11	1	1

Table 9. Correlations between climate data (temperature, precipitation and SPEI) and anatomical traits (TRW, RCTA, KH, KS, RVGI, DH) in O1, O2, U1 and U2 plots. Kruskal-Wallis test was used to compare means of anatomical traits among locations. Correlation coefficients, R higher than 0.54, significant at 95% confidence level, are indicated in bold and with asterisk (*).

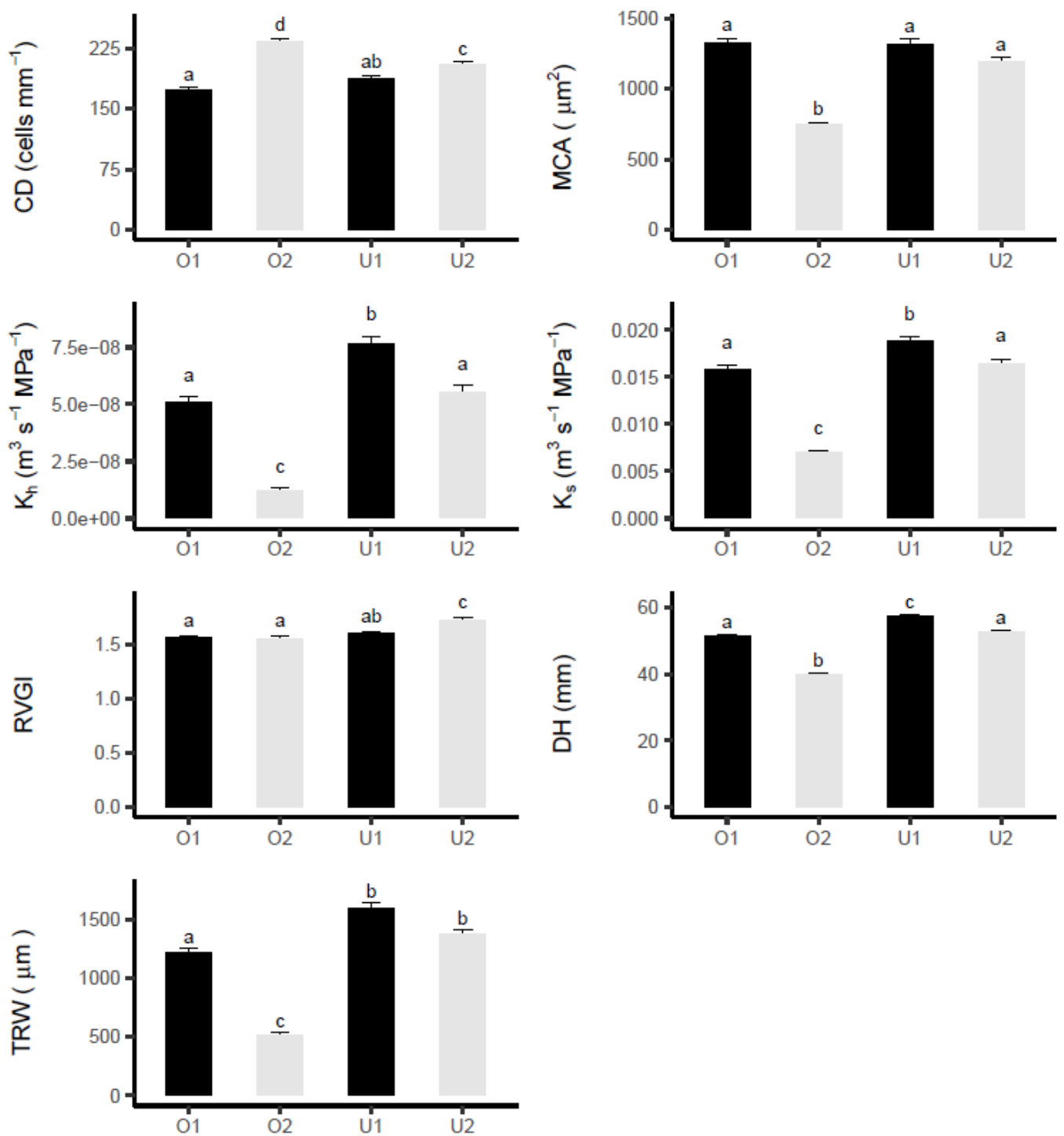


Fig. 14. Cell density (CD; cells mm^{-1}), mean cell size per ring (MCA; μm^2), accumulated potential hydraulic conductance (KH; $\text{m}^3 \text{s}^{-1} \text{MPa}^{-1}$), xylem-specific potential hydraulic conductivity (KS; $\text{m}^3 \text{s}^{-1} \text{MPa}^{-1}$, vessel grouping index (RVGI), overall mean hydraulic diameter (DH; mm), mean ring width (TRW; μm) in O1, O2, U1 and U2 plots. Different letters indicate significant differences of anatomical traits between locations. Differences were tested by a post-hoc Dunn test. Error bars show $\pm$ standard error values.

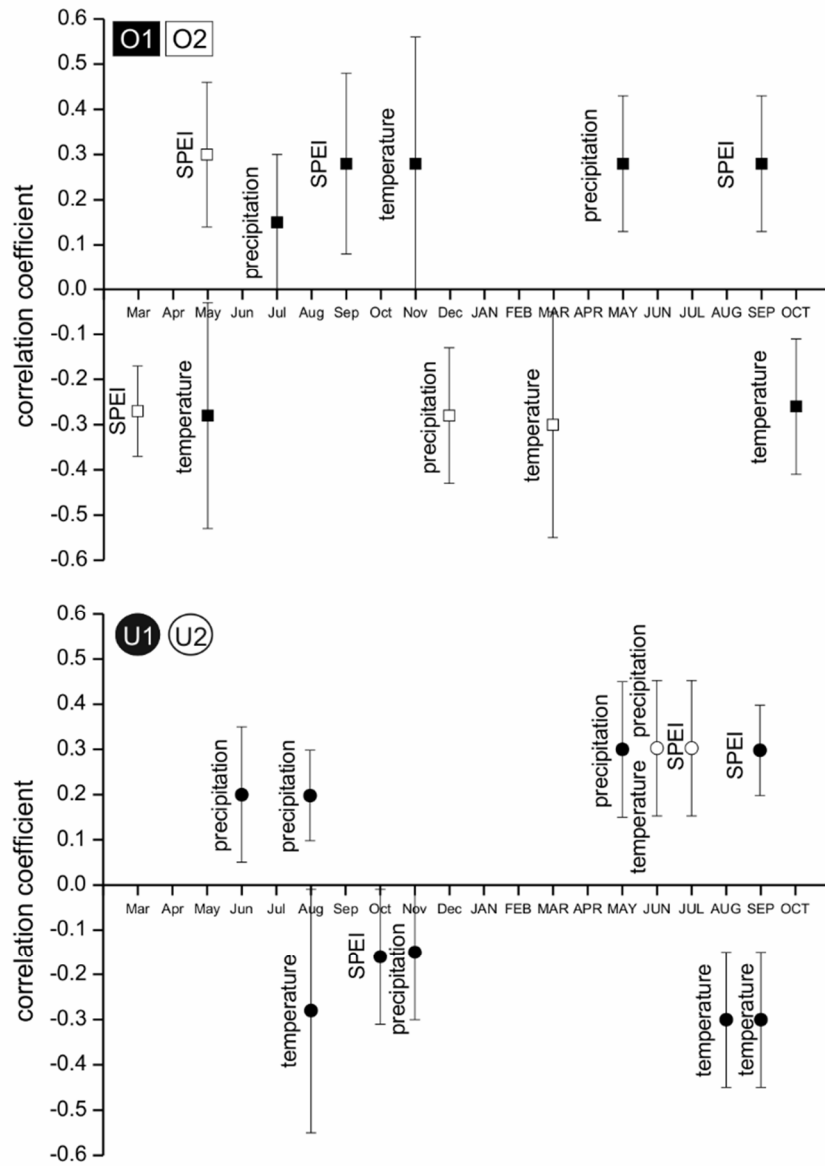


Fig. 15. Bootstrapped correlation values between DH and temperatures, precipitation and SPEI in O1 (black squares), O2 (white squares), U1 (black circles) and U2 (white circles). Correlations were calculated separately for each month for the period from March of the previous year (lowercase letters) to October of the current year (uppercase letters) in the period 1901-2015. Significant correlation values are reported ($P < 0.05$).

4. Discussion

4.1 Subalpine ecotone with beech and mountain pine

Climate and land-use changes concurred in affecting the growth of mountain pine and beech at the transitional ecotone between closed forest and krummholz of Majella Massif. The observed combination of climate and land cover changes had a strong impact also on vegetation shift, which in turn may affect the final set of benefits for local communities that these forests provide. This is particularly important for rural mountain communities, considering the recent abandonment of agro-forestry activities (mainly grazing) and of the reduction of associated goods (livestock productions, wood and non-wood forest products, etc.). For example, in PG the open areas are characterized by beech recruitment where young beech trees established within mountain pine krummholz. Here land cover varied from 37% to 49% for beech and between 26% and 41% for mountain pine (1954-2017) (Table 4). Variation in disturbance regime and land cover, related to climate (summer became increasingly drier in the period 1954–2013, in the study area) and land-use changes (human pressure decreased in the same period), impacted the ecotonal boundaries, creating favorable conditions for the establishment of beech at higher altitude and of mountain pine at lower altitude. For instance, high snow deposition may provide shelter against abrasion by wind and adequate soil moisture at the start of the growing season, though a deep snow cover may variably limit seedling establishment depending on the species (Camarero et al., 2000).

4.1.1 Beech stand

The structure of beech stands (Table 2) highlighted a wide intraspecific variability in response to environment at high altitude. Beech grew slowly in PE, where climatic and environmental conditions related to the altitude, limited plant growth (2127 m a.s.l.). Nevertheless, beech took, probably, advantage from the nurse effect exerted by mountain pine and expanded in density. The eldest mountain pines were in PE, where anthropogenic practices were absent because the topography makes it difficult to access the site; yet, mountain pine decreased in density. On the contrary, the youngest mountain pines were in BK, which suffered continuous forest cutting for production of charcoal in the 1950s (low values of MS in Table 6); nevertheless, in BK species-specific density fluctuation followed a pattern similar to PE, mountain pine still being the dominant species. Given the peculiarity of the Majella Massif, the protective role of krummholz on beech seedlings and

interactions with microtopography and microclimate warrant further studies (Holtmeier and Broll, 1992).

Dendroclimatological analysis was used: to define the influence of temperature and precipitation on tree growth during the vegetation season. In general, TRW was negatively correlated with maximum temperatures in beech, although being positively correlated with maximum temperatures in September and November of the previous year and October of the current year, at the highest elevation in PE. In PE, anthropic disturbance was less relevant than climatic constraint. Precipitation influenced tree growth in beech at the beginning of the growing season (May) and in July, in the last 30 years. The positive correlation observed at the beginning of the growing season can be related to the high altitude of this site, where the species grows at 2127 m of altitude in extreme life conditions. Beech has European-wide natural area, yet, ecophysiological and dendroecological studies revealed that populations at the southern margin of its distribution are sensitive to drought (Tognetti et al., 1995; Peñuelas et al., 2008; Piovesan et al., 2008; Fotelli et al., 2009; Tognetti et al., 2014; Bolte et al., 2016; Coccozza et al., 2016). Direct evidence of the impact of summer drought on beech growth was here provided by the positive correlation between TRW and precipitation in July, even at high elevation. Beech in BK suffered from anthropogenic disturbance, especially during the 1950s, when the forest was completely harvested. In addition to the relevance of the start of dry season on beech growth (Maselli et al., 2014), increasing damage from late spring frost in recent years may control inter-annual productivity variation on the Majella Massif (e.g., Bascietto et al., 2018).

4.1.2 Pine stand

Precipitation did not affect tree growth of mountain pine in the last decades. In PE, the late start of growth season can be related to the high elevation of the site. Palombo et al. (2014a) observed that temperature and precipitation in April and May played a key role in radial growth of mountain pine on the Majella Massif. The evolution of the subalpine ecotone on the Majella Massif was mainly related to spring and autumn climatic conditions, while on the Italian Alps, the radial growth of mountain pine and its expansion over the current climatic treeline were strongly influenced by high temperatures of May and July and precipitation of June (Pelfini et al., 2006). High temperatures and significant climate-growth relationships may explain amelioration of growing conditions of mountain pine over the current climatic conditions of the subalpine ecotone, contributing to an increase in the range distribution of this conifer species. Mountain pine is expanding towards higher and lower altitude, re-colonizing large areas formerly grazed and cut, especially where the soil is shallow and

rocky. Mountain pine is a pioneer species of avalanche chutes and abandoned pasturelands, threatening endemic herbaceous species and influencing local resource management (Dai et al., 2017). The response of forest communities and ecotonal vegetation to global change can, therefore, be influenced by interactions of single climatic and land-use components with tree species. On the other hand, ecotone evolution and vegetation shift in different elevations may modify the status of biodiversity refugia at high elevation on the Apennines (Stanisci et al., 2005).

Land cover in the mid of the twentieth century showed a closed mountain pine mat and beech forest stand with scattered vegetation (Table 4). The upward shifts of mountain pine *krummholz* above the current treeline appear to be driven by both climate and land-use changes (Palombo et al., 2013), whereas introgression of mountain pine downwards into the beech closed forest can be mainly related to the progressive abandonment of traditional forest management. Indeed, the effect of land-use changes was more important in the zone of transition between beech closed forest and mountain pine *krummholz* than in the upper treeline ecotone (e.g., Treml et al., 2016). Yet, over the last 60 years, beech forest recovered from clear-cutting during the postwar period. Nowadays, the upward shifts in recruitment of beech, in contact with mountain pine, take advantage from canopy shadowing, natural disease of mountain pine and high temperatures. In the MNP, since 1975, beech forest cover has expanded into abandoned farm lands and subalpine pastures at a rate of 1.2% year⁻¹ (van Gils et al., 2008), from the contiguous, mid-altitudinal beech stands. This is consistent with observation on forest expansion at the treeline in the Alps during the 20th century (Gehrig-Fasel et al., 2007). Forest cover is currently expanding in many mountain areas of the Italian peninsula (Motta et al., 2006). Transient forest expansion, due to the process of natural succession causing tree encroachment into abandoned farmland, represents a major land-use change with tremendous impacts on the mountain landscape. In concurrence with warming temperature, maturing secondary forests and increasing growing stock may result in increasing the risk of incurring disturbance events in the Apennines, as well as in the Alps (Bebi et al., 2017), and need smart management approach.

4.2 Elevational gradients of beech forest stands

The first hypothesis of growth traits in beech species, covarying with altitude was confirmed by our results; differences between plots in growth traits were determined by both different altitudes and climatic variables. Radial growth rates declined with altitude (Fig. 14, Table 9). Distinct DBH values of trees at different elevations were also related to plot-specific environmental conditions and management legacy, which also affected structural features and stand dynamics of beech both at the

lower elevation and at the subalpine ecotone. At low elevations, in U1 and O1, trees showed high proportions of conducting area in the stem and higher mean DH values. In O1 and O2, temperature influenced DH negatively at the beginning and at the end of the growing season (results also confirmed by the correlation with SPEI), while a positive influence of temperature in November could result in a lengthening of the growing season in O1 (Table 9, Fig. 15). Indeed, a clinal variation (north-south Europe) in xylogenesis duration has been observed by Martinez del Castillo et al. (2016) in beech, which was attributed to differences in temperature and precipitation in summer. Beech is also sensitive to yearly variation in weather conditions (Dittmar et al. 2003, Cufar et al. 2008), and deficient precipitation may cause early cessation of cambial cell division, as well as narrower annual ring widths (Giagli et al. 2016). A negative impact exerted by elevation have been found on the duration of the growing season in beech (Kraus et al. 2016, Prislan et al. 2013, 2018). In O2, lower temperature of March may contribute to the persistence of a larger snow pack in early spring with shortening of the growing season and possible consequences on hydraulic architecture (DH). Runoff of melting water before the start of the growing season may slow down, while the persistence of snow cover may reduce the exposure to damaging freezing temperature (Olano et al. 2013).

In the sampling areas tree growth is influenced by increasing temperature. In U1, the negative impacts of summer temperatures, especially in August and September, can be related to high potential evapotranspiration at low altitude (Levanic et al. 2009, Lebourgeois et al. 2010). Temperature in early spring has been found to affect tree ring widths in high mountains of Mediterranean environments (Di Filippo et al. 2007). Precipitation of spring and summer months influenced TRW and DH (with the exception of O2, the plot at the highest elevation). In Mediterranean context, groundwater recharge from spring precipitation favours a prompt initiation of the growing season, enabling trees to invest in secondary growth (De Soto et al. 2012). Nevertheless, in O1 low precipitation in July was a limiting factor in radial growth. In O2, a delay in the activation of the tree functionality at the beginning of the growing season was due to the altitude of the plot. The influence of altitude on tree growth and hydraulic traits was predominant over other environmental factors, such as slope and exposure of plots (O1 and O2 differed only for altitude). Environmental conditions at time of vessel formation determine hydraulic architecture (Fonti et al. 2010). Freezing-induced xylem embolism in beech at high elevation may increase throughout winter (Cochard et al. 2001).

In these Mediterranean mountains, temperature at the beginning of the growing season determined radial growth of beech at high elevation, probably in relation late-frost damage risks or growth-reactivation temperature requirements (Di Filippo et al. 2007). Correlation between temperature at

the end of the growing season of beech may reveal the existence of a second growth pulse at low elevation (O1) (Olano et al. 2013), after the period of Mediterranean summer drought (Olano et al., 2013, Camarero et al. 2013). In the Italian Peninsula, stem radial growth of broadleaved trees, including beech, has been found to be positively influenced by relatively high precipitation and low drought in summer months (Leonelli et al. 2017). Combined analysis of tree rings and stable isotopes has revealed a continuous enhancement in intrinsic water use efficiency and basal area increment at different sites along the Italian Peninsula, during the twentieth century (Tognetti et al. 2014), with potential enhancement of beech stand productivity (e.g., Chiesi et al. 2014). Although a longer growing season can be expected, following warming temperature, with an earlier spring start and later autumn end of carbon uptake period in temperate forests (Dragoni et al. 2011, Keenan et al. 2014), tree carbon balance response to an extended growing season is site-dependent and driven also by other environmental factors.

The studied marginal beech populations, in particular stands at higher elevation, had high sensitivity to environmental variability and trees showed anatomical adaptation traits to limiting conditions (in response to altitude) (O2), confirming our second hypothesis. Therefore, a reduction in DH with increasing altitude was expected. Hydraulic architecture was affected by climate and altitude, through adjustment in radial growth, RCTA, MCA, KH, and DH (Fig. 14; Table 9). Extreme climatic conditions at 2127 m a.s.l. (O2) limited the height to which trees might grow (mean tree height was 4 m). At higher altitudes, in stand with low density (U2 and O2), small vessel lumens and high RVGI, rather than privileging growth performance, preserved water conducting system from freeze-thaw events causing xylem embolism to some extent, ensuring high hydraulic safety (Lemoine et al. 1999). A low vessel size can be partially compensated by a high number of vessels formed in the ring, i.e., a higher CD (Diaconu et al. 2016, Eilmann et al. 2014). At lower elevations (U1 and O1), high hydraulic efficiency leads to high growth rates. Larger vessel lumens and higher hydraulic efficiency, promoted by warmer air temperature and soil moisture availability, resulted in greater growth rates at the cost of xylem safety (Hacke and Sperry 2001), increasing the risk of drought-induced cavitation (Stojnic et al. 2013). Negative relationships between CD and TRW in beech have been found in Pourtahmasi et al. (2011), Stojnic et al. (2013), Eilmann et al. (2014), Giagli et al. (2016) and Prislan et al. (2018).

When evapotranspiration is high, drought negatively affects vessel growth and, thus, can be reflected in reduced vessel size (Sass and Eckstein 1995, Arend and Fromm 2007, Eilmann et al. 2014). Different beech vessel features and wood formation patterns between years characterized by different amounts of precipitation have been found by Giagli et al. (2016). Nevertheless, any significant link

between precipitation amount and conduit size has been observed in beech by Prislan et al. (2018). It is possible that water availability becomes a limiting factor for growth of beech at Mediterranean latitudes or dry years, particularly in the case of hot and dry summers (Cufar et al. 2008). In fact, water availability directly affects vessel size, determining the cell turgor pressure necessary to stretch the primary cell wall of the forming cells (Castagneri et al. 2017). Precipitation and temperature of June and July regulated the radial growth pattern of these beech stands, as observed by Di Filippo et al. (2007) in eastern Alps. Low temperature at high altitude and high evapotranspiration at low altitude affected negatively beech growth in summer, as found by Fischer and Neuwirth (2013) in western Germany. With absence of frost events, warm temperature in spring triggers cambial activity and favours carbon assimilation, thus increasing growth rate of beech (Michelot et al. 2012). Soil water availability is also important in late spring and early summer, in correspondence of the peaks of high wood production rate (Primicia et al. 2013, Rossi et al. 2009). Substantial losses of tree productivity with increasing altitude in beech stands were observed in mountain beech, resulting from decreased photosynthetic and respiration rates (Coomes and Allen 2007).

Results of the present study contribute to a better understanding of the plasticity in xylem hydraulic architecture and the different strategies adopted by beech trees at different altitudes in Mediterranean context. Phenotypic plasticity over the life span of beech trees was a result of short-term to long-term physiological responses to climate variability and can be used to link local environment with xylem structure (Fonti et al. 2010). Intraspecific variation along environmental gradients, or between contrasting sites provides insights about the linkage between adaptation potential of tree species and functional attributes of wood structures (e.g., xylem anatomy) (e.g., Carlquist 1975, Baas 1986, Villar-Salvador et al. 1997, Wheeler et al. 2007). Variation in wood-anatomical characteristics represents adaptive structural solutions that a tree adopts in order to achieve an optimal balance among the competing needs of support, storage and transport under changing environmental conditions and phylogenetic constraints (Chave et al. 2009).

5. Conclusions

Ecotone dynamics, in Mediterranean mountains of the Majella National Park originated from increasing temperature (inducing a longer growing season and facilitating the upward shift of forest trees) and abandonment of past land-use (creating the opportunity for the introgression of mountain pines into beech stands, as well as the upward movement of beech). Spatial patterns and growth trends

of mountain pine and beech were affected differently by altered disturbance regimes, which may impact species-specific seedling encroachment and forest-krummholz ecotone evolution.

Vessel traits and hydraulic properties of beech in this Mediterranean mountain context differed between plots, following an altitudinal cline. Trees showed xylem plasticity in relation to anatomical traits and adaptation to limiting conditions. At lower elevation, trees had higher hydraulic efficiency and growth rates, though at higher risk of increased vulnerability to cavitation. In the present environmental conditions, vessel hydraulic characteristics and stem radial increments are directly related and may exhibit critical issues and thresholds related to altitude. Yet, precipitation is a limiting factor for stem radial growth and xylem vessel functionality in beech on the Majella massif and, probably, in other southern sites with a similar Mediterranean setting.

The combination of climate change and land use has a strong influence on tree growth and the expansion of forest areas, that can have positive or negative effects on local communities, particularly in the case of the recent abandonment of agro-forestry activities (mainly pastures) and the reduction of associated public use requirements (livestock production, timber and non-timber forest products, etc.). The results of the studies suggest that forest management and related changes can help to define an adaptive approach based on the resilience of forest ecosystems in the Mediterranean environment. The study stimulates further investigations towards: (i) the development of a resilient landscape mosaic configuration in fragile and threatened mountain forest environments, considering the driving forces of climate and land use; and (ii) the inclusion of the analysis of tree growth in decision-making processes at different institutional levels.

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I would like to finish this thesis in Italian, to express my feelings in the best way:

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7. Supplementary materials

7.1 Geology and geomorphology of the Majella massif

The Majella Massif is located in the Majella National Park (MNP), Abruzzo region, central Italy, along a north-south ridge at 32.5 km away from the Adriatic Sea. The Majella Massif has an overall area of 11 km² above 2500 m a.s.l., with 27 peaks over 2000 meters and the highest summit (Monte Amaro) reaching 2794 m a.s.l. (Stanisci et al., 2005).

The geological history of the Majella Mountains follows the structural geological evolution of the Central Apennines. These mountains are mainly characterized by carbonates from Lazio-Abruzzi Platform and the internal Apula Platform. The landscape is dominated by carbonatic lithologies, in which are well represented all the geological periods ranging from lower Jurassic to upper Miocene (i.e., from 200 to about 6 million years ago). The structural geological evolution of the area started during the upper Triassic (about 200 Ma) in a carbonatic platform environment, characterized by shallow water (between 0 and 150 m) where thick carbonate rocks layers were settled. There was therefore a succession of depositional phases with emergence phases of this platform, until the orogenetic “push”, which shaped the Apennines during the Pliocene (in the last 5 million years) and which contributed to the surfacing of the system at the current altitudes. After the emersion phase, these deposits were affected by strong erosional processes caused by meteoric waters, winds, thermal excursions and ice. In particular, the carbonatic lithologies are still affected by karst phenomena linked to meteoric waters, which having an acidic pH cause the dissolution of carbonates. In these lithologies the meteoric water, having a limited flowing surface (caused by the soil rifts and by karst phenoma), flows below ground and emerges downstream.

The Majella massif has a round shape thanks to the anticlinal axis and has also been modeled by the Quaternary glaciers that have left glacial cirques and top valleys (such as the Valle di Femmina Morta, from glacial origin and remodeled by karst phenomena (Fig. 16). Unlike other Apennine mountains are characterized by glacial valleys, during Quaternary glaciations this area was covered by a large ice cap (about 30 km²) which covered the higher portion of the chain, with a maximum thickness of 200 m (Catonica and Manzi, 2002). In addition on the eastern and northern sides, the massif is carved by deep river valleys, e.g., the Orfento Valley, the Mandrelle-S. Spirito and Taranta Valleys. The whole area shows traces of the ice modeling action. Ice tongues generated by an enormous cap glacier covered the entire summit, descending along the slopes of Majella Massif and modeling the entire area, from the summits to the bottom valleys. These deep “carves” differ greatly from each

other in length, depth and environmental peculiarities. The longest valley is that of Fara S. Martino (14 km) and spectacular are the valleys of Palombaro, Pennapiedimonte and the Valley of Orfento river. However, today this Massif appears as an arid mountain, even if the whole area broadly shares the high altitude vegetation characteristics of the Central Apennines. This high-altitude plateau, broadly sharing the main vegetation of the high-altitude central Apennines, exhibits some peculiar floristic and cenological characteristics, suggesting a different background to the Quaternary development of its vegetation (Blasi et al., 2005).

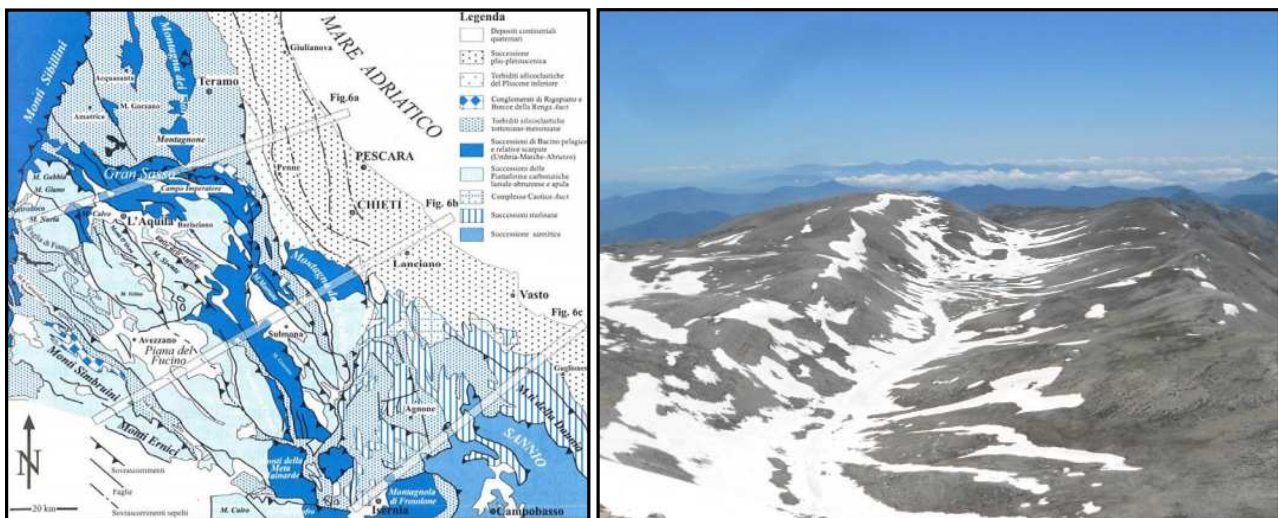


Figure 16. Structural and geological pattern of Central Apennine (from *Guide Geologiche Regionali-Abruzzo*, Crescenti et al., 2003). On the right Femmina Morta valley of glacial origin and modelled by karst phenomena (Picture by C. Calderaro).

7.2 Climate in Majella Massif

The climate variability of Majella Massif is influenced by two main factors:

- 1) the altitude ranges from 300 meters to 2795 m of Monte Amaro;
- 2) the conformation of the massif, which exposes the slopes to different types of atmospheric circulation.

According to the climates Köppen classification, there are four climates that characterize this area:

Sub coastal temperate (Cs) that influences the foothills and low-hill areas, especially towards the Adriatic Sea (the mean annual temperature (T) ranges between 10° C and 14.4° C, the mean T of the

coldest month ranges between 4° C and 5.9° C, 3 months with $T > 20^{\circ}\text{C}$, the annual temperature ranges between 16° C and 19° C);

Sub continental temperate (Cf) which affects higher altitudes referring to the temperate sub-coastal and the inner areas of low and medium mountain areas (with mean annual T between 10° C and 14° C; mean T of the coldest month between -1 and 3.9° C; 2 months with $T > 20^{\circ}\text{C}$, the annual temperature range between 16 and 19° C);

Continental temperate (Cf) which affects medium-high mountain areas, has sub-continental characteristics but with lower temperature values (mean annual T between 6 and 9.9° C, average of the coldest month between 0 and -3° C, average of the warmer month between 15 and 19.9° C, annual thermal excursion between 18 and 20° C);

Cold temperate (Dw), that characterizes the summits areas and the ridges of the massif (with average annual T between 3 and 5.9 ° C, average of the coldest month $< -3^{\circ}\text{C}$, average of the warmer month between 10 and 14.9° C; annual thermal excursion from 16 to 19° C).

In addition, the exposure of the slopes, the influence of the winds and the position of the massif in the Apennine chain imply a relatively moderate influence of the west wind. Although the mountains on the East side are significantly higher than the mountains located on the West side of the massif; there is a favorable exposure to cold and dry winds from the North and the Balkan area and to the warm and humid SE winds. Also the proximity to the sea mitigates the climate, but the shallow depth of the Adriatic sea does not allow the masses of water to significantly attenuate the cold winter (Pezzetta 2001). Generally, the average total precipitation exceeds 700 mm per year, with maximum values in November and December; minimum precipitation values are in July and August, making of the summer season the poorest period in terms of precipitation in the whole area (Fig. 17).

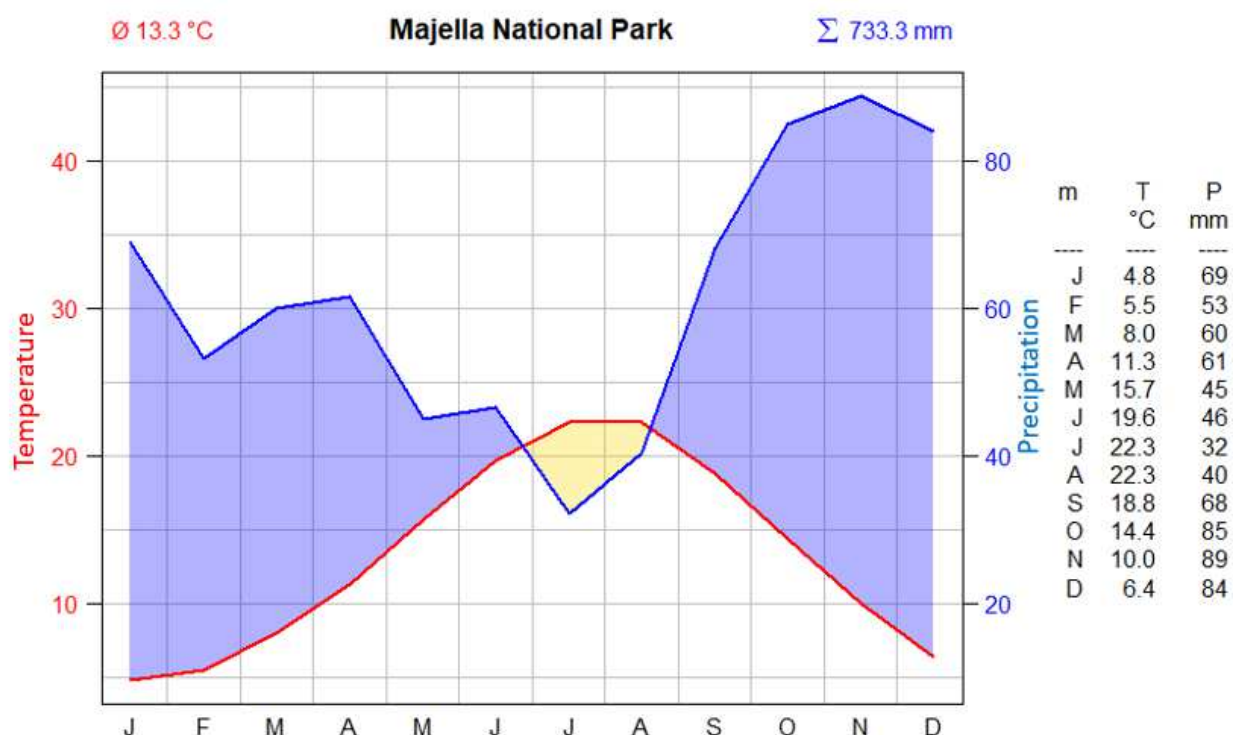


Figure 17. Mean temperature and precipitation data in Majella National Park in the sampling areas for the period 1901-2016, mean annual temperature (on the left side) was 13.3 °C and mean total annual precipitation (right side) was 733.3 mm. Temperature data derived from the CRU TS 4.01 gridded data set with 0.5° spatial resolution. Precipitation data available from monthly precipitation data recorded by the three local meteorological stations in the study area (Pescocostanzo, 1461 m s.l.m. - Lat 41 ° 53 '09"N Long 14 ° 04'. 14"E.; S. Eufemia a Maiella, 888 m s.l.m. - Lat. 42 ° 07 '00"N Long. 14 ° 01 '08"E; Palena, 767 m s.l.m. - Lat. 41 ° 59 ' 01"N Long. 14 ° 08 '15"E.). These stations located in the National Park are considered the most representative of the studied area.

7.3 Vegetation classification

With more than 2000 floristic species, the Majella National Park hosts 65 % of the flora of Abruzzo region, 37 % of Italy and 22 % of the European species (www.parcomajella.it). Vegetation in Majella is represented by several forest types. Each forest type has characteristic tree species composition and it is named with the dominant tree species.

The forests covers more than the half of the protected area, about two thirds are woodlands and for the remaining part is composed by shrubs. The more extended is the deciduous temperate forest, which is composed of various forms: beech, Turkey and white oak (*Fagus sylvatica*, *Quercus cerris*, *Quercus pubescens*), European hop-hornbeam (*Ostrya carpinifolia*), hygrophilous riparian

formations and a single population of birch (*Betula pendula*). The evergreen component is instead composed of dwarf pine stands, pine trees of indigenous black pine (*Pinus nigra* var. *italica*), reforestation of many conifers, juniper and the holm oak wood, that settles on the slope surfaces at lower altitudes. The most widespread physiognomy is the beech forest, which occupies the 30% of the Park territory. It is located in the mountain belt, between 1000 and 1800 m of altitude. At lower altitudes there are the oak woods and the mixed forests of deciduous thermophiles; at higher altitude, up to 2300-2400 m a.s.l., there are the sub-alpine shrublands, i.e., formations prostrate with mountain pine (*Pinus mugo* Turra subsp. *mugo*), juniper (*Juniperus communis* var. *saxatilis*) or bearberry (*Arctostaphylos uva-ursi*). As already mentioned, the Majella mountain pine population is the largest in the Apennines, it has a significant biogeographical and conservation importance, with the southernmost limit of its distribution range in Abruzzo. On the other hand, also the Lobel Maple tree (*Acer lobelii*), an endemic tree species linked to beech-woods, has its northern limit here. The Majella National Park hosts also old growth forests, characterized by the presence of large sized trees and abundant deathwood, as well as by a high diversity of species. Examples of old growth forests include the Bosco di S. Antonio in Pescocostanzo, and some portions of beech forest in the territories of Palena and Pizzoferrato.

At phytosociological level, the calcareous mountain pine stands of the Central Apennines are included in the endemic alliance Epipactido atropurpureae-Pinion mugo (Stanisci 1997), framed in the order Pino-Juniperetalia and in the Pino-Juniperetea class (Rivas-Martinez 1964), syntaxa related to the shrub and tree formations occurring beyond timberline in the Mediterranean area. The species characterizing this alliance are *Pinus mugo*, *Epipactis atropurpurea*, *Moneses uniflora*, *Silene multicaulis* and *Valeriana montana*. In particular in the National Park, the association Orthilio secundae-Pinetum mugo, between 2000 m and 2450 m, occupies the “pockets soil” occurring among the rocky ridges. The soils are eluvial nature, very rich in skeleton, with a high percentage of carbonates in solution, a pH from neutral to sub-alkaline and with a low amount of organic matter. Grouping in *Pinus mugo* and *Hypericum richeri* are well represented between 1800 m and 2100 m a.s.l., on slopes with medium acclivity and with different exposures; the soil is mature, deep, with pH from neutral to sub-alkaline, rich in organic matter and without carbonates in solution. Mountain pine is a protected species in the regional laws n° 45/79 of Abruzzo belonging to the priority habitat type 4070 in the European Habitats Directive (92/43/CEE). Habitat type: 4070 Scrub with *Pinus mugo* and *Rhododendron hirsutum* (Mugo-Rhododendretum hirsuti) these formations usually with *Rhododendro spp.* found occurs on dolomitic or calcareous substrates (Lasen and Wilhalm 2004) and play a major protection role.

7.4 Study area and National Park

The Majella National Park was established on the Majella Massif (MNP), Abruzzo region, central Italy, along a north-south ridge at 32.5 km away from the Adriatic Sea. The research area has a montane climate, with snowy winters and relatively moist summers (Van Gils et al., 2008). Mean annual temperature in the period 1901-2016 was 13.3 °C and mean total annual precipitation was 733.3 mm.

The Majella National Park is one of the five national parks of the Abruzzo region also called “the greenest region in Italy” and it is included between the provinces of L'Aquila, Pescara and Chieti.. The peculiarity of the park is that its area is included around the large limestone massif of the Majella and the Morrone mountain to the west side and Pizzi and Porrara mountains to the east side. More than 2100 plant species have been surveyed in the park, representing a third of all Italian flora; the animal species are more than 150. The park includes seven State Natural Reserves some of them are included in the sampling areas of the study.

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