



**UNIVERSITY OF NAPLES FEDERICO II**

**Department of Agriculture**

**PhD in Agricultural and Agri-food Sciences 32nd cycle**

**PhD Thesis**

**Treeline dynamics and local microclimate of *Fagus sylvatica*  
forests along the Apennine Mountains range**

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To my nephews and the future generation, so that they will learn respect the forests and benefit from these studies. This work is dedicated to Zoey and Alessia Greenberg

## Abstract

*Fagus sylvatica* is the dominant forest species in a wide altitudinal range of the Apennines, from about 1,000 up to 2,140 m a.s.l. The goal of this research project was to investigate climate, topographic, geographic and anthropogenic factors that determine the upper limit of the *Fagus sylvatica* forests (treeline) in the Apennines. The study of treeline responses to climate is strongly influenced by the spatial and temporal scale of the analysis. Three studies at different spatial scale, namely regional, landscape and local scale, have been carried out. At the regional scale, treeline elevation measured on satellite images in fifteen major mountain groups in the Apennines were correlated with selected climatic, geomorphological, and human disturbance variables. At the landscape scale study has been carried out on eight Apennine chains in order to assess treeline advancement and the mechanisms of beech recruitment above the present treeline. At the local scale the study was carried out at the southern latitudinal limit of the *F. sylvatica* range and investigated the role of the beech canopy cover in modulating near-ground microclimate. The result at regional scale showed that, the beech treelines across the Apennines are shaped by the multifaceted interactions between climatic constraints (low winter temperatures and low summer rainfall) and human disturbance, depending on the mountain group and peak considered. The study at landscape scale evidences that the treeline is going to advance upward thanks to the shrub facilitation effects which allow the establishment of *F. sylvatica* above the current altitudinal position of the treeline. The presence of a shrub cover is an indispensable condition for both recruitment and establishment of beech above the upper limit of closed forests, independently of shrub species and elevation. At local scale we stated that *F. sylvatica* canopy cover at high elevation is able to modulate microclimate in contrasting topographic sites of the mountain. The treelines under study are inside regional protected areas or in National Parks, where conservation of these ecotones is a priority.

Key words: Ecotone, treeline, European beech, climatic variables, anthropogenic impact.

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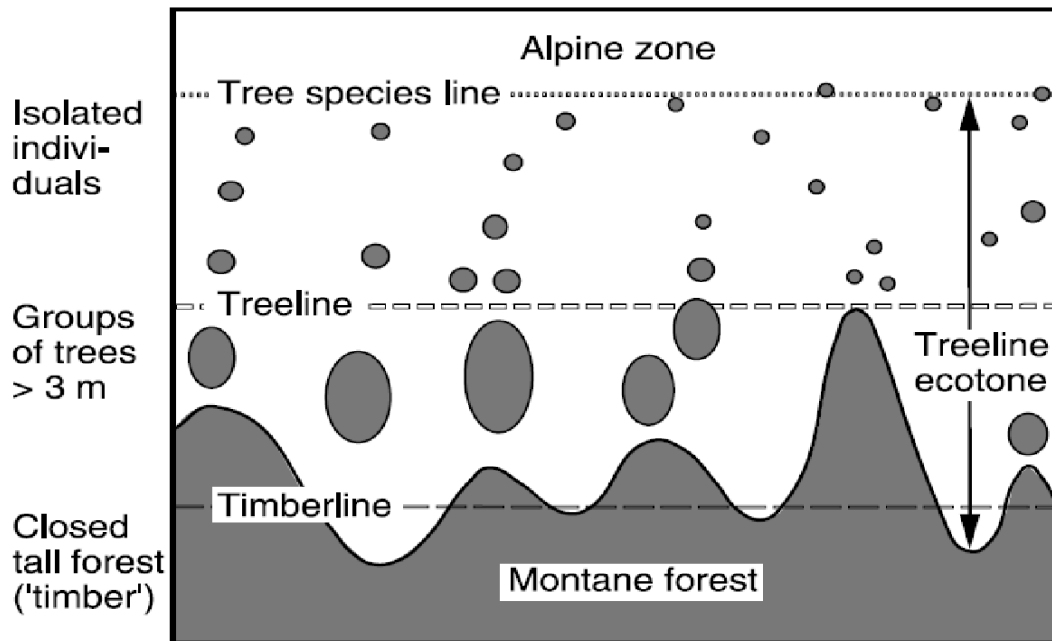
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# **1. Introduction**

## ***1.1 Treeline***

There is a general consensus that the current distribution at global to subcontinental scale of vegetation, particularly for temperate tree species, is controlled by climate (Prentice et al. 1992; Chuine and Beaubien 2001; Svenning and Skov 2004).

Indeed, the climate, by interacting with the physiology of the species, influences the structure and dynamics of the ecosystems (Woodward 1987). Because of their size, trees form the most obvious vegetation boundaries. However, since many of the environmental drivers of tree vigour change gradually and vary with topography, tree distribution boundaries are rarely sharp, and the transition from tree to shrub-only stages may be fragmented and stretching over a few meters. Such transition zones are called ecotones (Körner 2012). The treeline is a clear-cut ecotone and a highly visible ecological limit (Körner 1998). The upper treeline responds to changes in environmental conditions with a time lag of several decades or even centuries (e.g. Woodward 1990; Holtmeier and Broll 2005). Treelines world-wide exhibit striking similarities as well as differences both in structure and position. Some researchers prefer addressing the similarities (e.g. Körner, 1998; Körner and Paulsen, 2004) whereas others prefer emphasizing the differences (Holtmeier 2009) (Fig 1).



**Fig. 1** A schematic representation of the high-altitude treeline ecotone and the nomenclature used in Körner and Paulsen (2004).

Treeline position is commonly associated with the decrease in temperature as elevation increases; across sites around the globe, the mean air temperature during the growing season at the treeline appears to vary roughly between 5.5 and 7.5°C (Körner 1998; Körner and Paulsen 2004). However, although temperatures are an indicator of thermal conditions at the treeline, they cannot solely explain why a boundary exists (Holtmeier 2009).

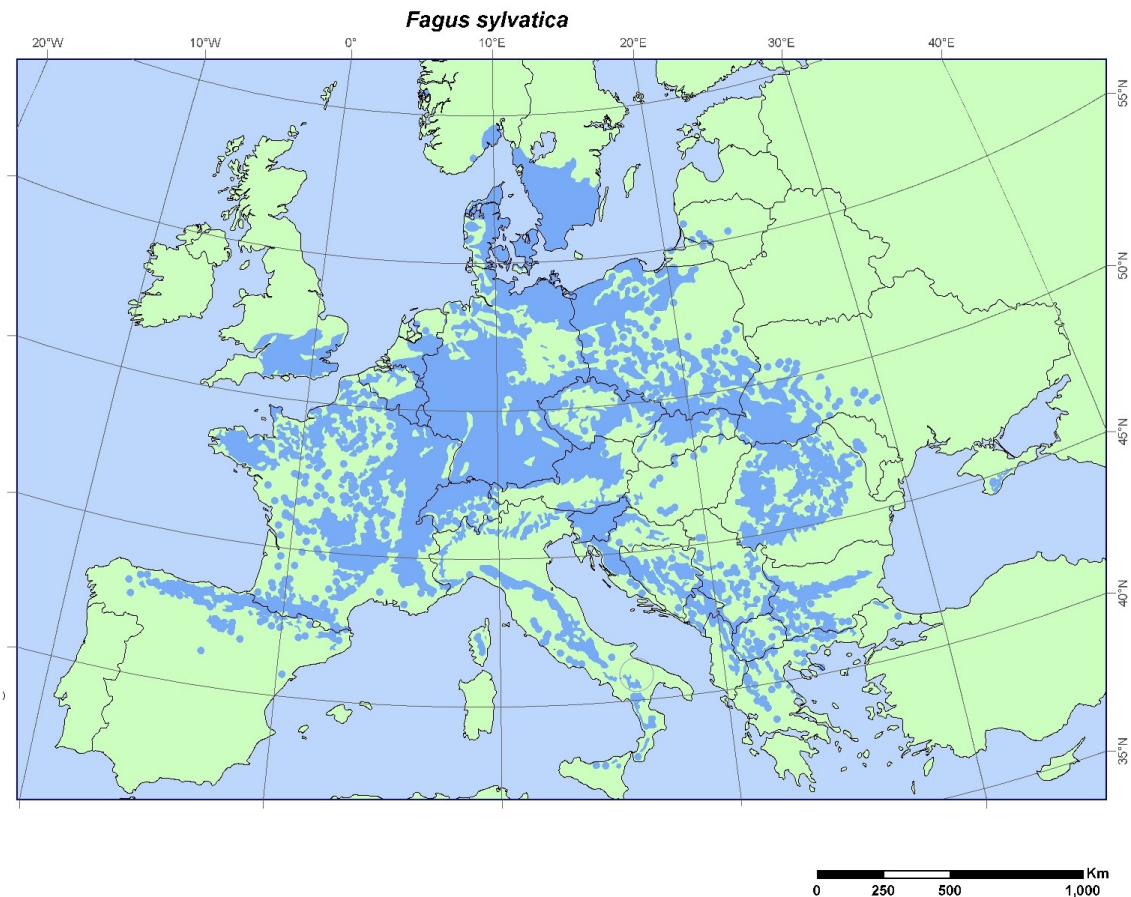
Körner (1998) has identified a number of mechanisms that could explain the treeline position at large scale patterns. However, the mechanisms behind their existence such as anthropic disturbance, drought, and site history, although are less consistent globally, act at smaller scales (Holtmeier and Broll 2005). Large- and small-scale mechanisms are not necessarily mutually exclusive. Large scale mechanisms refer to the stress and physiological tissue damage due to low temperatures or desiccation in the winter season. During the coldest season, the frost can damage cells by freezing or by photoinhibition. Other limits related to mechanical damage at high elevation are due to wind abrasion. At high altitude also reproduction is limited due to decreased pollination, seed

development, maturation, dispersal, and germination. Further, several eco-physiological theories explain the causal-effect relationships between low temperatures at the treeline and growth limitation due to the reduced development of new plant tissue.

Growing season temperatures are widely considered the main factor affecting the position of both latitudinal and altitudinal treelines (Tranquillini 2012; Körner 1998; Körner and Paulsen 2004; Körner and Hoch 2006); however, the role of winter temperatures and precipitation regimes have also proved to be critical (Jobbagy and Jackson 2000; Camarero and Gutierrez 2004; Harsch et al. 2009). Körner (1998, 2007) and Körner and Paulsen (2004) found constant mean ground temperature values of the growing season at the treeline worldwide. These values were set equal to  $6.7 \pm 0.8^{\circ}\text{C}$  by Körner and Hoch (2006). Successive statistical modelling confirmed data from *in situ* measurements suggesting a minimum growth season temperature of  $6.4^{\circ}\text{C}$  globally (Paulsen and Körner 2014). Only in a few cases (e.g. *Fagus sylvatica* Mediterranean treelines) the temperatures at the treeline were found to be substantially higher, a phenomenon interpreted as due to genus-specific boundaries (Körner and Paulsen 2004).

### ***1.2 About European beech species***

The genus *Fagus*, is typical of the European cool-temperate, Asian and North American belt. In Europe *F. sylvatica* spreads from the Sicily in Southern Italy (c.  $37.7^{\circ}$  N) up to Bergen in South Norway (Jalas and Suominen (1988) (Fig 2).



**Fig. 2.** Distribution map of Beech (*Fagus sylvatica*). Genetic Resources Programme (EUFORGEN) [www.euforgen.org](http://www.euforgen.org)

The history of its late Holocene expansion in Southern Europe corresponds to the climatic changes that led to warmer winter conditions (Huntley 1996). Although thermal climate is the most important overall factor in determining the beech distribution (Fang and Lechowicz 2006), very little is known about the relationships between the *Fagus sylvatica* altitudinal limits and the climate (Fang and Lechowicz 2006). Hofmann (1991) suggested a mean annual temperature of 6°C, Pavari (1931) cited a warmest month mean temperature lower than 20°C, and Lausi and Pignatti (1973) reported a growing season of 110–150 days with a daily maximum of 10°C or over, while Dahl (1980) suggested a timberline coldest month mean temperature requirement of around –2.5°C.

*F. sylvatica* is a fast growing, shade tolerant species at seedling stage, with limited tolerance to drought and vulnerable to the early spring frosts that damage the new leaves and inflorescences and



limit its distribution in a continental climate (Larcher 1980; Packham et al. 2012). The beech shows a preference of an oceanic climate with annual rainfall exceeding 1000 mm and it is reluctant to the lowlands and karstic basin, where temperatures are very high (Hofmann 1961, 1991).

### ***1.3 Treeline in the Apennine chains: environmental and anthropogenic factors***

The Apennine mountains extend from Liguria to Sicily, and are surrounded by two seas, the Tyrrhenian and Adriatic Sea, with 200 peaks above 2,000 m a.s.l, reaching their highest point at the Gran Sasso (2,912 m a.s.l.) (Soldati and Marchetti 2017). Areas above the timberline can be regarded as an 'archipelago' of alpine islands on the border between the Central European and the Mediterranean regions in Italy (Ferrari, 2018). In the Apennine mountain chains, the prevailing species is *F. sylvatica* that dominates the vegetation belt from 800 m a.s.l. up to the treeline (Bonanomi et al. 2018). The climate of the Apennines is a mountain variant of the Mediterranean type, with the mean temperature ranging from 0 to 11 °C in January and 24 to 28 °C in July. The total annual precipitation varies between 600 and 4500 mm with frequent winter snowfall above 1000 m a.s.l. (Vacchiano et al. 2017).

The beech forest is widespread all along the Apennine mountains in Italy both on limestone and volcanic mountains. The Northern Apennines host most of the beech coppices having mediocre or discreet vegetative conditions (Hofmann 1961, 1991). In the center and southern Apennines, the carbonate platform offers a much more favourable soil to beech forests. Brown eutrophic Mediterranean soils and rich humus guarantee a cation richness of soils, weakly leached thanks to a summer dryness. The summer drought is also one of the factors that limits the recolonization of the beech into the secondary prairie at high elevation (Bonanomi et al. 2018).

Regarding the Apennines, few studies have been carried out, in order to assess the factor explaining the European beech treeline elevation, taking into account both climate (Pezzi et al. 2008) and other variables more related to local mountain features and land use history (Bonanomi et al. 2018).

#### ***1.4 Study cases and related specific objectives***

Vegetation at the upper limit of the forest has been worldwide an essential subject of study, specially related to species' responses to environmental changes. In Europe these studies have been carried out especially in northern Europe (Poljanec et al. 2010; Geßler et al. 2007) and in the Alps referring mainly to coniferous species (Motta and Nola 2001).

Although *F. sylvatica* in the Apennine has been extensively investigated under several perspectives (i.e. Travaglini et al. 2012; Vacchiano et al. 2017) so far, studies on the treeline ecotone are widely lacking.

Previous studies carried out by Bonanomi et al. (2018) evidenced that the current position of the treeline in the Apennines is broadly and heavily depressed as a result of a complex interaction between climatic factors and the past human pressure.

In this context, the present work has the specific aims of investigate in detail the features of the present beech treeline and the factors affecting its current distribution.

Since the local factors can override general climatic trends and the assessment of treeline responses to climate is strongly influenced by the spatial and temporal scale of the analysis (Holtmeier and Broll 2005) three studies at different spatial scale, namely Apennine scale, landscape scale and local scale, have been carried out:

##### **1) Climatic and anthropogenic factors explain the variability of *Fagus sylvatica* treeline elevation in fifteen mountain groups across the Apennines.**

We correlated treeline elevation, measured on satellite images, in fifteen major mountain groups in the Apennines with selected climatic, geomorphological, and human disturbance variables in order to assess site-specific feature and factors of the treeline elevation testing the hypothesis that:

1a) Mean annual temperature is more important than winter climate in determining the *F. sylvatica* treeline;

1b) the *F. sylvatica* treeline is higher in the warmer southern aspect compared to the colder northern sides; and

1c) human activity negatively affects *F. sylvatica* tree line elevation.

## **2) Shrub facilitation promote the treeline advancing of *Fagus sylvatica* across the Apennines (Italy)**

The landscape scale study has been carried out on nine Apennine chains in order to assess treeline advancement and the mechanisms of beech recruitment above the present treeline. Spatially fine-scale distribution data of *F. sylvatica* seedlings and saplings in areas above the treeline with or without shrubs was obtained through two field campaigns.

Specifically, we tested the hypothesis that:

2a) *F. sylvatica* requires nurse plant to colonize open area over the treeline;

2b) the nurse effect is species-specific, being higher for *Vaccinium myrtillus* compared to *Juniperus communis* and *Pinus mugo*; and

2c) nurse effect is stronger at low- compared to high-elevation treelines.

## **3) *Fagus sylvatica* stand structure modulates near-ground climate in a Mediterranean treeline**

The third study, carried out at local scale at the southern latitudinal limit of the *F. sylvatica* range, investigated the role of the beech canopy cover in modulates near-ground climate precipitation and temperature.

Specifically,

3a) we explored the variability in soil microclimate imposed by topographic conditions and seasonal changes in vegetation cover;

3b) we described systematically the effects of canopy cover on near-ground air temperature and soil moisture in contrasting environments, such as open areas and closed forest stands at the high-altitude vegetation limit.

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**2. Climatic and anthropogenic factors explain the variability of *Fagus sylvatica* treeline elevation in fifteen mountain groups across the Apennines. For. Ecosyst. 7, 5 (2020).**

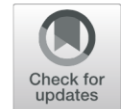
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Forest Ecosystems

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# Climatic and anthropogenic factors explain the variability of *Fagus sylvatica* treeline elevation in fifteen mountain groups across the Apennines



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## **Abstract**

### **Background**

*Fagus sylvatica* forms the treeline across the Apennines mountain range, with an average elevation of 1,589 m a.s.l. Previous studies evidenced that the current position of the treeline in the Apennines is heavily depressed as a result of a complex interaction between climatic factors and the past human pressure. In this study we correlated treeline elevation in the fifteen major mountain groups in the Apennines with selected climatic, geomorphological, and human disturbance variables in order to investigate in detail the site-specific features affecting the current treeline distribution.

### **Results**

Treeline elevation was lowest in the North Italy (Apuan Alps), while the highest treeline was found in Central Italy (Simbruini). An absolute maximum treeline elevation of *F. sylvatica* exceeding 2,000 m a.s.l. was found on 13 mountain peaks in Central and Southern Italy. Noteworthy, treeline elevation was largely lower on warmer south-facing slopes compared to northern slopes, with values several hundred meters lower in the Gran Sasso and Velino-Sirente. Although the causes of this pattern are still unknown, we argue that treeline elevation on south-facing slopes may be limited by the combination of climatic constraints (i.e. summer drought) and human disturbance. Evidence of a pervasive anthropogenic effect depressing treeline elevation was found in the North (Apuan Alps) Central (Gran Sasso, Velino-Sirente, Sibillini) and Southern part of Apennines (Pollino). By contrast, treeline elevation of the Laga, Simbruini, and Orsomarso mountain groups appears less affected by past anthropogenic disturbance. Finally, we recorded in the several mountain groups (i.e. Majella, Marsicani and Pollino) the coexistence of very depressed treelines just a few kilometers away from much higher treelines, among the highest ever recorded for *F. sylvatica*.

### **Conclusions**

Finally, we argue that *F. sylvatica* treeline across the Apennines is locally shaped both by the interaction of low temperatures experienced by the species in its earliest life stages in snow-free open spaces with summer soil water depletion and human disturbance.

**Keywords:** Anthropogenic impact, Latitudinal gradient, Mean annual temperature, Population density, Summer drought, Winter temperature.



## ***2.1 Introduction***

The treeline is a well identifiable ecological boundary representing the upper ecological limit for forest growth and development. Treelines range worldwide from a few meters above sea level in high latitudinal regions to more than ~4,000 m a.s.l. in the Himalayan mountain range and in the Andean Cordilleras (Körner 1998). In recent decades, several studies have sought to shed light on the physiological and ecological factors affecting treeline altitude at regional and global scales (Harsch et al. 2009; Wang et al. 2017). It is widely agreed that temperature is the most important limiting factor for tree growth and development at high altitude (Körner and Paulsen 2004). Limiting temperature, however, at local scale interacts with mountain topography, soil quality, and biotic factors like herbivores and anthropogenic disturbance that may substantially change treeline shape and elevation (Macias-Fauria and Johnson 2013; Ameztegui et al. 2016). In this regard, several studies have shown that drought, recurrent fire and logging can dramatically depress treeline elevation compared to the species potential based on climatic stress alone (Piper et al. 2016; Bonanomi et al. 2018). For instance, aspect controls the amount of solar radiation reaching surfaces (Monteith and Unsworth 2013), thus affecting air, soil and vegetation temperatures (Wieser and Tausz 2007). As a consequence, at mid-latitudes in the Northern Hemisphere, south-facing slopes receive much more direct solar radiation than comparable northern slopes. Thus, treeline elevation is expected to be higher on south-facing warmer slopes than on their cooler north-facing counterparts. However, in the Mediterranean area, which is frequently subjected to drought and soil moisture depletion in the summer season, south-facing slopes can be more prone to drought than north-facing slopes, causing a substantial lowering of treeline elevation (Piper et al. 2016; Bonanomi et al. 2018).

Most previous research aimed at identifying the environmental factors controlling treeline elevation, studied natural sites with limited disturbance, discarding areas affected by human activities (Körner and Paulsen 2004). However, this approach yields few insights into the current treeline position which is the net interaction between ecological factors and past and present human activities. This

especially holds in densely inhabited inland areas, as found in Western Europe and the Mediterranean basin: several studies carried out in the Alps, the Pyrenees, as well as the Apennines indicate a significant lowering of actual treeline elevation caused by past human activity in terms of fire, grazing and logging, creating secondary grassland in place of high elevation mountain forests (Pignatti 1998; Tinner et al. 1996; McNeill 2002).

Worldwide, the treeline is commonly formed by evergreen conifer species in mountains of boreal and temperate regions (Körner 2012), with broadleaf evergreen species dominant in tropical latitudes with less accentuated seasonal extremes (Jobbágy and Jackson 2000). Instead, much less common are treelines formed by broadleaf deciduous species. Notable exceptions are treelines formed by *Nothofagus* species in South America, and by *Fagus sylvatica* in the Mediterranean basin (Körner and Paulsen 2004). *F. sylvatica* is a highly competitive species which maintains a high growth rate up to late maturity, with limited tolerance to drought and to spring frosts (Nolè et al. 2018; Allevato et al. 2019) which may seriously damage new inflorescences and leaves, thereby limiting distribution of the species in a continental climate (Larcher 1980; Packham et al. 2012). Although *F. sylvatica* is present at sea level in Northern Europe and Scandinavia (Randin et al. 2013), in the Apennines mountain range this species dominates the vegetation belt from 800 m a.s.l. up to the treeline, mixed with *Abies alba* only in more thermophilous low-elevation Mediterranean beech forests (Di Pasquale et al. 2014; Rita et al. 2014). Recently, in a study on *F. sylvatica* treeline elevation in the Apennines, Bonanomi et al. (2018) reported an average elevation of 1,589 m a.s.l., with considerable variability among peaks ranging from less than 1,000 m a.s.l. to the highest site reaching 2,141 m a.s.l. This study, however, did not investigate the variability of treeline elevation within different mountain groups forming the Apennines. In this regard, several attempts have been made to identify specific features of treelines in different mountain groups, including the Northern Apennines (Pezzi et al. 2008), the Majella (Palombo et al. 2013), the Sibillini (Vitali et al. 2018), as well as Gran Sasso and Laga (Mancini et al. 2016). However, to date no studies have made a

systematic comparison of current treeline distribution across different mountain groups in the Apennines.

To fill this gap, we first determined current treeline distribution in the fifteen major mountain groups in the Apennines, thus providing an unbiased data set. We then compared treeline elevation in different mountain groups with special attention to the differences associated with slope aspect. Finally, we analysed the relationships between treeline distribution with selected climatic, geomorphological, and human disturbance variables to explore the factors that affect *F. sylvatica* treeline distribution. We tested the following hypotheses: (i) the treeline is higher in the cooler northern aspect compared to the warmer southern sides; (ii) mountain groups surrounded by populous areas have more depressed treelines; (iii) and treeline elevation is more variable in mountain groups which are more subject to human pressure.

## ***2.2 Materials and Methods***

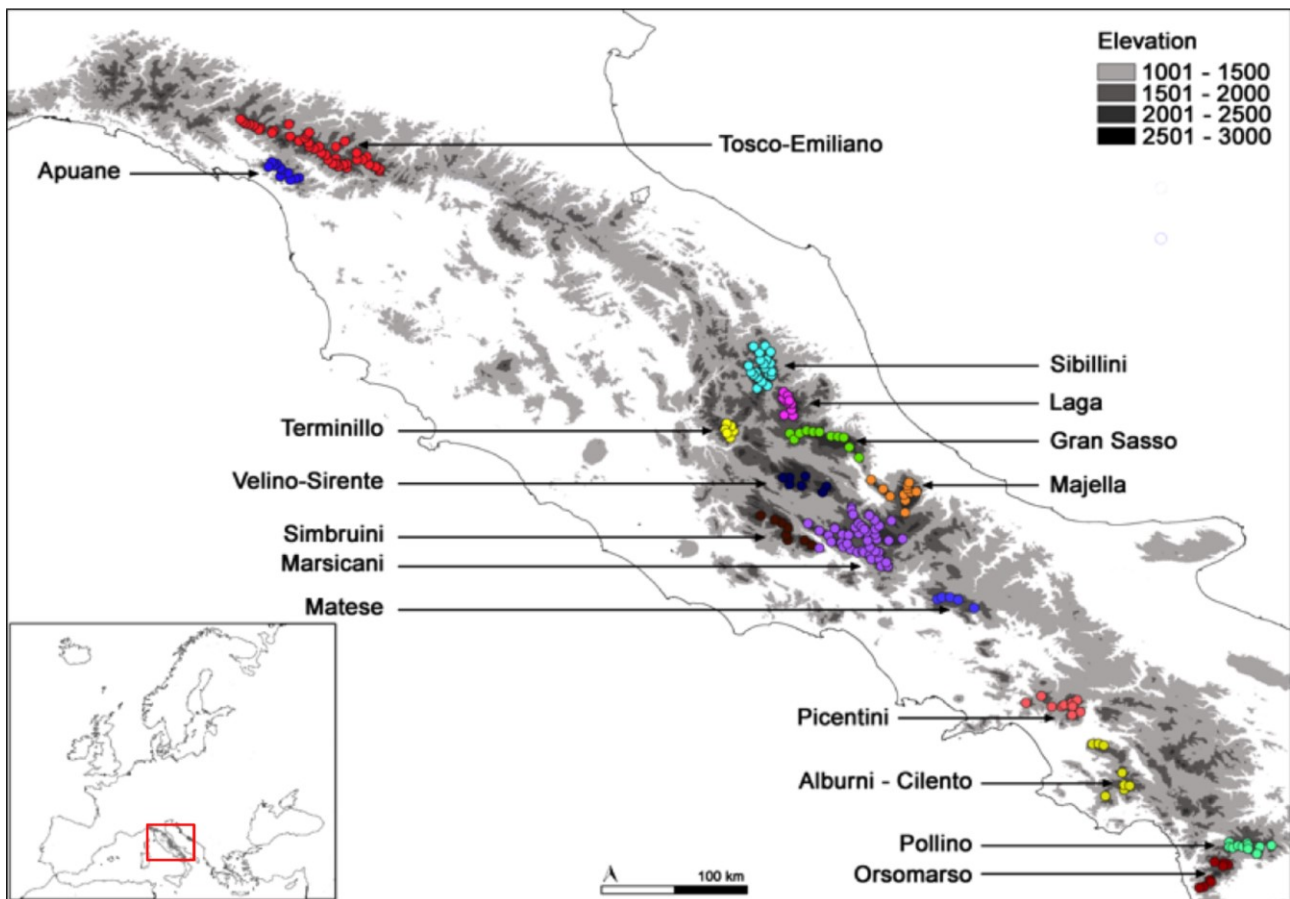
### ***Study area***

The Apennines is a ~1,200 km-long mountain range, running like a backbone down the Italian peninsula from north to south, ranging in latitude from 38°N to 44°N. The Apennines include 261 major and secondary peaks above 2,000 m a.s.l., with the highest point at the Gran Sasso (2,912 m a.s.l.). The Apennine substrate mainly consists of limestone, with occasional arenaceous-pelitic flysch in Northern and Central Italy.

*F. sylvatica* is the most common species in the mountain belt between ~800 m a.s.l. up to the treeline. Almost monospecific stands of *F. sylvatica* are recorded at the treeline (Hofmann 1991; Piovesan et al. 2005), coexisting with relict conifer species only at a few locations. For instance, *Picea abies* can be found in the northern Apennines (Magini 1972), while *Pinus heldreichii* subsp. *leucodermis* forms treelines in the southern Apennines in the Pollino group (Todaro et al. 2007).

For the purpose of this work, we specifically selected only mountains peaks with an elevation above 1,500 m a.s.l. since few of the mountains below this elevation show evidence of a treeline. For our

purposes, the mountain peaks of the Apennines were clustered into 15 main groups based on a well-recognized geographical criterion (Almagià 1959). Specifically, the following mountain groups were identified from the northern to southern Apennines: the Apuan Alps, Tosco-Emiliano, Sibillini, Laga, Terminillo, Gran Sasso, Velino-Sirente, Majella, Simbruini, Marsicani, Matese, Picentini, Alburni-Cervati, Pollino, and Orsomarso (Figure 1).



**Figure 1.** The 15 selected Apennine mountain groups, indicated with different color dots, where *Fagus sylvatica* treeline elevation was measured in all the mountain peaks belonging to each group. Overall, 224 mountain peaks were included in the study.

### *Treeline altitude assessment*

To determine the current *F. sylvatica* treeline elevation we used a recently published data set (Bonanomi et al. 2018). Briefly, the Apennine treeline position was mapped on Google Earth Pro™ (Google Inc., Mountain View, CA, USA), using the time series images ranging from 2004 to 2011, with which the treeline boundaries of all Apennine mountain peaks were digitized, amounting to a

total of 302 mountains. Here, the data set was restricted to mountain peaks belonging to the same selected geographical group and excluding isolated mountains (Supplementary Table S1). The present data set includes 224 peaks that, in fact, include all peaks within each mountain groups. For each peak (N=224) the whole treeline i.e. the boundary lines that connect the highest patches of forest, were identified and digitalized to measure the maximum, minimum and average elevation. This analysis was carried out on the four aspects of each mountain peak, thus providing the complete assessment of treeline elevation for each peak.

Treeline position was mapped on the four aspects of selected mountain peaks, with accuracy of the Google Earth-measured points. The accuracy of the Google Earth-measured data was checked by field measurements on 80 peaks distributed along the whole Apennines, corresponding to 35.7% of geolocated waypoints, with a Garmin Montana® 600 GPS device equipped with a barometric altimeter. Overall, we found a negligible deviation among Google Earth and GPS measurement, being in average of +0.3 and -0.2 m for lowest and highest treeline points, respectively (Bonanomi et al. 2018).

### ***Variables associated with the treeline***

In a previous study (Bonanomi et al. 2018) we analysed the explanatory capability of 58 variables to predict treeline distribution across the Apennine. Here, based on the previous work, we selected the 13 variables most closely correlated with treeline elevation across the entire mountain chain to assess their capability to explain the difference observed among the 15 mountain groups. The variables were grouped into three classes: climatic, geographical and topographical, and anthropogenic variables (Table 1).

**Table 1.** Variables considered in the analysis of *Fagus sylvatica* treeline elevation in different mountain groups within the Apennines.

<b>Variable</b>	<b>Unit</b>	<b>Symbol</b>
<i>Geographic &amp; topographic</i>		
Peak elevation	m a.s.l.	PE
Latitude	degree	LAT
Distance from the sea	km	SD
Aspect	°	A
Slope	%	SLP
<i>Climatic</i>		
Mean annual temperature	°C	MAT
Mean temperature of warmest month	°C	MTWM
Mean temperature of coldest month	°C	MTCM
Mean temperature of warmest quarter	°C	MTWQ
Mean temperature of coldest quarter	°C	MTCQ
Annual precipitation	mm y <sup>-1</sup>	AP
<i>Demographic</i>		
		HP 1860
Population density within a 10.0 km radius around each mountain peak at three time points (1860, 1921, and 2011)	n km <sup>-2</sup>	HP 1921
		HP 2011

With regard to climatic variables, mean annual temperature (MAT), mean temperature of warmest month (MTWM), mean temperature of coldest month (MTCM) mean temperature of the warmest quarter (MTWQ), mean temperature of the coldest quarter (MTCQ), and Annual Precipitation (AP) were selected.

Data were extracted from the global climate database WorldClim 2.0 (<http://www.worldclim.org>; Hijmans et al. 2005) at a spatial scale resolution of 1 km<sup>2</sup>. In the WorldClim database, the

temperature is calculated as the spatial average of grid squares that include the selected point and adjusted according to their average elevation. Data were then normalized, following the method of Jobbágy & Jackson (2000), to remove the effect of the elevation of individual grid squares by reporting the temperature at sea level for each mountain peak by a  $0.006^{\circ}\text{C m}^{-1}$  adiabatic lapse rate (Barry 2008). For cumulative annual rainfall, data were collected from the Bioclimates of Italy because of the higher spatial resolution compared with WorldClim for the Apennines. In brief, these rainfall data were obtained with a calibration process, via regression kriging, of the WorldClim (1.4), with a large data set from local meteorological stations (Pesaresi et al. 2017).

With regard to geographical and topographical variables, most of the selected mountain groups share similar bedrock (i.e. limestone), with the exception of the Tosco-Emiliano and Laga groups that have arenaceous-pelitic flysch substrata (Supplementary Table S1). Data for bedrock type were obtained from the maps of the National Cartographic Portal of Italy ([www.pcn.minambiente.it/GN](http://www.pcn.minambiente.it/GN)). Additional geographical information concerning treeline position i.e. peak elevation (PE), latitude (LAT), distance from the sea (SD), aspect (A) and slope (SLP) was also included in the dataset (Table 1).

Finally, human impact was indirectly quantified using population density around each mountain peak as a proxy. Specifically, we used the population within a 10 km radius around each mountain peak in three dates: 1860, 1921, and 2011 (named HP1860, HP1921, and HP2011, respectively). This variable was selected because a very detailed census of human population is available in Italy at very fine resolution (7,998 municipalities with ~10 years resolution for the last 150 years, [www.istat.it](http://www.istat.it)). Other parameters that could be a good proxy for human impact such as the amount of wood removed by cutting, the stock of grazing animals (cow, sheep, goat, etc.), and road network were not considered in this study because their distribution are very sparse in time and space.

### ***Data analysis***

For each mountain group, maximum, minimum and average values of treeline elevation (TLE) were calculated. The number of mountain peaks differed for each mountain group as follows: Apuan

Alps (11), Tosco-Emiliano (40), Sibillini (24), Laga (11), Terminillo (9), Gran Sasso (11), Velino-Sirente (7), Majella (11), Simbruini (8), Marsicani (48), Matese (5), Picentini (10), Alburni-Cervati (8), Pollino (12), and Orsomarso (9).

The role played by aspect in treeline elevation was analysed by focusing on northern and southern mountain faces. For each mountain group we calculated the differences between north and south average treeline elevation ( $\Delta$  average TLE north - average TLE south) and between north and south maximum elevation ( $\Delta$  maximum TLE north - south). Finally, for each mountain group we calculated the difference between the maximum treeline elevations recorded within the group and the average values of the same group ( $\Delta$  maximum TLE – average TLE). The significance of the index is to quantify the depression of the treeline compared to the maximum values recorded within each homogeneous mountain group.

In order to increase explicative power of multivariate analysis, hierarchical clustering of the 13 geographical, demographic and climatic variables were performed on average values for each Apennine chain. Prior to clustering analysis, values for each variable are normalized through mean subtraction and divided by their standard deviation in order to avoid biases from scale disparities of the variables. It then makes it possible to derive meaningful distances between samples, using Euclidean distance. Results of Euclidean distance resemblance matrix were plotted in dendrogram.

The same pre-treatment and multivariate analytical approach were performed for dataset generated from treeline elevation (TLE) variables (average TLE, maximum TLE, minimum TLE,  $\Delta$  average TLE north - average TLE south aspects and  $\Delta$  maximum TLE - average TLE). Additionally, the normalized dataset generated from Treeline variables were stressed in Principal component analysis (PCA), in order to visualize specific association between Apennine mountain groups and TLE attributes. To further emphasize the common relation between TLE and mountain groups clustering calculated on Euclidean distance are overlaid in loading plots diagram. Similarity profile tests (SIMPROF) were applied as multivariate permutational test ( $N^\circ$  of permutation: 999) to each



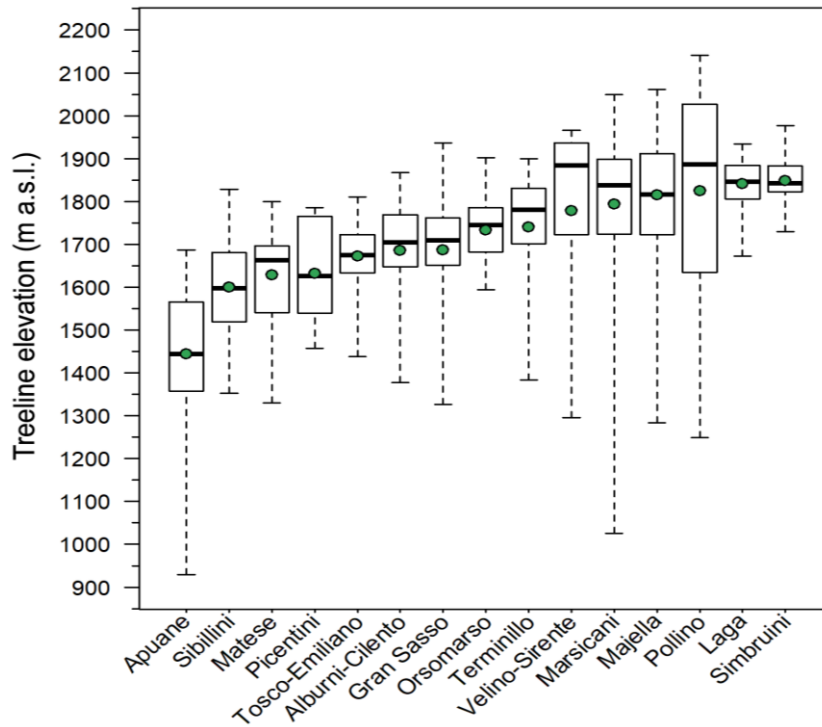
normalized dataset to obtain significant clustering among mountain groups. Dendrograms, PCA of TLE data and SIMPROF tests were generated in Primer-v7 (Clarke and Gorley 2015).

A further multivariate approach by using principal component analysis (PCA) was performed to assess how the intrinsic variation in the 13 selected geographical, climatic and demographic variables explain treeline elevation (i.e. minimum, average and maximum) in each mountain peak belonging to different mountain groups. In order to assess the association between the 13 variables and the treeline elevation, we followed the approach suggested by Legendre & Legendre (2012) for supplementary variables. We plotted treeline elevation values as loading vectors on bi-dimensional PCA space even if it was not used to compute the eigenvalues of the same ordination space and do not contribute to the specific ordination of mountain peaks in score plot.

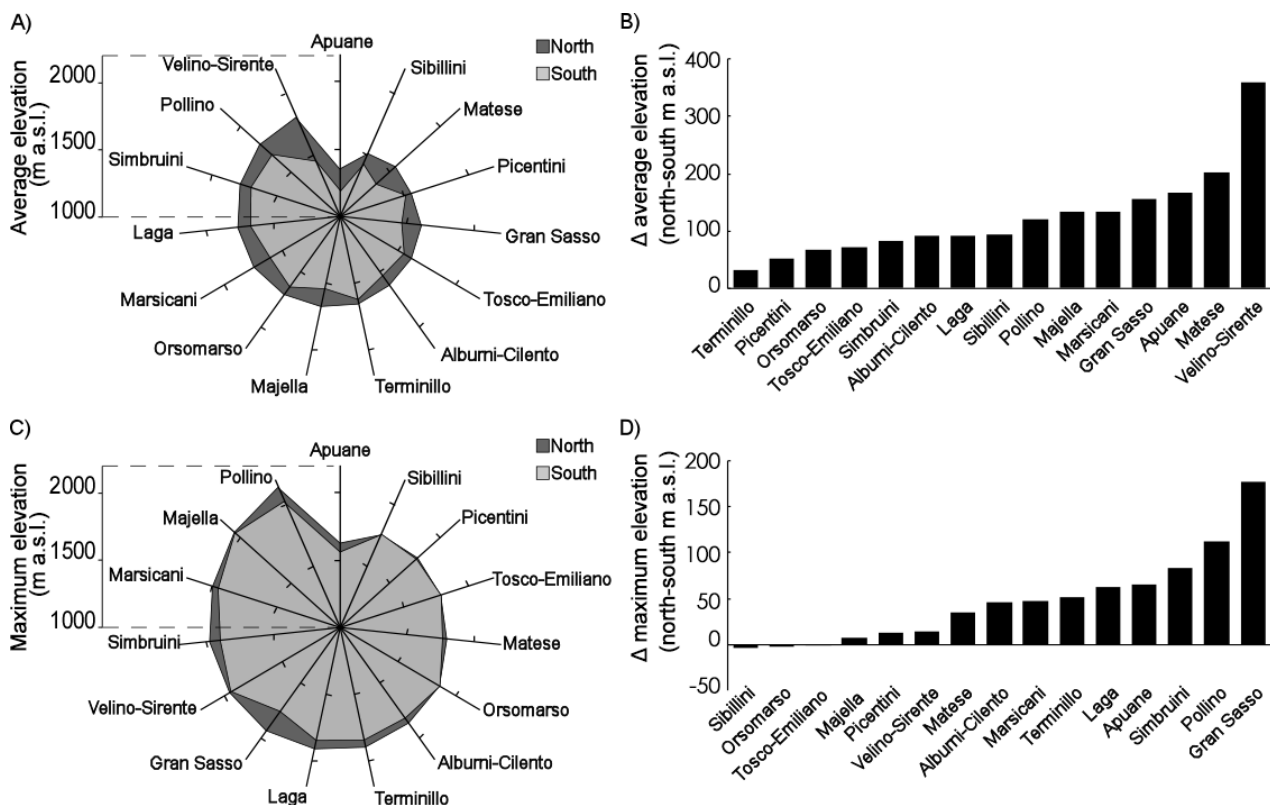
### ***2.3 Results***

In all, 2,895 km of treeline on 224 mountain peaks were measured for this study. The absolute maximum treeline elevation ranged between 1,687 in the Apuan Alps to 2,141 m a.s.l. in the Pollino massif (Figure 2). Absolute maximum treeline elevations exceeding 2,000 m a.s.l. were found on 13 mountain peaks, namely five on Pollino, five also on the Majella, and three in the Marsicani group. As regards the average treeline elevation, the lowest value of 1,286 m a.s.l. was found in the Apuan Alps, while the highest was 1,752 m a.s.l. in the Simbruini. High values were recorded also in Laga, Orsomarso, Pollino and Terminillo (Figure 2). By contrast, very low average treeline elevations were recorded in the Sibillini, Gran Sasso, Velino-Sirente, and Matese. The current analysis revealed that aspect greatly affected treeline elevation. Treeline elevation was higher in northern aspects compared to southern in all mountain groups, with south-facing treelines across the Apennines, on average, 127 m lower (Figure 3a,b). We found very high values of  $\Delta$  average TLE north – south in the Velino-Sirente, Matese, Apuan Alps and Gran Sasso with, instead, low values in the Tosco-Emiliano, Orsomarso, Picentini and especially Terminillo groups.

Interestingly, we found  $\Delta$  maximum TLE north – maximum TLE south very close to zero in Majella, Picentini and Velino-Sirente, with slightly negative values in Orsomarso, Tosco-Emiliano and Sibillini (Figure 3,c,d).

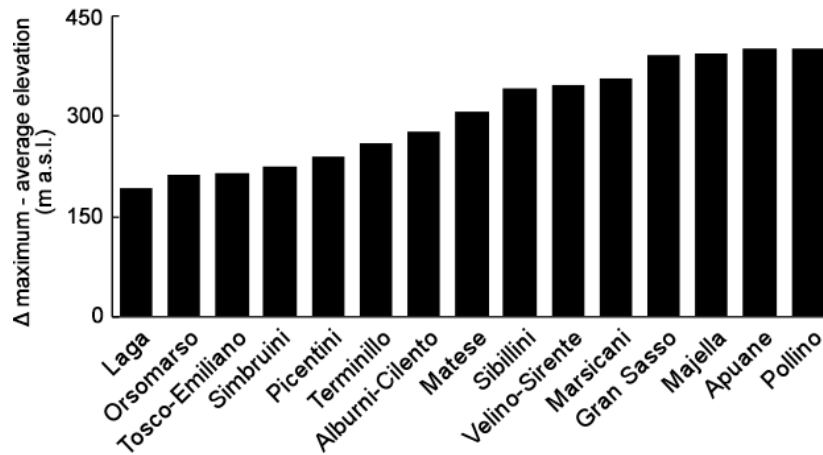


**Figure 2.** Distribution of the maximum treeline elevation of *Fagus sylvatica* measured in all the mountain peaks (N=224) of the 15 selected Apennine mountain groups. The top and bottom edges of the box are the 1<sup>st</sup> and 3<sup>rd</sup> quartiles, respectively; above and below bars indicate maximum and minimum values, respectively; the central line indicates the median value; green circles indicate the average value.



**Figure 3.** *Fagus sylvatica* treeline average and maximum elevations in the 15 selected Apennine mountain groups according to aspect: A) north (dark gray) and south (light gray) average elevation, B) differences between north and south average elevation, C) North (dark gray) and South (light gray) maximum elevation, D) differences between north and south maximum elevations. Within each mountain group, the maximum treeline values is the absolute highest elevation measured; average treeline elevation values are calculated as a mean of all peaks belonging to the respective mountain group.

By contrast,  $\Delta$  maximum TLE north – maximum TLE south attained very high values for Simbruini, Pollino and especially Gran Sasso. Finally, the  $\Delta$  maximum TLE – average TLE (i.e. the differences between absolute maximum elevation minus the average treeline elevation) was very high for Pollino, the Apuan Alps, Majella and Gran Sasso, with the lowest values recorded in Laga (Figure 4).



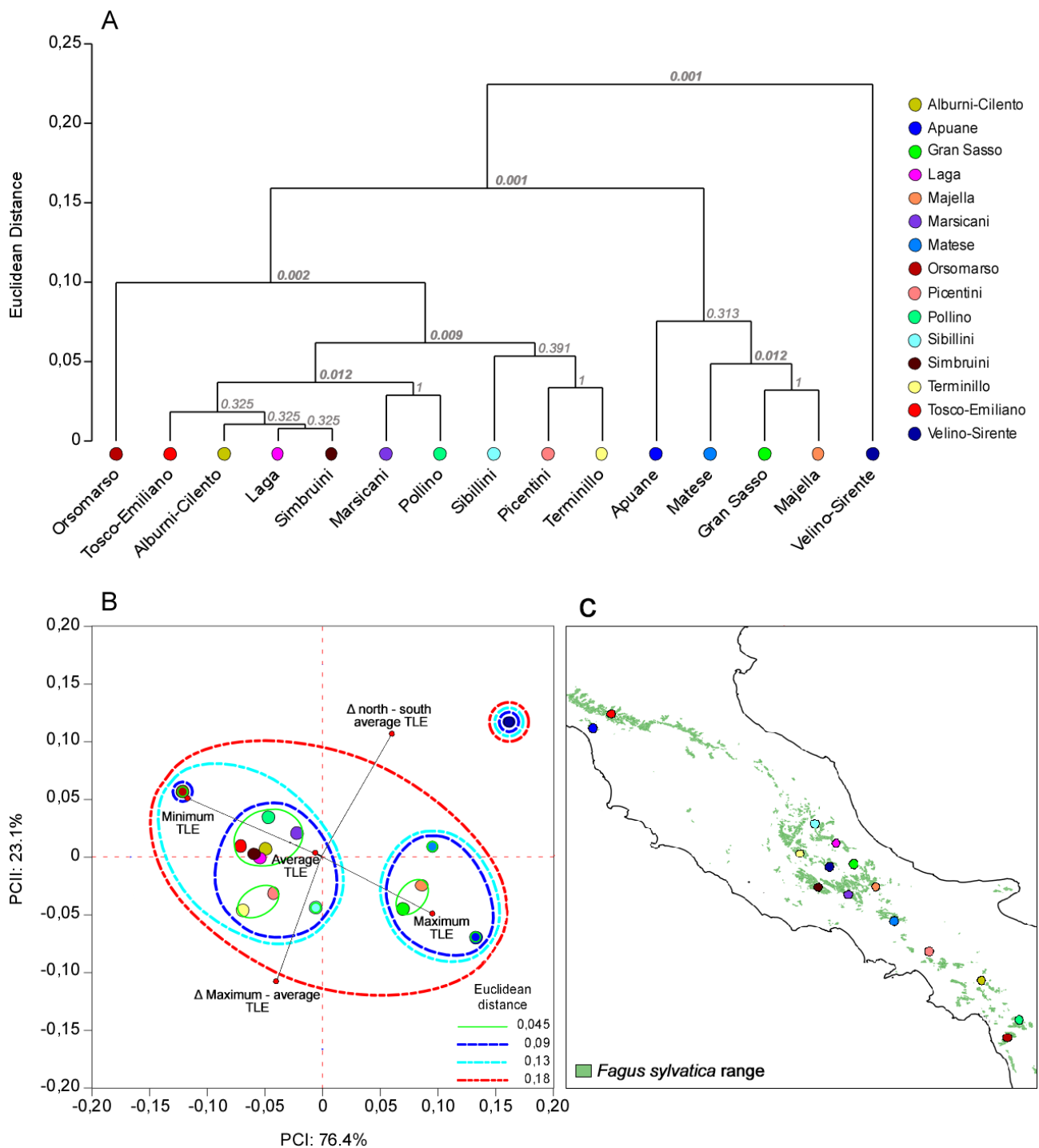
**Figure 4.**  $\Delta$  maximum – average treeline elevation (differences between absolute maximum elevation and the average treeline elevation) for *Fagus sylvatica* treeline in 15 selected Apennine mountain groups.

The hierarchical clustering of the fifteen mountain groups based on the geographical, demographic and climatic variables show significant differences between mountain groups and are shown in dendrogram (Figure S1). The most distant mountain group is Apuane, forming single cluster at Euclidean Distance (ED) value of 8.15, with respect to all the other mountain groups ( $p$  0.001). At 5.05 ED value two internal clusters are formed ( $p$  0.001) including a first group formed by Orsomarso, Pollino, Picentini, Alburni-Cilento and Matese and a second composed by the remaining mountain groups. Notably, in the second group an additional cluster node is formed by Tosco-Emiliano mountain group and the others at ED of 4.77 ( $p=0.002$ ). Internally to the first and the second groups other less significant clustering take place and are shown in Fig S1.

Principal component analysis (PCA) of mountain groups based on TLE parameters explains overall 99.5% of the total variance in the dataset (PCI: 76.4% and PCII: 23.1%) and is used in combination with ED clustering of the mountain groups (Figure 5a and b). In detail, multivariate data analysis showed that Velino-Sirente mountain group forms single cluster at Ed of 0.22 ( $p<0.001$ ), this clustering mainly caused by higher level of positive association with  $\Delta$  average TLE in north and south aspects and negative association with  $\Delta$  maximum TLE - average TLE. A second clustering occurs at 0.16 ED value at significance level of  $p<0.001$ , leading to the formation of a distinct group characterized by level of Euclidean distance below 0.08 ( $p =0.32$ ). This last cluster,

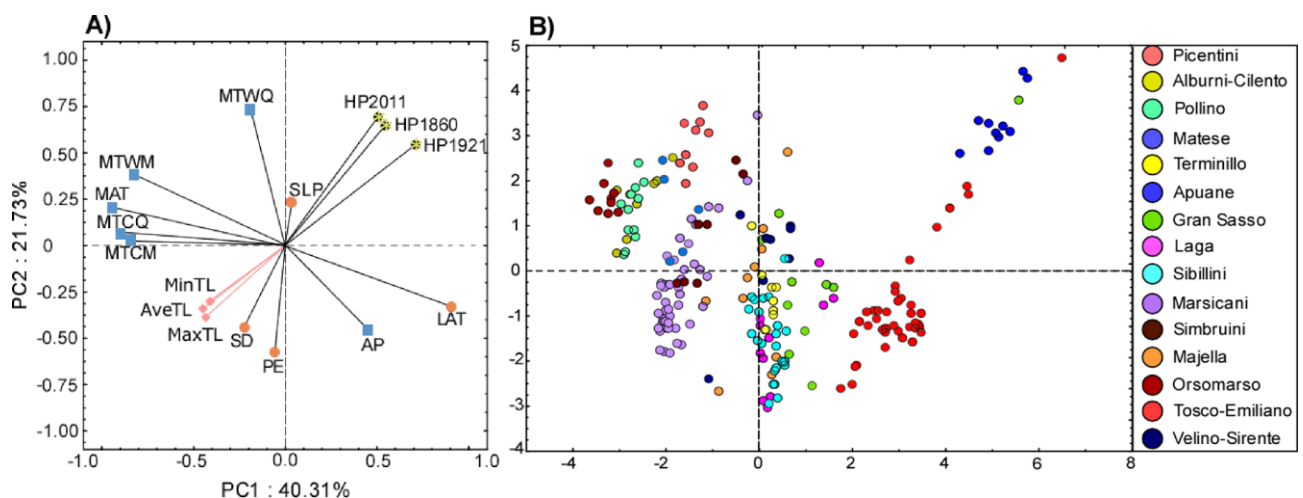
containing Apuane, Matese, Gran Sasso and Majella, is mainly due to positive association with maximum TLE values and negative association with the minimum TLE values.

Conversely, the other cluster forms two subordinate clusters at 0.10 ED with single cluster composed by Orsomarso and the other cluster containing all the other mountain groups. Segregation of Orsomarso is given by the strong positive association with minimum TLE and negative association with maximum TLE. The other mountain groups, namely Pollino, Marsicani, Tosco-Emiliano, Alburni-Cilento, Laga, Simbruini, Sibillini, Picentini, and Terminillo are clustered by a slight positive association with minimum TLE and  $\Delta$  maximum TLE - average TLE. Further, sub-clustering at 0.06 ED and corresponding significance levels are shown in Figure 5.



**Fig 5.** Comparative multivariate data analysis among mountain groups. Panel A shows hierarchical ordination of Apennine mountain groups according to Euclidean distance calculated on treeline elevation (TLE): maximum TLE, minimum TLE, average TLE,  $\Delta$  average TLE north aspect - average TLE south aspect,  $\Delta$  maximum TLE - average TLE variables. Grey numbers in correspondence of the nodes report  $p$  value, in bold significant differences. Panel B shows specific association of treeline attributes with Apennine mountain groups, clustering of mountain groups is performed through overlay function of Euclidean distance. Panel C shows the geographical distribution of the fifteen selected mountain groups throughout the Apennine *Fagus sylvatica* range.

The Principal component analysis (PCA) based on 13 variables provided a satisfactory ordination of the treeline elevation across the 15 mountain groups, with the first two eigenvalues accounting for 62.04% (40.31, and 21.73%, respectively for the first and second components) of the total variance. In Figure 6 we report the loading vector variables (i.e. for each parameter value actually recorded, and how they relate to the PC axes), in bi-dimensional space. The first PCA component highlights the importance of mean annual temperature (MAT), minimum temperature of the coldest month (MTCM), and latitude, although the last variable had the opposite effect. The second PCA component indicates the importance of human population which is negatively associated to minimum, average and maximum treeline elevations in most of the mountain groups (Figure 6).



**Figure 6.** Principal Component Analysis (PCA). Loading plots of 15 selected *Fagus sylvatica* treeline elevations according to: A) topographic, anthropogenic and climatic variables and B) relative Score plots Segregation variables according to relative loading plots. For topographic and geographic variables acronyms are: peak elevation (PE), distance from the sea (SD), latitude (LAT) and slope (SLP); for climatic variables: mean annual temperature (MAT), mean temperature of warmest month (MTWQ), mean temperature of coldest month (MTCM), mean temperature of warmest quarter (MTWQ), mean temperature of the coldest quarter (MTCQ) and annual precipitation (AP). For anthropogenic variables: population density at 10.0 km radius around each mountain peak in the year 1860 (HP1860), 1921 (HP1921), and 2011 (HP2011). Minimum treeline elevation (MinTL), Average treeline elevation (AveTL) and Maximum treeline elevation (MaxTL) were also plotted as supplementary variables (red vectors) following Legendre & Legendre (2012).

PCA also revealed a large variability within the Tosco-Emiliano, Gran Sasso, and Marsicani groups, with more homogeneous conditions within Orsomarso, Picentini and the Apuan Alps. Treeline elevation in the Apuan Alps is strongly and negatively associated with population, which also affects Tosco-Emiliano, albeit, in the latter case, with a substantial contribution of latitude. Settlements around mountains explain a large variability also for Gran Sasso, Majella, Velino-Sirente and Marsicani with a minor role, instead, for Orsomarso. Treeline elevation of Orsomarso and Pollino was associated with MAT, MTCM and with a contribution of MTCQ. Finally, topographical variables had no great influence, although latitude (LAT) played an important role in the distribution of the treelines of the Picentini in concomitance with annual precipitation (AP).

#### **2.4 Discussion**

This study revealed a large variability of *F. sylvatica* treeline elevation among as well as within the 15 mountain groups analysed. Our survey revealed that treeline elevation is the results of both climatic factors and anthropogenic disturbance that play a different role across the Apennine mountain range. First, we recorded a remarkable depression of treeline elevation in all mountain groups compared with the expected climatic potential, suggesting a pervasive anthropogenic effect. Moreover, we found that treeline elevation was consistently lower on warmer, south-facing slopes of all mountain groups analysed. This pattern, although still not explained, could be associated to a synergic interaction between climatic constraints (e.g. summer drought) and human disturbance (e.g. logging and grazing pressure) that may leads to the loss *F. sylvatica* canopy viability and of their regeneration capability. According to our hypothesis, we found within mountain groups the coexistence of a very depressed treeline, in several cases with elevation of ~1,000 m a.s.l., with very high treeline placed well above 2,000 m a.s.l.. The co-occurrences of such variability in treeline elevation is sites that are few kilometres apart suggest that factors other than climate control this



pattern. In this context, we argue that high elevation treeline exist in very remote and inaccessible suspended valleys that protected it from past and present anthropogenic disturbance. On the other hands, very depressed treeline are located in accessible areas that was extensively exploited in the past centuries. Hereafter, we discuss the treeline patterns and the potential causative factors for each of the 15 mountain groups analysed.

### *Northern Apennines*

Apuan Alps had the lowest average treeline in Italy (814 m a.s.l.), lower than the adjacent Tosco-Emiliano. Moreover, the Apuan Alps have a very high value of  $\Delta$  Maximum TLE – Average TLE, which indicate that the treeline could potentially reach high elevations, but the average values are heavily depressed. The Apuan Alps and the Tosco-Emiliano group are situated at a similar latitude and share a similar climate, with very high rainfall and a limited summer drought (Fратиanni & Acquaotta 2017). The most striking feature of the Apuan Alps which may explain the depressed treeline is the very high population density around this mountain group, with several large towns (e.g. Massa Carrara, Viareggio) situated a few kilometers from the main peaks. As early as 1861, the human population numbered  $\sim$  83,000 and  $\sim$  88,000 around Mt. Pisanino and Punta Carina, respectively, two of the most important peaks in this group. More importantly, the mountain group was intensively exploited in pre-Roman times (Bruschi et al. 2004) and in recent centuries for its marble deposits (Carmignani et al. 2007), causing a dramatic change in mountain morphology and hence the complete removal of forest cover on several peaks. PCA analysis confirmed that past and present human population density is the most important explanatory variable for the low treeline elevation in this mountain group.

The Tosco-Emiliano group has a higher treeline elevation than the Apuan Alps, despite the similar climate and latitude. Moreover, it has low values of both  $\Delta$  average TLE north – average TLE south and of  $\Delta$  maximum TLE – average TLE, suggesting that it has been subject to more limited human disturbance compared to the nearby Apuan Alps. Therefore, the highest treeline, recorded at 1,811

m a.s.l. in the Monte Prado peak (2,054 m a.s.l.), probably reflects climatic limitations (Pezzi et al. 2008), the group lying at the boundary of the Northern Apennines and thus experiencing much colder weather conditions compared to mountain groups in the Central and Southern Apennines. Finally, PCA analysis indicates that rainfall affects treeline elevation in this group, which is indeed the wettest in the Apennines. In this regard a weak but positive correlation between treeline elevations across the Apennines with the amount of summer precipitation was documented (Bonanomi et al. 2018). Here we speculate that high rainfall can alleviate summer drought, especially in southern aspects, contributing to the presence of a high elevation treeline also on the southern slopes of these mountains.

### ***Central Apennines***

The Apennines in central Italy comprise nine main mountain groups, namely the Sibillini, Laga, Gran Sasso, Terminillo, Majella, Velino-Sirente, Simbruini, Marsicani, and Matese. Blasi (2010) placed the potential elevation limit of *F. sylvatica* in central Italy at 1,900 m a.s.l. However, we found eight sites where the treeline elevation exceeded 2,000 m a.s.l. (five in the Majella and three in the Marsicani group). The existence of several sites located well above the threshold of 2,000 m a.s.l. clearly demonstrate that the climatic potential of *F. sylvatica* is much higher than previously thought (Blasi 2010). Currently, we are focusing on these study sites to better define the upper climatic limitation of *F. sylvatica* in areas subject to minimal anthropogenic disturbance. The discovery of very high treeline, most of which are located in remote and inaccessible valleys, highlight the general and widespread treeline depression of Central Apennines. In fact, in all mountain groups analysed the average treeline elevation occurs several hundred meters below its potential climatic limit.

Sibillini had the lowest average treeline in central Italy (1,202 m a.s.l.), with also a relatively low absolute maximum (1,828 m a.s.l.). This mountain group is characterized by very ample and characteristic altitudinal grasslands (Catorci et al. 2008; Costanzo et al. 2009; Allegrezza et al.

2013) with *F. sylvatica* often limited to very steep, rocky slopes (Supplementary Fig. S1). Moreover, the southern section of the group is largely deprived of forest cover which, even today, is intensively exploited for agricultural purpose at altitudes up to 1,500 m a.s.l., i.e. Piano di Castelluccio, Norcia. These multiple lines of evidence suggest a pervasive negative impact of human activities such as agriculture and intensive grazing even at high elevations which may well have lowered the treeline in this group. The comparison between the Sibillini and Laga, a mountain group located less than 10 km south, is very informative. In central Italy, Laga had the highest average treeline (1,831 m a.s.l.), coupled with the lowest  $\Delta$  maximum TLE – average TLE (192 m a.s.l.), showing a very limited variability of treeline elevation in this group (Supplementary Fig. S1).

These results are the opposite of the Sibillini, although the two groups share similar climatic conditions. Our analysis suggests that the treeline position in the Laga group is explained by two factors: the bedrock type and the human population density around these mountains. Laga is the only group in central Italy with arenaceous-pelitic flysch substrata, all other groups having limestone bedrock. A flysch substrate is much less permeable to rainfall than limestone, hence being able to retain large amounts of water in the soil and thus reducing summer drought (Gisotti 1983; Adamoli et al. 2012). As a result, trees are likely less affected by recurrent summer drought even at the treeline and in the southern faces of mountain peaks. Moreover, Laga had a very low past and present human density that, likely, do not provide a strong pressure on forests and, so, preserves an ample and continuous forest cover.

Gran Sasso and Velino-Sirente are two limestone groups with several high elevations and prominent peaks. Gran Sasso and Velino-Sirente also share low average treeline elevation with high values of  $\Delta$  average TLE north – average TLE south. Indeed, the southern slopes of these mountains groups are almost devoid of forest cover with, for instance, the Campo Imperatore plateau (the largest in central Italy covering more than 75 km<sup>2</sup>) completely covered by grassland from 1,600 m up to 2,300 m a.s.l. (Supplementary Fig. S1). Our PCA revealed that past human population is the

most important explanatory variable for the low treeline elevation in the Gran Sasso group: both the groups have very large (>50,000 inhabitants) ancient cities dating back to Roman times, located just at the base of the southern face of the main peaks, i.e. L'Aquila for Gran Sasso and Avezzano for Velino-Sirente. Human exploitation of the latter area goes back to Roman times during which reclaimed a large plateau covered by a natural lake for agricultural purposes in Avezzano (Burri & Petitta 2004). Moreover, in these two groups the differences between mountain aspects become striking, with the north face often covered by *F. sylvatica* up to 1,800-1,900 m a.s.l, while south faces have treelines that in several cases lie below 1,200 m a.s.l.

Bonanomi et al. (2018) first reported that *F. sylvatica* treeline elevation is lower on warmer, southern aspects compared to the colder north across the Apennines. This counterintuitive pattern, considering the current theory proposed to explain treeline elevation (Körner 2012), has been hypothesized to be the result of a combination between water shortage, and alteration of microclimate conditions when *F. sylvatica* cover is removed for pasturage. Allegrezza et al. (2016) reported that, at the treeline on south-facing mountain slopes, plants outside the canopy cover may experience very high soil and air temperatures (up to 38°C) and intense summer drought which restricts *F. sylvatica* regeneration capability on open patches. In this regard, *F. sylvatica* itself can act as an ecosystem engineer by modifying forest microclimate thanks to its canopy cover and thus facilitating seedling establishment. Hence, we speculate that depression of treeline on southern mountain faces is due to the loss of engineering capability of *F. sylvatica* after canopy removal which, if intact, modulates a positive feedback on microclimate buffering temperature extremes, increasing soil and air moisture by limiting wind impact (Jones et al. 1997). Since self-shading buffers local microclimate, we hypothesize that this effect will be more important in southern than in northern aspects where air and soil temperature are already buffered by the reduced solar radiation. In this regards, intense anthropogenic disturbance could exacerbate the stressful impact of intense solar radiation, high daily temperature and summer drought on southerly exposed vegetation gaps, with negative effects on the capability of *F. sylvatica* to regenerate and recolonize the

disturbed areas that rapidly become grassland. In this context, the Velino-Sirente group had better represent this stressful ecological condition for *F. sylvatica* treeline because combine a very high human pressure with the driest climate because of its position in the interior of the Italian peninsula (Pesaresi et al. 2017). Future work is needed to test this multifaceted hypothesis, comparing gap and closed forest microclimates in connection with eco-physiological studies that focus on the *F. sylvatica* regeneration niche (Grubb 1977) in northern and southern slopes expositions.

Majella is a large and compact massif composed of a high elevation plateau (average elevation >2,600 m a.s.l.), with steep and topographically complex external faces (Whitehead 1951). The Majella treeline shows large variability, with the highest absolute values in central Italy (2,061 m a.s.l.) and five sites where the treeline exceeds 2,000 m a.s.l. but, at the same time, several sites with a treeline below 1,200 m a.s.l. (Supplementary Fig. S1). The considerable variability observed in the treeline within the Majella cannot be explained by climatic factors but is likely the result of uneven past human activities, since large population inhabits Majella. Treelines appear especially depressed in close proximity to settlements and to external mountain faces that were more accessible for timber exploitation. In Majella, however, depressed treelines coexist with a very high treeline that only occurs in remote and almost inaccessible hanging valleys (Supplementary Fig. S1), an observation that supports the human accessibility hypothesis. That said, the occurrence of several treelines at elevations >2,000 m a.s.l. on all mountain aspects, including the southern slopes, raises the ecological climatic potential of *F. sylvatica*.

The Marsicani mountain group has the most peaks (48 in our analysis), with many showing a large variability in treeline elevation. In three sites, absolute maximum treeline elevation exceeded 2,000 m a.s.l. (i.e. Monte Greco, Terratta, and Monte Rotondo) and, in several cases, high and low treelines coexist within the same peaks (e.g. Monte Marsicano, La Meta). In this large and heterogeneous group, the treeline elevation is negatively associated with human population but positively with the minimum temperature of the coldest quarter of the year. Bonanomi et al. (2018) found that the winter climatic effect was stronger in high elevation peaks (>1,900 m a.s.l.),

reporting for the first time that winter temperature affects *F. sylvatica* treeline elevation in addition to the well known impact of MAT and growing season temperature (Körner and Paulsen, 2004). In this regard, the Marsicani appears a complex group where climate mostly control treeline elevation in high elevation peak, while human disturbance seems more important in low elevation mountains. In addition, in the Marsicani group the past human pressure was likely uneven distributed also at low elevations because previous studies discovered the most ancient *F. sylvatica* old-growth forest of Europe in this geographical area (Piovesan et al. 2005).

### ***Southern Apennines***

The Picentini and Alburni-Cilento mountain groups in southern Italy have low elevation peaks, the highest point being Mt. Cervati (1,899 m a.s.l.). In these groups, PCA indicates the importance of mountain peak elevation as a physical limiting factor for treeline elevation, given that the ecological potential of *F. sylvatica* is well above 2,000 m a.s.l. at this latitude (Bonanomi et al. 2018). As a consequence, in several peaks *F. sylvatica* reaches the top of the mountain (e.g. Mts. Gelbison, Mercori, Panormo, Polveracchio), especially in the northern aspect. On the other hand, in these two groups with their low elevation peaks, the contribution of climatic factors to treeline elevation is of less importance.

Located at the southern limit of the carbonatic continental Apennines, the Pollino massif includes five peaks exceeding >2,150 m a.s.l. Average treeline elevation is high in Pollino, which comprises five sites with treelines higher than 2,050 m a.s.l., including the highest site ever recorded for the continental distribution of *F. sylvatica* at 2,141 m a.s.l. on Mt. Serra del Prete. Indeed, the latter site demonstrates that in southern Italy the climatic potential distribution is well above 2,000 m a.s.l., probably lying around 2,100 m a.s.l. Despite this, in many places treeline elevation in the Pollino group is very low (often lower than 1,200 m a.s.l.), causing the large variability in treeline elevation observed in the group. Here, the occurrence of the highest treeline in a mountain group with relatively low elevation peaks could be explained by the co-existence of several sites that were little

disturbed, if at all, by human activities and, on the other hand, by other peaks that were heavily exploited for timber and intensive grazing. Further studies are needed to explain the uneven treeline distribution in this mountain group.

Orsomarso, located a few kilometers to the west side of Pollino, shares a similar climate, being characterized by higher MAT and MTCQ than other groups located in the central and, especially, northern Apennines. In Orsomarso the treeline has a high average elevation but, unlike the nearby Pollino group, the lack of mountain peaks with elevation above 2,000 m a.s.l. explains the absence of a very high treeline. By contrast, Orsomarso has very low values of  $\Delta$  average TLE north – average TLE south and  $\Delta$  maximum TLE – average TLE indexes, all proxies of limited anthropogenic disturbance. Unlike the Pollino massif, the Orsomarso group has a low population density and is physically isolated, with few mountain roads and several peaks that are quite difficult to reach even today. These factors support the poor accessibility hypothesis and may well explain the very extensive forest cover of this group as well as the poor variability of treeline elevation observed between contrasting mountain aspects.

## **2.5 Conclusions**

Our survey of the *F. sylvatica* treeline along the Apennines revealed that treeline elevation is, on average, several hundred meters depressed in all the mountain groups analysed. We found evidence of a pervasive anthropogenic effect across the Apennines, with a strong impact in northern (i.e. Apuan Alps), central (Gran Sasso, Velino-Sirente, Sibillini) as well as in southern Apennines (i.e. Pollino). By contrast, the treeline elevation of some mountain groups (i.e. Laga, Simbruini, and Orsomarso) appears less negatively affected by past anthropogenic disturbances.

According with our expectations, treeline elevation was largely lower on warmer south-facing slopes, with values several hundred meters lower in Gran Sasso, Velino-Sirente, Matese, and Pollino. Although the causes of this pattern are still unknown, we argue that it could result from a combination of climatic constraints (e.g. summer drought) and human disturbance that, by causing

to the loss of the microclimate buffer capability of *F. sylvatica* canopy may hamper tree seedling regeneration and open the way for secondary grassland colonization. Further studies are needed to test this hypothesis.

Finally, we found in some groups of central (Majella and Marsicani) and southern Apennines (Pollino) the coexistence of a very depressed treeline with, a few kilometres apart, the highest treeline ever recorded for *F. sylvatica*. We explain this variability of treeline elevation with the coexistence, in the same mountain group, of very remote and almost inaccessible valleys with mountain slopes which, instead, were easily accessible and then extensively exploited for timber, charcoal production and grazing. In conclusion, our results show that the *F. sylvatica* treeline across the Apennines is shaped by the multifaceted interactions between climatic constraints (low winter temperature and low summer rainfall) and human disturbance, with their relative importance, that depends on the mountain group and considered peak.



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### **3. Shrub facilitation promotes treeline advancing of *Fagus sylvatica* across the Apennines (Italy)**

#### ***3.1 Introduction***

Treeline is the ecological boundary representing the upper elevation limit for forest development that, in temperate and tropical climates, occur a high elevation (Körner 1998). Treeline has been observed worldwide and can be formed by both evergreen and deciduous species (Lenz et al. 2013). Climate play a pivotal role in determining treeline elevation, with deficit in growing season temperature having a primary role (Körner 1998). However, the anthropogenic disturbances, i.e. fire, grazing, and logging, may significantly depress treeline elevation in respect to its climatic potential (Feeley and Silman 2010).

In recent decades, knowledge has been achieved concerning the advancing of treeline in relation to anthropogenic disturbance (Holtmeier and Broll 2007) plant-plant interaction (Gaire et al. 2017), and climatic changes. It is largely recognized that temperature is the most important limiting factor for growth and development at the treeline (Grace et al. 2002). In this regards, climatic changes with projection of increasing global temperature, is expected to promote tree expansion at higher elevation worldwide (Lindner 2010). However, a meta-analysis (Harsch et al. 2009) reported inconsistent response of treeline advancement to recent climatic warming, suggesting that other factors like topography, edaphic properties, disturbances and the presence of competing vegetation may override the positive effect of cold stress alleviation (Lembrechts 2018).

Transition from seedling to sapling establishments are key phases of tree life cycle, being especially critical in stressful environments as occurs in alpine ecosystems (Krishnadas and Comita 2019). At the treeline, seedling is subject to multiple stresses, including wind desiccation (Holtmeier and Broll 2007), mechanical damage (Harsch and Bader 2011), spring frost (Allevato et al. 2018), extreme fluctuation of soil and air temperature in the daily cycle, and even lack of symbiotic microbes in the soil (Bonanomi et al. 2008). Under these conditions, positive plant-plant interaction may alleviate

environmental stress and facilitate seed germination and seedling establishment. For instance, shrub canopy but also large rocks may provide shade that reduce the risks of desiccation and photoinhibition (Germino and Smith 1999; Bader et al. 2007), could protect from animal browsing (Luo and Dai 2013), and improve plant nutrition thanks to the formation of localized fertility islands (Allegrezza et al. 2016). Conversely, neighbour's plants may also compete with tree seedlings for nutrients, water and light at the treeline (Lachmuth 2019), reducing physiological performances and hampering the colonization of not forested vegetation patches (Honnay 2005). For instance, in Tibetan Plateau, Liang et al. (2016) reported that shrubs, mainly *Rhododendrum* species, located just above the treeline strongly inhibited tree establishment and, consequently, slowed the upward movement of the trees.

The variable effects of the neighbour plants on tree establishment depends on the specific nurse–beneficiary combination in interaction with underlying environmental conditions (Callaway 1997). Generally, the beneficial effect of nurse depends on plant architecture that modulate local microclimate, and chemical traits that control organic matter and nutrient cycling. All these factors, however, varies with the nurse species and, within species, with the ontogenetic phase of the life cycle (Gómez-Aparicio et al. 2005). For example, *Juniperus communis* shrub provide a biogenic amelioration of soil quality and canopy microclimatic, but only large shrubs and not young individuals act as nurse for woody species (Allegrezza et al. 2016). On the other hand, the response of beneficiary plants depends on their capability to take advantage of the environmental changes induced by the nurse. For example, broadleaf compared to coniferous seedling is more prone to suffer for high temperatures during the day, frost in the night, and drought related desiccation (Brosersen et al. 2019). In this regards, *Fagus sylvatica* seedling is prone to early spring frosts (Allevato et al. 2018) and, later in the growing season, is very intolerant to summer drought (Piovesan et al. 2008). Seedling desiccation is especially important in Mediterranean climates where summer precipitation and soil moisture availability can interact negatively with high temperature

also at the treeline (Weisberg and Baker 1995; Lloyd and Graumlich 1997; Allegrezza et al. 2016; Piper et al. 2016).

In the Apennines, the current treeline position, mainly formed by the deciduous *Fagus sylvatica*, is largely depressed compared to its climatic potential as a result of past human activity (Bonanomi et al. 2018). However, in the last decades a substantial abandonment of economic activities like logging, burning, and pastoral uses in mountain areas was observed in Europe (Cairns and Moen 2004). Moreover, average temperatures have risen substantially in the Mediterranean basin in the last decades (Vacchiano et al. 2017). The combination of higher average temperature with the reduced pressure of human activities driven to a significant treeline advance in several mountain groups (Gehrig-Fasel 2007), including *Pinus nigra* and *Pinus heldreichii* in the Apennines (Vitali et al. 2019). However, no information is available about the response of *F. sylvatica* to climatic warming and land abandonment at the treeline. Based on the specific *F. sylvatica* eco-physiology, we expect that this species would be able to recolonize at forested patches higher elevation not only in presence of nurse plant that provide safe sites for seedling establishment. To test this hypothesis, we selected seven mountains having different treeline elevation, rock substrate, and potential nurse plant to assess if *F. sylvatica* treeline is advancing across the Apennines. Specifically, we selected the three most abundant shrubs at the treeline ecotone with contrasting ecological traits: two evergreen coniferous species (i.e. *Juniperus communis* L. and *Pinus mugo* Turra) and the deciduous *Vaccinium myrtillus* L. The inclusion of three nurse species, two substrate type (i.e. limestone and flysch substrata), and a broad range of treeline elevations (from ~1,600 m to ~2,100 m a.s.l.) offer the opportunity to assess the relative importance of plant facilitation in determining the advance of *F. sylvatica* treeline at its southern distribution limit. To achieve this aim, we collected spatially fine-scale distribution data of *F. sylvatica* seedling and sampling in transect ( $N=71$ ) having or not the presence of shrubs. By assessing recruitment distance from treeline, age, size, and architecture we were able to assess if shrubs promote or not treeline advancement. Specifically, we tested the hypothesis that: (i) *F. sylvatica* requires nurse plant to colonize open area over the treeline; (ii) the

nurse effect is species-specific, being higher for *V. myrtillus* compared to *J. communis* and *P. mugo*; and (iii) nurse effect is stronger at low- compared to high-elevation treelines.

### **3.2 Materials and Methods**

#### **Study sites**

The Apennines is a 1,200 km long mountain chain ranging from 38°N to 44°N, with 261 peaks above 2,000 m a.s.l.. Along the Apennines the treeline is dominated by *F. sylvatica*, with occurrences of few and relict populations of *Pinus* species (*P. nigra*, and *P. leucodermis*) respectively in the central and southern Apennines (Todaro et al. 2007), and *Picea abies* in the Northern section. The Apennine is largely formed by limestone substrata, with occasional arenaceous-pelitic flysch in the Laga groups (Bonanomi et al. 2018). The climate is a mountain variant of the Mediterranean type, with mean temperature ranging from 0 to 11 °C in January and from 24 to 28 °C in July; the total annual precipitation varies between 600 and 4500 mm, with frequent winter snowfall events above 1000 m a.s.l. (Vacchiano et al. 2017). In our analysis, we selected seven mountains peaks differing each other for i) treeline elevation, ii) substrate type, and iii) shrub species above beech treeline, regarded as potential nurse plants (Table 1).

Treeline elevation ranges from 1640 m a.s.l. in Sibillini to 2140 m a.s.l in Pollino. All sites share a similar limestone bedrock type with the only exception of Laga having arenaceous-pelitic flysch. A flysch substrate, compared to limestone, is more permeable to rainfall have a larger capability of store water in the soil and present a lower soil pH (Adamoli et al. 2012). The acidic pH of Laga soils explain the unique presence of *V. myrtillus* in this mountain group (Pignatti 1982). Sampling sites were carefully selected after extensive aerial photographs assessment of treeline derived from a previous study (Bonanomi et al. 2018, 2020). The selected sites fulfilled the following requirements: i) treeline dominated by *F. sylvatica* with closed canopy (tree cover >90%); ii) the co-occurrence in the same site of areas with and without shrub cover (maximum topographic

distance between paired sites of 1,000 m); iii) the lack of geomorphic constraints that limit upward treeline advancement.

### ***Nurse plants profiles***

*V. myrtillus* is a deciduous, rhizomatous shrub having aerial shoots erect, 10-60 cm tall. The distribution is in N W Europe, Iceland to N. Portugal and Spain, Italy, Macedonia to Asia and Central and N. Europe. In Italy, it can be found from the Alps to the central Apennine in shrubland and pastures mainly between 1200 and 2000 m a.s.l.. and much rarely between 300 and 2800 m a.s.l.. Its presence is strictly related to humic and acid soil (Pignatti 1982).

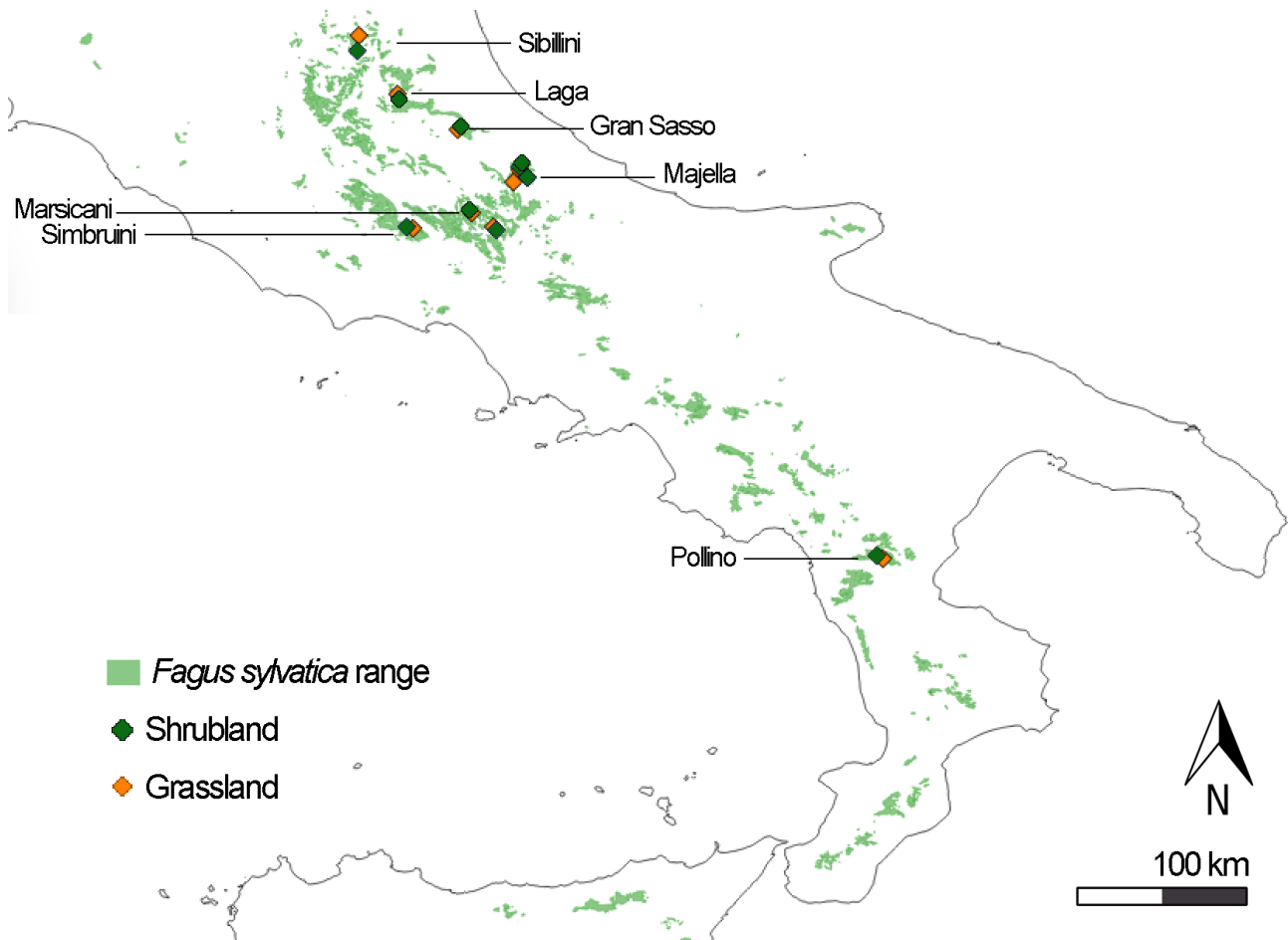
*Juniperus communis* is a gymnosperm and one of the most widespread plant species, it is a shrub or tree rarely attaining a height of 150 cm. The geographic distribution covers most of the Northern Hemisphere (Adams 2008). In Italy, it can be found on the Alps mainly above the treeline, in the northern and central Apennine mainly between 1500 and 2500 m a.s.l..

*Pinus mugo* is a gymnosperm, with a shrub or tree habitus attaining a height of 5 m. The geographic distribution covers encompassing Central and Eastern Europe. In Italy, it can be found in the Alps and central Apennines, in shrubland and pastures mainly between 1400 and 2700 m a.s.l. (Christensen 1987).

### ***Field survey for assessment of treeline advancement***

During the summer 2017 and 2018, we surveyed nine treeline sites in seven mountain chains (Fig.1, Table S1).





**Figure 1** Study sites. Paired areas with shrubland or grassland vegetation cover above the beech treeline on seven Apennine mountain chains.

In each treeline site, we established four rectangular transects, at least 20 m apart from each other in the area with shrub cover and additional four transects in the area without shrub cover. A total of 68 transects [(8 study sites \* 2 areas \* 4 transects) + (1 study site \* 1 areas\* 4 transects)], having 10 m wide x 100 m length size (Table S1), were placed along the mountain slope. The lower border of each transect was positioned at the current treeline defined as the upper limit of continuous forest with a canopy cover  $\geq 90\%$  and tree height  $\geq 3$  m. Corner points of each transect were accurately geolocated with a Garmin Montana® 600 GPS.

In each transect, the relative position (i.e. x and y coordinates with respect to the fixed plot) each living and dead seedlings, saplings and trees were recorded. For each individual, the following

parameters were recorded: stem diameters at base and breast height (1.30 m), architecture i.e. growth form (single or multi-stem), distance from the treeline, relative position according to shrub canopies, i.e. inside or outside a shrub canopy.

For each tree with basal diameter >5 cm, one core was extracted with a direction parallel to the slope using an increment borer. Smaller seedlings and saplings were cut with a scissor at the base and a stem disks was obtained. In each transect both cover and eight all shrubs species were recorded.

### ***Laboratory measurements***

Overall, cross sections of stems of 200 trees were sampled. The age structure of all plots was determined by dendrochronological methods. All cores were mounted on wooden strips. In order to make visible the ring boundary, we flattened the core surface with a stainless-steel surgical blade or we sanded cross sections by a series of progressively finer sandpaper (from p120 to p 400). Each cross section was observed with the help of a stereo microscope (magnification 10x-40x). Tree ring width measurements were made to the nearest 0.001 mm using LINTAB (Digital LINear TABLE for tree ring measurement). In order to reach maximum precision of the tree ring count, tree ring series were cross dating visually.

### ***Shrub canopy cover estimation***

In order to calculate the proportion of shrub canopy cover (SCC) of *P. mugo*, *J. communis* and *V. myrtillus* in each transect, visual photointerpretation of the satellite images available in Google Earth pro was performed. If shrubs did not reach the top boundary of the transect, percentage of shrub cover refers to the density of the shrub canopies in the portion of transect that they occupied.

The Google Earth images is referred to the year 2018. The vector data were imported, managed and analysed in the open source QGis software (QGIS Development Team, 2019).

### **Data analysis**

A logistic regression model was applied in order to test the hypothesis of shrub-cover facilitation on seedling establishment of *F. sylvatica*. The effect of the percentage shrub canopy cover on establishment/recruitment of *F. sylvatica* seedlings was examined. The logistic model includes as binary response variable the occurrence of *F. sylvatica* seedlings inside (IN) or outside (OUT) the shrub crown-cover and as predictor variable the percentage of shrub cover. The equation of the logistic model was the following:

$$g(x) = \beta_0 + \beta_1(SCC)$$

where  $g(x)$  represents the probability of occurrence of *F. sylvatica* seedlings,  $SCC$  is the percentage of shrub canopy cover, and  $\beta_0$  and  $\beta_1$  are the intercept and slope parameters, respectively. Since the probability of occurrence of beech seedlings inside the shrub canopy cover increases with increasing degree of canopy cover, we test the null hypothesis ( $H_0: \beta_1=0$ ) that there is no relationship between the shrub canopy cover and occurrence of *F. sylvatica* seedlings by means of Z test (Zar 2013). Logistic regression was performed by means of generalized linear models (GLM) assuming a logit link function for binary response variables (IN-inside and OUT-outside). Parameters of logistic model were assessed by means of maximum likelihood estimation method (MLE).

To evaluate the advancing of *F. sylvatica* treeline ecotone the relationship between the distance of *F. sylvatica* trees from the treeline and their age was analyzed. The relationship was evaluated by means of a non-parametric Spearman rank correlation (Zar 2013). Correlation between distance and age of *F. sylvatica* trees was determined separately in each of the three shrub cover species (*J. communis*, *V. myrtillus* and *P. mugo*) and in open areas covered by grassland.

Both management and analysis of data were performed in R by using the package Jtools version 2.0.0, (Jacob and Long 2019) at level of significance  $\alpha = 0.05$ .

### 3.3 Results

#### Treeline stand structure attributes

The treeline elevation ranges between a minimum of 1641 m a.s.l. to a maximum of 2082 m a.s.l. (Table 1). Above these treelines, the shrub cover is mainly represented by *J. communis* followed by *P. mugo* and *V. myrtillus*. Their percentage cover change across the treeline, with the lower values ranging between 15 to 68% observed for *J. communis* and the higher values of 100% detected for *P. mugo* and *V. myrtillus*. In addition, the shrub average total height was higher for *P. mugo* followed by *J. communis* and *V. myrtillus* (Table 1). *F. sylvatica* trees growing above the treeline ecotone showed an average total height that range between 1.3 and 7.0 m. Additionally, the highest heights were observed in the sites covered by *P. mugo*, while in *J. communis* and *V. myrtillus* were registered the lower *F. sylvatica* total heights (Table 1). On treelines below the 2000 m, the average basal stem diameter of *F. sylvatica* ranged between 4.0 cm to 6.6 cm. In contrast, above the 2000 m the stem diameter was higher in the sites covered by *J. communis* than *P. mugo*.

**Table 1** Summary of the stand structure variables for shrub species (*J. communis*, *P. mugo* and *V. myrtillus*) and European beech (*F. sylvatica*) above treeline ecotone. Numeric values represent mean and 1<sup>st</sup> standard deviation.

Study site	Treeline elevation (m a.s.l.)	Shrub species	Shrub canopy cover (%)	Average total height of shrub species (cm)	Mean density (n ha <sup>-1</sup> )	Average total height of beech (m)	Average basal stem diameter of beech (cm)	Average beech tree age (years)
Sibillini	1641	<i>J. communis</i>	16 ± 3.2	49 ± 14	110	2.1 ± 1.6	6.6 ± 4.7	19 ± 9
Gran Sasso	1753	<i>J. communis</i>	57 ± 7.4	67 ± 15	23	2.4 ± 0.7	4.0 ± 1.1	29 ± 15
Simbruini	1760	<i>J. communis</i>	56 ± 6.3	45 ± 18	63	2.7 ± 3.7	5.5 ± 4.1	25 ± 13
Majella 2	1900	<i>J. communis</i>	68 ± 2.7	26 ± 8	90	1.9 ± 1.9	5.9 ± 7.2	17 ± 11
Laga	1905	<i>V. myrtillus</i>	100	17 ± 2	143	1.3 ± 1.0	4.8 ± 3.4	16 ± 8
Majella 1	2010	<i>P. mugo</i>	100	300 ± 40	53	7.0 ± 1.0	17.0 ± 2.4	22 ± 17
Pollino	2020	<i>J. communis</i>	15 ± 2.1	35 ± 9	17	2.3 ± 1.2	23.8 ± 31.1	29 ± 3
Majella 3	2042	<i>P. mugo</i>	100	149 ± 18	67	3.2 ± 1.3	10.3 ± 5.6	65 ± 40
Marsicani	2082	<i>J. communis</i>	60 ± 4.7	26 ± 9	90	1.4 ± 1.6	24.6 ± 15.8	21 ± 13

The mean age of *F. sylvatica* ranged between a minimum of 16 years in mountain sites covered by *V. myrtillus* to a maximum of 65 years in sites covered by *P. mugo*.

Association between beech density and elevation, percentage of shrub cover and mean height of the shrubs calculated with Spearman rank correlation are not significant (Table 2).

**Table 2** Spearman rank correlation between density of beech plants above the treeline and the variables associated with the study area, namely treeline elevation, shrub cover percent and mean height of the shrubs.

Variables	Spearman's (rho)	p-Value
Beech density - elevation	-0.16736	0.66691
Beech density - shrub cover	0.33903	0.37211
Beech density - shrub height	-0.51046	0.16027

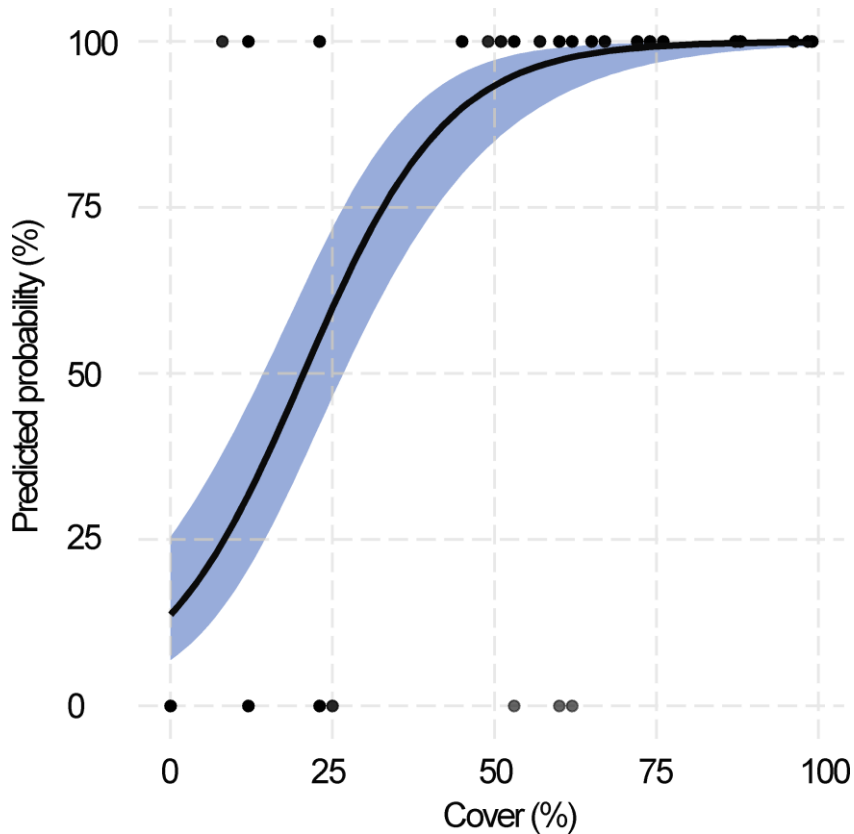
### Shrub facilitation

According to Z test the probability of the occurrence of the *F. sylvatica* inside a canopy cover of shrub species was independent by degree of cover. In detail, the slope parameter ( $\beta_1$ ) of logistic model resulted highly significant, while the intercept parameter ( $\beta_0$ ) (Table 3).

**Table 3** Summary statistics of logistic model parameters. The parameters  $\beta_0$  and  $\beta_1$  are respectively the intercept and slope of the model.

Parameter	Estimate	Standard error	Z-value	p-value	Lower 95%	Higher 95%
$\beta_0$	-0.873	0.491	-1.779	0.752	-3.023	0.810
$\beta_1$	0.068	0.013	5.205	0.013	0.010	0.084

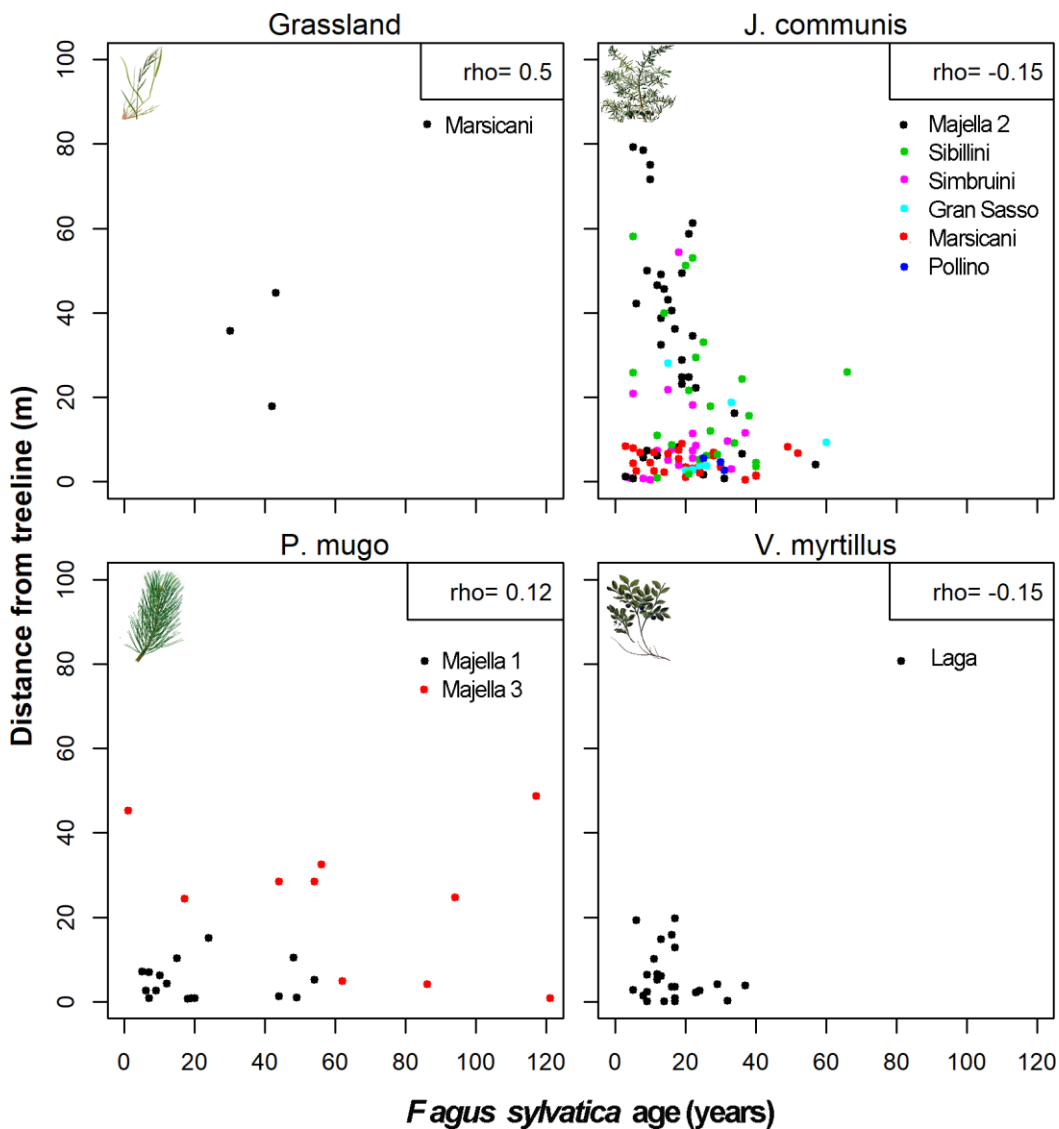
The odds ratio ( $e^{\beta_1}$ ) for percentage shrub cover was estimated as 1.07, which means that for 1% increase of the canopy cover a shrub has a 1.07 more chance of having a *F. sylvatica* tree inside the canopy cover than outside. Accordingly, the plot of predicted probabilities of occurrence of *F. sylvatica* clearly showed a logistic relationship with the degree of shrub canopy cover (Figure 2).



**Figure 2.** Predicted probabilities from logistic regression model of the occurrence of the *F. sylvatica* individuals in relation to shrub canopy cover. Blu band represents the 95% confidence interval. Open circles represent *F. sylvatica* individuals observed inside (1) and outside (0) the shrub canopy cover.

### **Relationship between distance and age**

The correlation between distance from treeline and age of the recruited *F. sylvatica* trees was not significant for all type of canopy cover. A negative correlation was observed in mountain sites covered by *J. communis* ( $\rho = -0.15$ ,  $p=0.11$ ) and by *V. myrtillus* ( $\rho = -0.15$ ,  $p=0.776$ ). In contrast, mountain sites covered by grassland and *P. mugo* the correlations were both positive ( $\rho = 0.50$ ,  $p=0.1$  and  $\rho = 0.12$ ,  $p=0.56$ , respectively) (Figure 3).



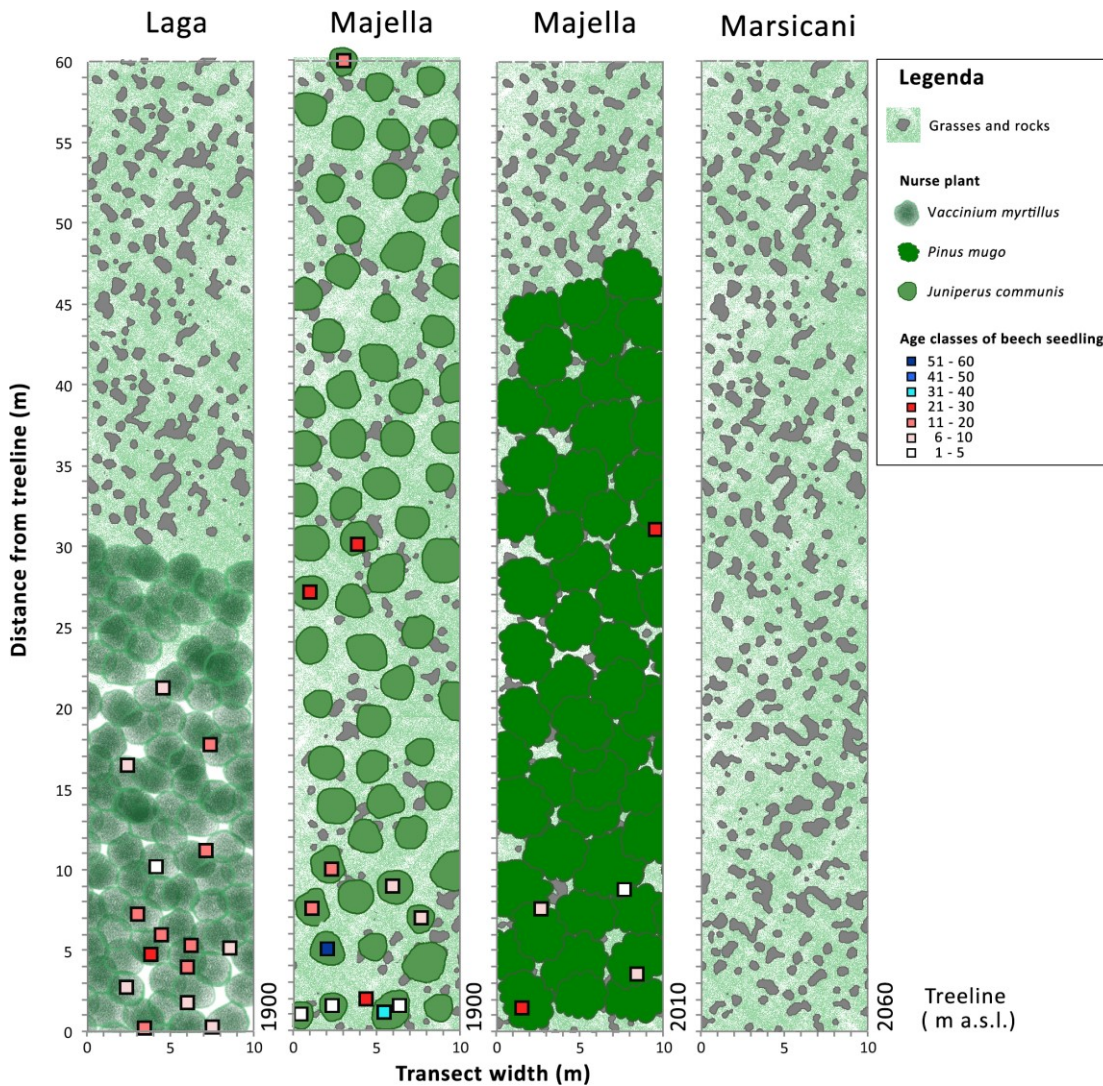
**Figure 3** Scatterplot of age (year) and distance (m) from treeline of *F. sylvatica* trees growing in: a) grassland; b) *Juniperus communis*; c) *Pinus mugo* and d) *Vaccinium myrtillus* shrub cover. Rho represents the Spearman rank correlation value.

### Mechanism of recruitment

Recruitment of new individuals (1-10 years old) is ongoing at most of the sites with the exception of Pollino and Gran Sasso, both also recording the lowest densities of colonizing trees above the treeline (17 and 23 individuals ha<sup>-1</sup> respectively).

The negative correlation between age and distance from treeline both in the *J. communis* and *V. myrtillus* shrubland, even if not significant, indicates that beech trees become younger as distance from treeline increases. This feature suggests a progressive colonization starting from the treeline to

upward. Among the juniper shrublands, it is interesting to note two extreme opposite patterns: one in Majella, where young beech plants (mainly between 3 and 25 years old) spread throughout a long distance from the treeline, and the other in Marsicani Mts. where beech trees, between 3 and 52 years old, are constrained in the first 10 meters from the treeline.



**Figure 4.** Spatial distributions and age of the *F. sylvatica* trees in 4 representative plots: Laga (M. Gorzano), Majella (M. Amaro), Majella (M. Cavallo), Marsicani (M. Greco) of the Apennine treelines. The colours of the squares indicate the tree class age.



### **3.4 Discussion**

Our analysis shows that recruitment and establishment of new individuals of *Fagus sylvatica* occur above the present treeline in all the studied mountain chains, regardless treeline form (namely Krummholtz and abrupt), elevation and location.

This is consistent with what might be expected as a result of both increasing global temperatures and reduction of anthropogenic activities. Indeed, worldwide, multiple lines of evidence support recent recruitment beyond treeline limits consistent with observed rates of recent warming (Suarez et al. 1999; Gamache and Payette 2005; Truong et al. 2007; Shiyatov et al. 2007, Harsch et al. 2009). In view of the changes in economic structure and historical disturbance by anthropogenic factors, recent shrubs and trees encroachment of abandoned alpine pastures has also been documented for Central Europe, following the progressive decline of herbivore pressure linked to traditional agro-pastoral practices at high elevation (Holtmeier and Broll 2007; Gehrig-Fasel et al. 2008; Vitali et al. 2019).

Beech individual's density values are very heterogeneous, both between paired areas, namely shrubland and grassland, and between different shrubland types. A clear pattern separates the shrublands from the grasslands above the treeline, where beech individuals were always present and absent/episodic, respectively.

This array evidences the absence of beech regeneration in open grassland areas above the treeline. The few three adult trees found in a grassland area in the Marsicani chain at 2060 m a.s.l. should be considered as residual trees. Both their old age between 30 and 43 years, their long distance from the present tree line and above all that the present maximum treeline elevation recorded in the Marsicani mountain group is ~180 m higher than the sampled one (Bonanomi et al. 2020) let us to suppose that these sparse trees might belong to a past continue canopy forest and that at that site the past treeline was higher than the present one. In the Marsicani mountain group in several cases, high and low treelines coexist within the same peaks suggesting a very heterogeneous relative contribution of climatic and human disturbance on treeline elevation (Bonanomi et al. 2020).

As hypothesized, the presence of the shrub canopy cover represents a major environmental driver feature operating at local scale in controlling both recruitment and establishment of new beech. In this sense, the logistic model clearly shows that in shrubland areas the probability of the occurrence of *F. sylvatica* under a shrub canopy is independent by the degree of shrub cover. Indeed, even at very low cover degree, beech individuals can be found preferentially in the shrubs' microsite.

Literature reports ample evidence of facilitative relationships as a widespread ecological phenomenon. (Callaway and Walker 1997) Intra and inter-specific associations have been found in many different ecosystems, and facilitative relationships have been found above all in harsh environmental conditions such as high elevation treelines and arid and semi-arid biomes. Plants may promote the life of other plants by ameliorating micro-environmental characteristics through several mechanisms. For example, they may have facilitative effects by altering substrate characteristics, by trapping seeds in subcanopy litter; or even indirectly, by introducing other beneficial organisms such as soil microorganisms, mycorrhizae, by attracting more pollinators or by eliminating potential competitors and providing protection from herbivores. At treeline, a preeminent role of the canopy cover in buffering the understory climate temperature extremes that mitigate the effect of wind and regulate soil moisture has been also reported (Bonanomi et al. 2018; Allegranza et al. 2016; Hadley and Smith 1986; Camarero and Gutiérrez 2002). In severe environments such as high elevation treelines, both seedling survival and growth of new individuals depends on the availability of existing trees or shrubs, that serving as shelter, provide safe microsite conditions, protect new seedlings, and thus promote treeline advances (Akhalkatsi et al. 2006; Batllori et al. 2009; Grau et al. 2013; Lyu et al. 2016).

In all the shrubland studied areas, no clear relationship between density and the considered variables (treeline elevation, shrub cover %, shrub height) has been found. A very weak negative relation exists only between treeline elevation and density of beech plants in the areas with juniper. This evidence suggests that the shelter effect of the shrub canopies is effective in a number of environmental conditions and is not linked to the shrub species. Camarero and Gutiérrez (2002)

report a shrinking effect on the recruitment of *Pinus uncinata* of dense and low shrubs (e.g. *Rhododendron ferrugineum* and *J. communis*). In our study, the nursing effect overrides the light needing even when the shrub cover is 100% as in the case of *V. myrtillus* and *P. mugo*. This is consistent with the autecology of *F. sylvatica* which seedlings are shade-tolerant able to persisting as small trees for long periods in the forest understorey.

The highest density of *F. sylvatica* saplings found in *V. myrtillus* shrubland is somewhat surprising. Indeed, several studies have demonstrated significant root competition of ericaceous shrubs with tree seedlings (Jäderlund et al. 1997; Titus et al. 1995; Nilsson 1994; Messier 1993; Messier and Kimmins 1991). Further, the broadleaf habitus of this shrub does not guarantee effective protection from winter stressful condition. However, in Mediterranean climates, seedling desiccation is especially important, since low precipitation and scarce soil moisture availability can affect recruitment and growth also at the treeline (Weisberg and Baker 1995; Lloyd and Graumlich 1997; Piper et al. 2016; Allegrezza et al. 2016). In this regard, Bonanomi et al. (2018) evidenced that overheating, and summer drought are among the major constraint limiting treeline elevation of beech. Indeed, during the spring and summer season, shrub canopy cover, could both mitigate the high summer temperatures by providing shadow and also trap winter snow and retard its melt, ensuring sufficient moisture for seedling recruitment and survival. In this sense, a facilitative effect of shelter rocks too, has been suggested by Vitali et al. (2019) for *Pinus heldreichii*, but this does not apply to European beech because it suffers a lot in rendzic soils because the rooting is strongly hindered.

A clear spatio-temporal colonization pattern above the treeline is absent. Indeed, both the age of the beech individuals and their spatial distribution, namely the distance from the present treeline, is somewhat in homogeneous between the considered areas. A common date for the beginning of the colonization above the treeline is lacking, but a major recruitment occurred at the beginning of the nineties. In figure 4, we report four exemplificative recruitment patterns namely in *V. myrtillus*, *J. communis*, *P. mugo* and grassland. We should speculate that this different pattern might be related to

different land use histories i.e. different time of abandonment of agro-pastoral activities and a greater impact of grazing by wild ungulates on the Marsicani Mts and Majella (Van Gils et al. 2008, 2012, Palombo et al. 2014), or a major role of microdentis as agents of seed dispersal in the Majella site. In both the *P. mugo* shrubland, the presence of both seedling and sapling (i.e. 1-20 years old) indicates that recent recruitment is occurring. However, the presence of adult trees laying at far distance from the present treeline suggests that past forest was probably extending several meters above the present treeline and that what is happening now, is an infilling or recolonization pattern where old trees act as outposts of the tree species line.

### **3.5 Conclusion**

Our results provide clear evidence that in several Apennine mountain sites treeline is going to advance thanks to shrub facilitation effect which allows the establishment of *F. sylvatica* above the current altitudinal position of treeline. The presence of a shrub cover is an indispensable condition for both recruitment and establishment of beech above the upper limit of closed forest, independently by both the shrub species and elevation.

To sum up, although a clear nursing effect has been stated, further studies must be devoted to shed light on the nature of facilitative mechanism (e.g. climate buffering, seed trapping, wind protection, physical protection from wild-grazing) and on the relative roles of topographic features (e.g. elevation, slope, aspect). Alpine treeline ecotones have received much attention recently due to their potential as indicators of climate change. In this context, investigations on the role of preexisting vegetation in the establishment and survival of seedlings above the treeline, can have a fundamental role since disregarding the mechanism of plant-plant interaction could result in unrealistic prediction of treeline dynamic response to environmental change.

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## **4. *Fagus sylvatica* stand structure modulates near-ground climate in a Mediterranean treeline**

### ***4.1 Introduction***

The dynamic of forest stands undergoes spatio-temporal variations because of continuous feedbacks with biotic and abiotic factors (including disturbances), with emphasis on local climatic conditions. Such interactions allow exchanges of energy and matter between the canopy and the surrounded atmosphere playing an important role in the modification of the canopy cover, stand composition, and eco-physiological behavior of trees (Jones 1992). On a global scale, there is a general consensus that macro-climatic factors such as temperature and/or precipitation exert a major role in controlling growth, distribution as well as health status of forests. Specifically, temperature sets rather narrowly defined growth-physiological limits to trees particularly at their limit of distribution (Alvarez-Uria and Körner, 2007; Lenz et al. 2014a; Rossi et al. 2016). For instance, in a global comparison of rooting-zone temperatures at high-elevation, Körner and Paulsen (2004) proposed a thermal threshold of 6.7 °C (even with some exceptions) during the growing season as the thermal limitation to plant tissue formation for tree species living at the upper forest boundary. Not by chance available global/regional climate data layers e.g., WorldClim (Fick and Hijmans, 2017), and CRU TS (Harris et al., 2014), among others, are primary tools in ecological research to understand important implications for the functioning of forest biomes, forecast potential species range distribution and land-use variations in ongoing climate change. However, at the finer scale, we still know relatively little about forest microclimate gradients over time and across spatial scales, where meaningful factors such as wind, slope orientation, snow cover, soil type, forest structure and human impact among others, may lead to highly heterogeneous forest microclimate ( Clarke 2017; Zou et al. 2007). It has been proven that, even within areas of moderate topography, ecologically significant gradients in soil moisture and near-surface air temperature can occur between slopes of different inclination and

orientation, i.e., a 2.5–3 °C mean annual temperature difference between north and south-facing slope recorded by Rorison et al. (1986). Roughly equivalent, Ackerly et al. (2010) focusing on a small mountainous landscape in California assessed that thermal variability across this topographically complex area may span from 3 to 8 °C. Such a topoclimatic variability at local scales constituted a potential important buffer in ecosystem response to climate variability providing microrefugia where species persisted locally amidst unfavorable regional climatic conditions (Alvarez-Uria and Körner 2007; Lenoir et al. 2013; Lenz et al. 2014a; Macias-Fauria and Johnson 2013).

In this context, the forest canopy has also been recognized to influence the dynamics of soil-plant-water interactions at both local and landscape-scale (Aussenac, 2000; Breshears et al. 2009; Zou et al. 2007) creating a microclimate whose characteristics depend on either the general climate itself or the physical characteristics of the vegetation cover. Tree canopy *i.e.*, leaf area and related supporting branches have substantial effects on interception of rainfall, incoming/outgoing short-longwave solar radiation, and wind, resulting in a reduced lateral transfer of humidity and heat, and buffering against heat loss overnight (Baldocchi and Xu, 2007; Komatsu, 2005; Lenoir et al., 2013). Branches, leaves, and needles reflect and absorb part of the incoming solar radiation during the day, allowing less energy to reach the ground below the canopy (Aussenac, 2000). The degree of absorption is largely determined by stand structure, tree density, species composition, and leaves distribution (Arx et al., 2012; Ehbrecht et al., 2019; Gaudio et al., 2017). During the night, infrared heat released from both the ground and plants is partly held back by the canopy above (Groot and Carlson, 1996). As a consequence, forested areas usually cool down less during the night and limit daytime air warming. Several authors showed that this smoothing effect on temperature daily amplitudes is most pronounced on warm, sunny days and in dense stands, but also depends on physiographic settings (see above), ground vegetation layer, and soil moisture (Arx et al., 2012). The buffering and decoupling capacities due to canopy cover further increases the probability for understory plants, including tree

seedlings, to persist locally. The canopy shelter phenomena create cooler and wetter conditions for seedlings establishment (and in general for tree species sensitive to high temperatures or drought) and have important implications for species redistribution under anthropogenic climate change. Such 'forest influence' on microclimate is spatio-temporal heterogeneous, particularly at the edge between treeless areas and the forest patches (De Frenne et al., 2019; Renaud et al., 2011). Quantitative data about spatio-temporal relationships between understory microclimate and local open-field macroclimate showed the difference to the open area is greatest at noon and in the early afternoon when daily minimum values are recorded (Arx et al., 2012). For instance, in a comparison between open-field and below-canopy conditions for different forest types of the Alps, Renaud et al. (2011) found the greatest temperature differences for beech and beech–silver fir forests with summer values 6 °C to 8 °C lower below-canopy compared to open-field. More recently, De Frenne et al. (2019) in a global analysis of 714 paired temperature data points, confirmed that tree canopies buffer forest floors against both maximum and minimum open-field temperatures. The mean and maximum understory temperatures were, on average, cooler than macroclimate temperatures by  $1.7\pm 0.3^{\circ}\text{C}$  and  $4.1\pm 0.5^{\circ}\text{C}$ , respectively. Conversely, the minimum temperatures of the forest understory were  $1.1\pm 0.2^{\circ}\text{C}$  warmer than the temperature in the open-field.

Understanding whether and how the buffering capacity of forests may vary over time and across topographical features requires further insight into temperature variations over seasons, and their relations to tree phenology and stand characteristics, particularly in environments where trees grow at the edge. In such landscapes, commonly referred to as treeline, microclimate experienced during different seasons is limiting for plants when their physiological tolerances are exceeded (Harsch and Bader 2011; Körner et al. 2016). Here, small fluctuations of environmental parameters may determine changes in the specific architectural and functional components of plant (e.g. *krummholz sensu* Harsch and Bader 2011), patterns of tree establishment and mortality, which in turn alter trees spatial distribution (Bertrand et al. 2011; Lenoir et al. 2017).

In this work, we systematically evaluated how the spatio-temporal variability associated with canopy cover influences the dynamics of soil surface microclimate reflected in near-ground temperature and soil water content. To this, we selected the highest *Fagus sylvatica* treeline in the Mediterranean mountainous area as an experimental site, near to the southern limit distribution of the species (Bonanomi et al. 2018). Our main goal was to explore the variability in near-ground microclimate imposed by topographic conditions and seasonal changes in vegetation cover. We described the effects of canopy cover on the near-ground air/soil temperature and soil moisture in contrasting environments, such as open areas and closed forest stands at the high-altitude tree vegetation limit.

## **4.2 Materials and Methods**

### **Study site**

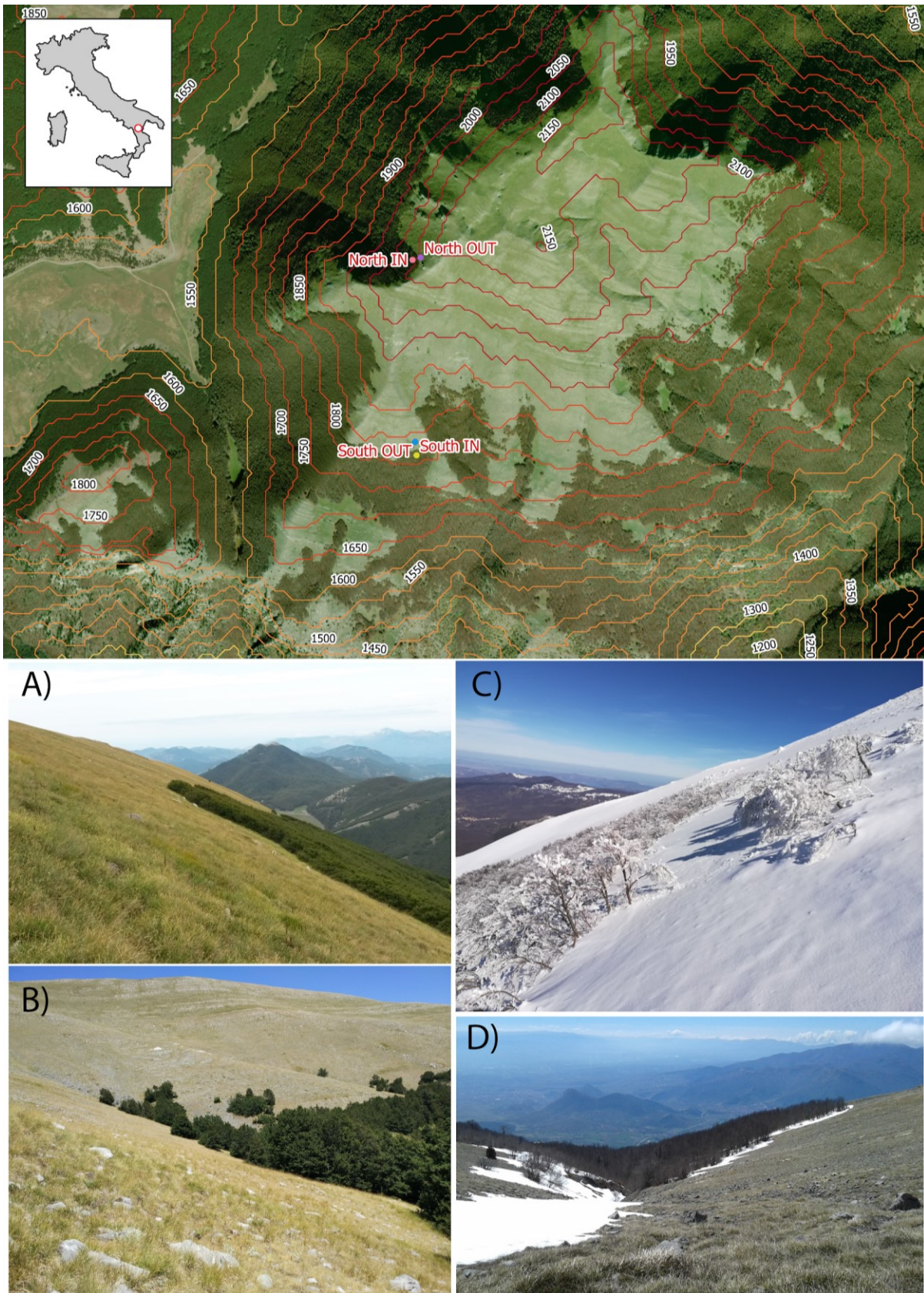
The study was conducted in the Serra del Prete mountain (39°54' N, 16°08' E; elevation: 2,181 m a.s.l.), Southern Apennine, Italy, near to the southern limit of European beech (*Fagus sylvatica* L.) distribution. The climate of the site is characterized by warm summers (average July-August temperature of 13.5 °C) and cold winters (average December-February of -2.6 °C). The mean annual temperature is 5 °C and snow cover persists from November to May. Annual precipitation is 1,583 mm, irregularly distributed throughout the year, with only 7.6% falling during summer months. On the western mountain-side, fog and low clouds carried by perturbations from the close Tyrrhenian Sea mitigate soil water depletion during the dry summers. The soil originates from a fissured grayish limestone with Haplic Calcisol in the forest and shallow rendzic Leptsol and large outcropping rocks under the grassland above the treeline (FAO Soil Classification System).

The stands, dominated by mono-stem and mono-layer beeches, were managed until 1960 up to 1,900 and 1,700 m a.s.l. at the north and south aspects, respectively. Above these elevations, the regeneration strategies switches from seed to layering, resulting in changes in structure from single- to multi-stem, more pronounced in the North-West than South aspect.

## Fieldwork

Two experimental plots were established at the study site differing in slope orientation and stand structure (mono-stem vs. multi-stem, Fig. 1). Near-ground microclimate measurements were performed below-canopy on North-West (2,043 m a.s.l.) and South (1,835 m a.s.l.) aspect. Each experimental stand has an open field near-ground microclimate measurement reference, in order to document the buffering effect of the canopy cover on near-ground microclimate.

Air temperature and relative humidity at 10 cm above ground and soil temperature and moisture at 10 cm depth were monitored below-canopy and in a near grassland open-field. In each site, we deployed a data logger (Em50 Decagon Devices, Inc, Pullman, WA, USA), powered by a 12 V battery replaced after six months, and equipped with (i) an air temperature/humidity sensor (VP-3; Decagon Devices, Inc, Pullman, WA, USA), which measured respectively temperature and relative humidity of air with 0.1°C and 0.1% resolution and (ii) two integrated soil temperature and moisture sensors (5TM; Decagon Devices, Inc, Pullman, WA, USA) placed horizontally in the undisturbed mineral soil, at 10 cm depth (B horizon). Measurements were recorded every minute and averaged per half hour May 2016 and June 2017. Temperature records were occasionally lacking due to repeated blackouts of the data collection due to lightning.



**Figure 1.** High elevation *F. sylvatica* canopy cover in the study site (Serra del Prete, 2181 m a.s.l. in the southern Apennines) with abrupt and 'krummholz' treeline form (*sensu* Harsch and Bader, 2011) at South and North-West facing slope, respectively. The markers indicate the locations of air and soils temperature and humidity sensors below-canopy (IN) and open-field (OUT) positions, at southern (1,747 m a.s.l) and northern-western exposition (2042 m a.s.l.). Contour lines represent 50 m intervals. Pictures A) and C) show Serra del Prete, north-west face in summer and winter, respectively. Snow depth in C) was 2.5-3.0 m. B) and D) show Serra del Prete, south face in summer and winter,

respectively. Pictures have been taken by G. Bonanomi. Image on the above map is from Google Earth Pro™ (Google, Inc. Mountain View, CA, USA).

### **Stand attributes**

Stand attributes were measured in transects of 5 m x 10 m on both treelines (Table 1). Diameter at breast height, basal stem form (i.e, length:height ratio in the first 2 basal meters), total height and height of live crown base insertion on the stem were measured for all sampled trees. Plant area index (PAI) was measured in summer during the fully leafed period with the LAI 2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA).

### **Data Analysis**

We calculated the standard deviation (SD) on the long-term raw data to examine the variation of the data and detect statistical outliers. Values exceeding the range of mean  $\pm$  3 SD were considered as potential outliers and were then inspected manually and excluded from the successive analysis if they did not occur. In winter, soil temperatures

fluctuated near zero and was considered in the analysis as a proxy of the residence time of snowpack. To report summary statistics, we carried out a multilevel-modeling framework using intercept-only linear mixed-effects models (LMMs) without fixed predictor variables but using nested month, day and hour as a random intercept term to account for random variability. The intercept of intercept-only models represents the average magnitude of the temperature offset of forests in summer (JJA), winter (DJF), and through the growing season (from May to September) while accounting for the non-independence among replicates from the same measurement. When fitting our intercept-only LMMs, we used the restricted maximum likelihood method in the *lmer* function from the *lme4* package (Bates et al., 2015) in R version 3.6.02 (R Core Team, 2019).

We tested for non-linearity of the relationships between the average temperatures outside the forest and the forest temperature offset (i.e., the difference between the the below-canopy and the open-field temperature) during the growing season using General Additive Mixed Models (GAMMs) for both stands including open-field temperatures and daytime (as sin and cos of hours) as fixed effects

and month-day as random ones with the *mgcv* package (Wood, 2017). We assessed how open-field temperatures predicted variation in the forest floor temperature during the growing season. We fitted LMMs with open-field temperatures and daytime (as sin and cos of hours) as fixed effects and month and day as a nested random effect using restricted maximum likelihood in the *lmer* function from the *lme4* package. We also performed  $\chi^2$  test by comparing the univariate LMM including a single predictor with the baseline intercept-only model. Goodness-of-fit was determined by calculating the marginal and conditional coefficient of determination ( $R^2$ ) as previously reported using the '*r.squared GLMM*' function in the *MuMIn* package (Burton, 2019).

### **4.3 Results**

#### ***Stand structure attributes according to elevation and aspect***

Peculiar forest attributes were detected at the stand on the northern slope where tree regeneration strategies switched from seed to vegetative layering (Table 1). In particular, the stem density was about seven-time higher at 2,043 compared to 1,752 m a.s.l., while the basal area increased by 93% and the plant area index (PAI) of 110%, respectively. On the contrary, stem sizes reduced by 92% and 181% for diameter and total height, respectively. The mean height of the live crown approached forest floor (~1 m vs. ~10 m for north-western and southern slope, respectively) and stem shape switched from decumbent (or upright) to procumbent at increasing mountain elevation. The stem base height (first 2 m) exacerbate its sabre-form and was tightly in contact with forest floor at northern treeline compared to southern treeline (basal stem form: 1.36 vs. 1.06, respectively). At the southern slope the mono-stem and mono-layer canopy are proxy of past forest practices.

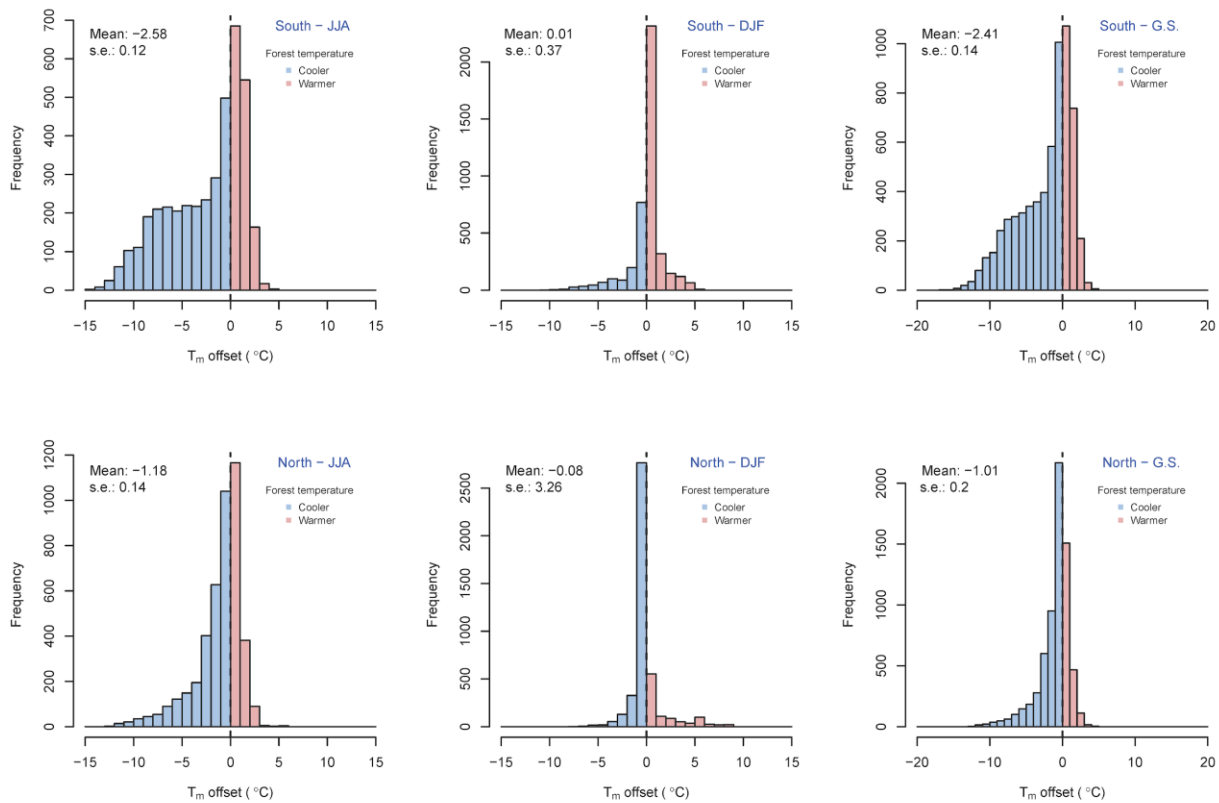


**Table 1.** Summary of *F. sylvatica* treeline stand structure attributes studied in the Serra del Prete (southern Apennines). In the southern slope secondary prairie substitute beech forest starting from 1,800 m a.s.l.. In brackets values of 1<sup>st</sup> standard deviation are reported.

	North-West	South
Elevation (m a.s.l.)	2040	1752
Slope (%)	68.5	40
Stem density (n. ha-1)	7651	1167
Basal area (m <sup>2</sup> ha-1)	50.48	60.1
Mean diameter at 1.30 m (cm)	10.57 (8.81)	20.93 (14.87)
Mean total height (m)	5.13 (3.01)	16.37 (5.01)
Mean live crown base height (m)	0.93 (0.20)	10.38 (3.06)
Mean height-to-live crown (m)	5.01 (2.81)	8.45 (3.46)
Mean stem form index (-)	1.36 (0.23)	1.08 (0.12)
Plant Area Index (PAI)	4.33 (0.11)	3.68 (0.35)

### ***Microclimatic differences between open field and below-canopy conditions***

Throughout the monitored period, the minimum temperature recorded was -10.1 °C at 2:00 am on November 30<sup>th</sup> 2016 and -9.8 at 0:30 am on January 8<sup>th</sup>, at South below the canopy and North open-field, respectively; the maximum air temperature was 39.45 °C at 3:30 pm on July 12<sup>th</sup> 2016 (South exposition, open-field). The large temperature variability was observed in April and May when temperature experienced high daily fluctuation (Table S1, Supplementary Fig. S1, and S2).



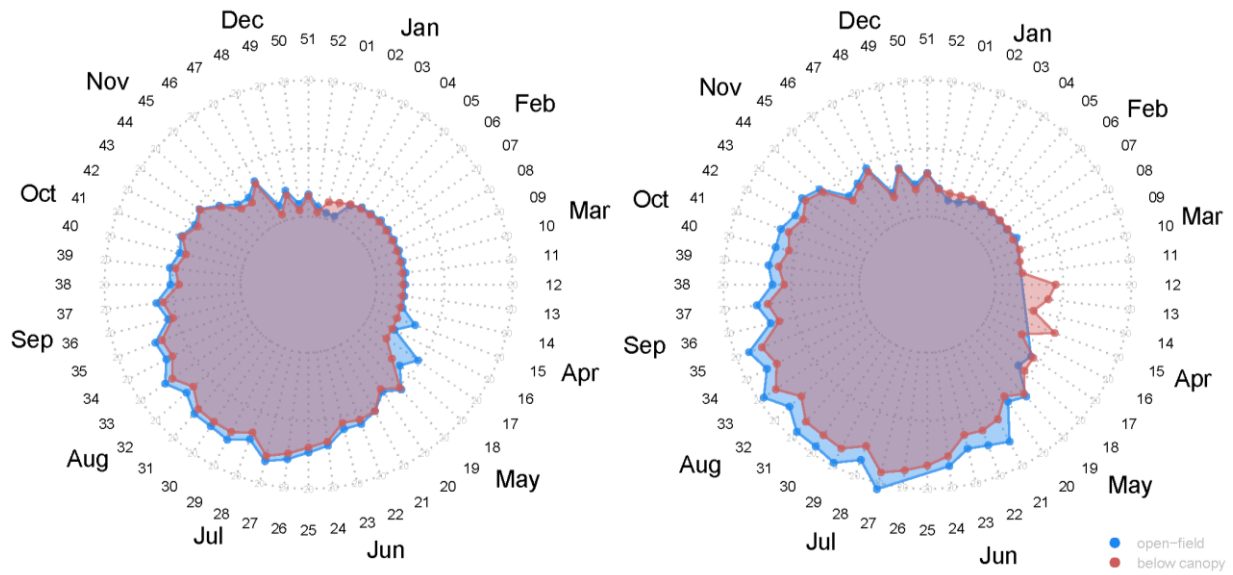
**Fig. 2.** Temperature offset values for average mean temperatures during summer (JJA), winter (DJF), and the growing season (G.S., i.e, from May to September). Mean temperatures are consistently cooler under-canopy (microclimate) compared to open-field (macroclimate). Temperature offset (mean  $\pm$  s.e.) are based on mixed-effects models with months, days, and hours as nested random-effect term (full statistics is reported in Supplementary Material Table S2). Y-axis scales are not fixed.

Overall, daily and weekly patterns for selected treeline stands indicated that canopies buffer forest floors against average (Fig. 2 and Fig. 3), maximum, and minimum open-field (Supplementary Figs. S3, and S4) temperatures. In summer, the below-canopy temperatures were, on average, cooler than open-field ones by  $2.58 \pm 0.12^{\circ}\text{C}$  and  $1.18 \pm 0.14^{\circ}\text{C}$  for south and north aspect, respectively (mean  $\pm$  s.e., mixed-effects models: both  $p < 0.001$ ). This is particularly evident in August for the treeline at the south-facing slope, where a maximum temperature difference of about  $10^{\circ}\text{C}$  between open-field and below-canopy is recorded. No significant offset was found for the

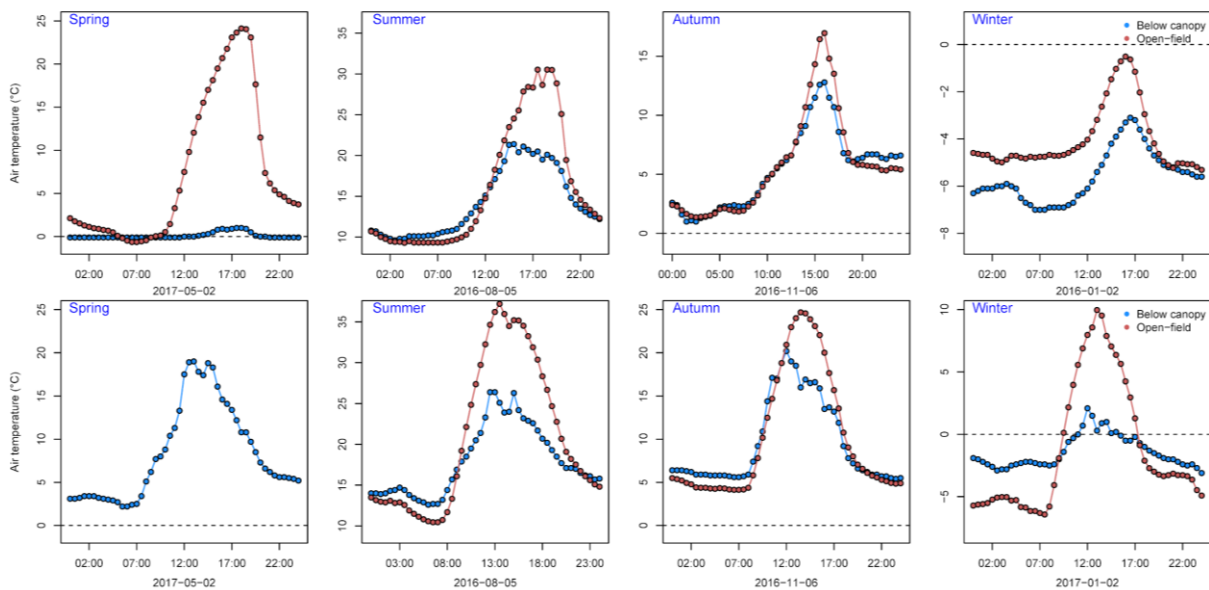
average temperature in winter (DJF) for South and North aspect (mixed-effects model: not significant; Supplementary Table S2). During the growing season (i.e., from May to September), the below-canopy temperature was, on average, cooler than open-field one by  $2.41 \pm 0.14^\circ\text{C}$  and  $1.01 \pm 0.20^\circ\text{C}$  for South and North aspect, respectively (Fig. 2; mixed-effects models,  $p < 0.001$ ). Considering the maximum temperature in summer, they were cooler under-canopy than open-field by  $8.63 \pm 0.4^\circ\text{C}$  and  $5.42 \pm 0.81^\circ\text{C}$  for South and North aspect, respectively (mixed-effects models: both  $p < 0.001$ , Supplementary Fig. S3). Conversely, the minimum temperature of below-canopy was  $0.90 \pm 0.17^\circ\text{C}$  and  $0.31 \pm 0.14^\circ\text{C}$  warmer than the open-field (Supplementary Fig. S4).

Uncoupled spatio-temporal pattern of temperatures between sampled sites was common in our dataset, mostly during spring. For instance, at the north-facing treeline, a large offset (more than  $5^\circ\text{C}$ ) in the average temperature in April (between the 15<sup>th</sup> and 16<sup>th</sup> week of the year) between the under-canopy and open-field conditions was found (Fig. 3). At this time, the snowpack under the canopy at north-facing slope persists compared to the adjacent open-field where it has already melted due to the increase of seasonal temperatures (see Figure 1D for an example of below-canopy snow persistence). On the other hand, in the spring clear sky night time like on April 20<sup>th</sup> 2017 (Supplementary Fig. S2) the open-field average temperature dropped to  $-2.7^\circ\text{C}$ .

The buffering effect of the forest canopy against the average temperature is observable in almost all the periods of the year, especially in the central hours of the day where the open-field temperatures peaked (Fig. 4). Conversely, the average below-canopy temperature at both sampled stands were warmer than in the open-field during the night.

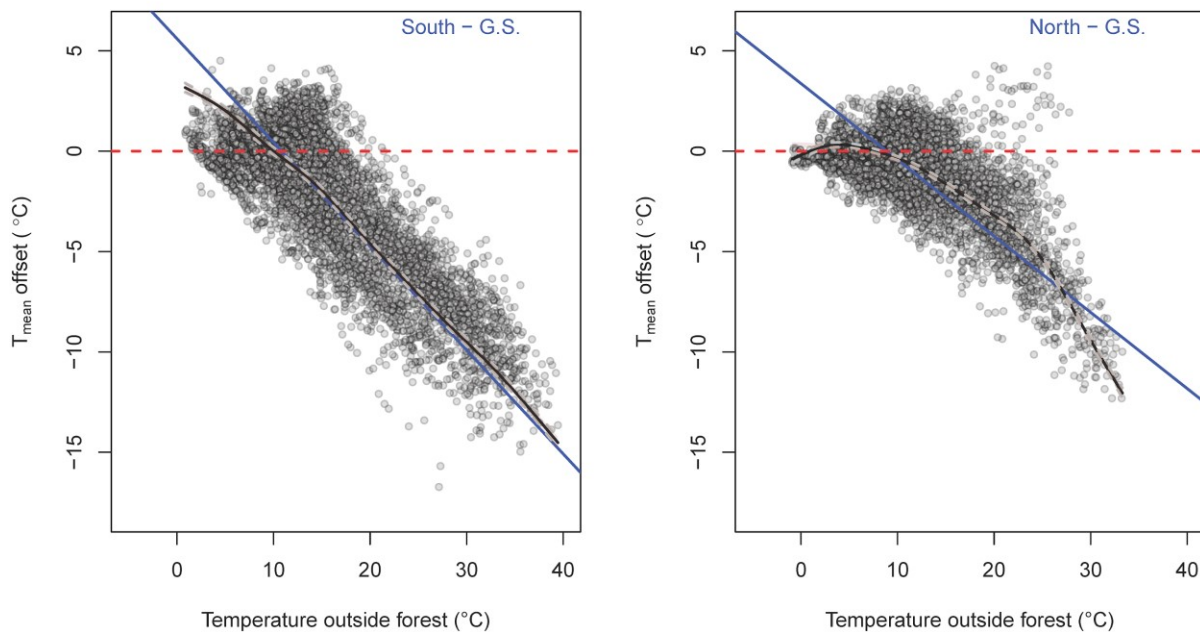


**Figure 3.** Average weekly near-ground air temperature recorded in the open-field (blue) and below the forest canopy (red) at North (left) and South (right) aspects. Black numbers in the radar charts are the week number while grey numbers are the temperature (in °C).



**Figure 4.** Diurnal patterns in near-ground air temperature for a selected random day for each season (from left to right: spring, summer, autumn, winter). The *F. sylvatica* treelines on the northern and southern slopes are shown on top and bottom panels, respectively. Blue and red lines represent the near-ground surface temperature below-canopy and related open-field, respectively.

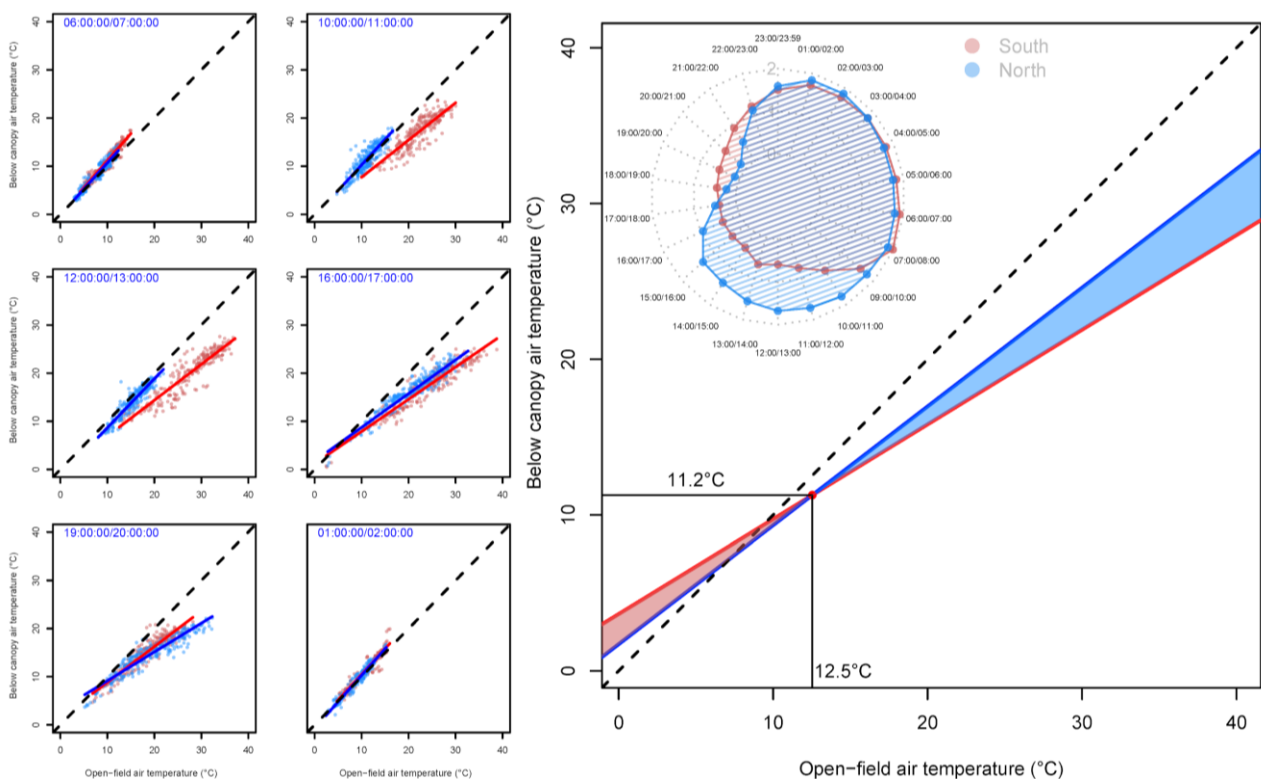
During the growing season the observed patterns of the temperature offset against open-field temperature appear to be linear (Fig. 5 and Supplementary Table. S3), apart from slight deviation for the northern stand a temperature  $<10^{\circ}$  and  $>27^{\circ}$  °C. The slope of the fitted regression lines, computed by means the mixed-effects models, was steeper for the treeline facing south (slope=-0.51) compared to north (slope=-0.37).



**Figure 5.** Testing for non-linearity of the relationships between the average near-ground temperatures in open-field (set as reference) and below-canopy temperature offset during the growing season (from May to September) using General Additive Mixed Models (GAMMs) for South (left panel) and North (right panel) treelines, respectively. Solid black lines show the fitted GAMMs with month, day and hour as nested random-effect term (dashed grey lines and grey shaded areas between the dashed lines show the standard error around the predicted values); solid blue lines show the fitted linear mixed-effects models (LMMs) with nested random-effect term for South (intercept=5.6, slope=-0.51;  $p < 0.001$ ) and North (intercept=3.37, slope=-0.37;  $p < 0.001$ ); red dashed lines show the null line (temperature offset = 0 °C or below-canopy equals open-field temperature). G.S. represent growing season from May to September.

The linear mixed model between below-canopy temperatures and the open-field temperatures during the growing season (from May to September) summarizes the microclimatic buffering effect of treeline forest canopies. The fitted lines measure below-canopy microclimate variability and can be represent strength and magnitude of ‘decoupling’ when the reference sensor represents open-field conditions (Fig. 6). At contrasting aspects, canopies showed substantial differences ( $p$ -value  $< 0.001$ , ANCOVA with aspect as dummy) in their ‘buffering capacity’ i.e., the cumulated area between the fitted regression lines in Figure 6 (sensu Davis et al., 2019). Figure 6 highlights that as

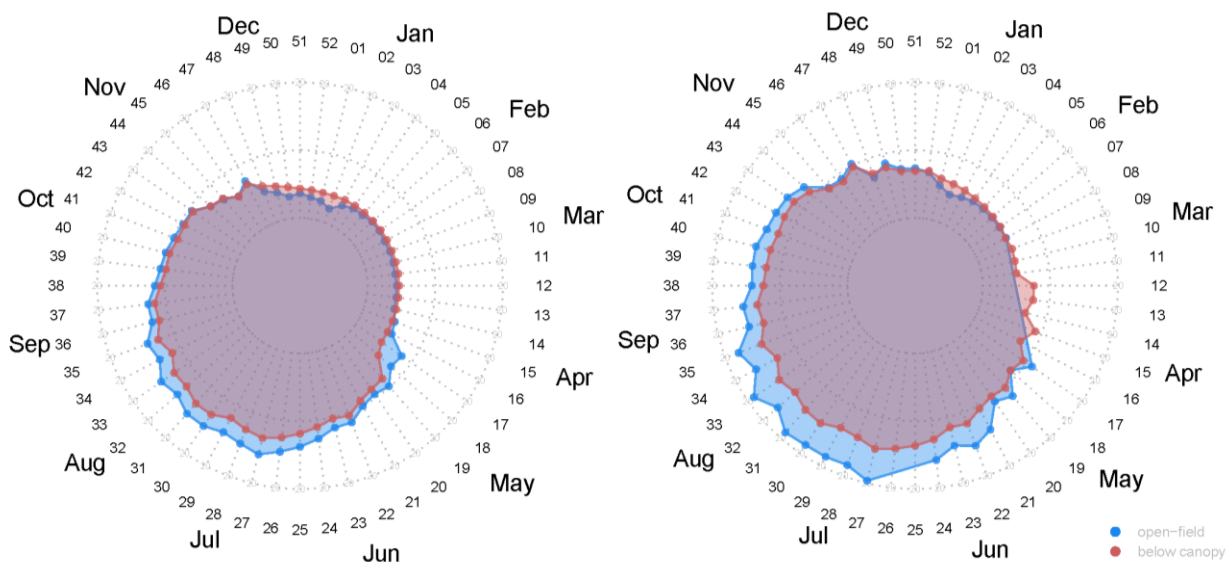
the air temperature of open-field increases, the related near-ground temperature under the canopy increases with less rhythm at the southern treeline (slope coefficient of 0.60) compared to the north-facing treeline (slope coefficient of 0.76). For instance, at the southern treeline the near-ground temperature below-canopy may result either higher or lower than the northern treeline, depending on the reference temperature. However, the pattern of decoupling of below-canopy temperature against the open-field follows a rather strong relation with the daytime. In details, both the understorey average temperature at the North and South aspect are quite coupled with the open-field temperature from 23:00 p.m. to 7:00 a.m.; then during the forenoon, from 10:00 a.m. to 13:00 a.m. the average temperature at the south aspect decoupled with the open-field temperature, while at the north aspect the temperature is still coupled. In the afternoon till sunset (from 16:00 a.m. to 21:00 a.m.), both the below-canopy average temperature at the North and South aspect are quite decoupled with the open-field temperature (Figure 6).



**Figure 6.** Relationship between near-ground open-field (set as reference) and below-canopy daily mean temperature of the growing season (from May to September). Blue and red circles represent the mean daily temperature of north-west

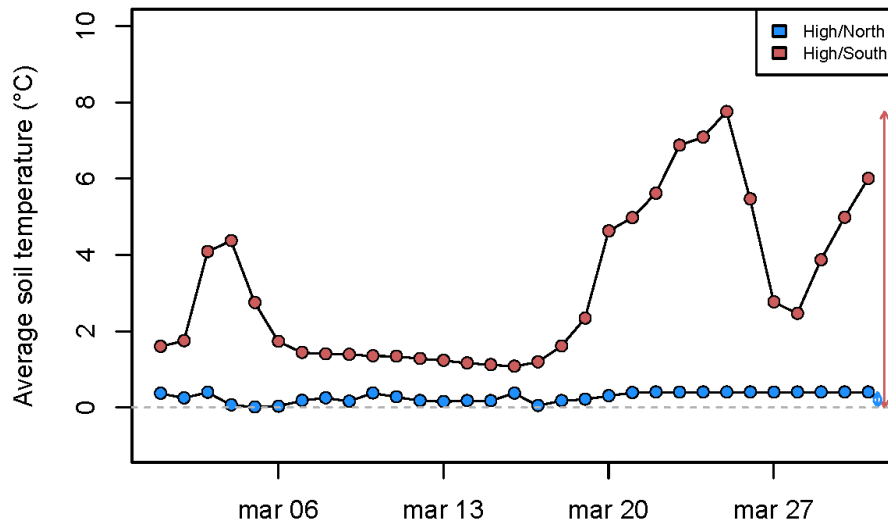
and south treelines, respectively. Full line represents linear regression fit (North, blue line: intercept= 1.73, slope=0.76; South, red line: intercept= 3.65, slope=0.60). The dashed black line represents the 1:1 relationship. Positive values (shady pink area) indicate overall near-ground warmer conditions under canopy than at the reference site, while negative values (shady blue area) indicate cooler air under canopy than reference conditions. Full statistics are reported in Supplementary Material Table S4.

The average temperature of the soil showed less weekly variability than air (Fig. 7, and Fig. S6 for average daily soil temperature). However, the offset between the understory and open-field conditions were much higher than the near-ground air temperature. Such a difference is particularly high in the summer months where at low elevation southern aspect was on average 13°C. In winter, the offset between temperatures is positive, meaning warmer temperatures below the canopy because of the cover effect (*i.e.*,  $T_{\min}$  higher inside). This could be an important effect particularly in these winter months, where the temperature is buffered by the shelter that trees provide.



**Figure 7.** Average weekly soil temperature recorded in the open-field (blue) and below the forest canopy (red) at the North (left) and South (right) aspect. Black numbers in the radar charts are the week number while grey numbers are the temperature (in °C).

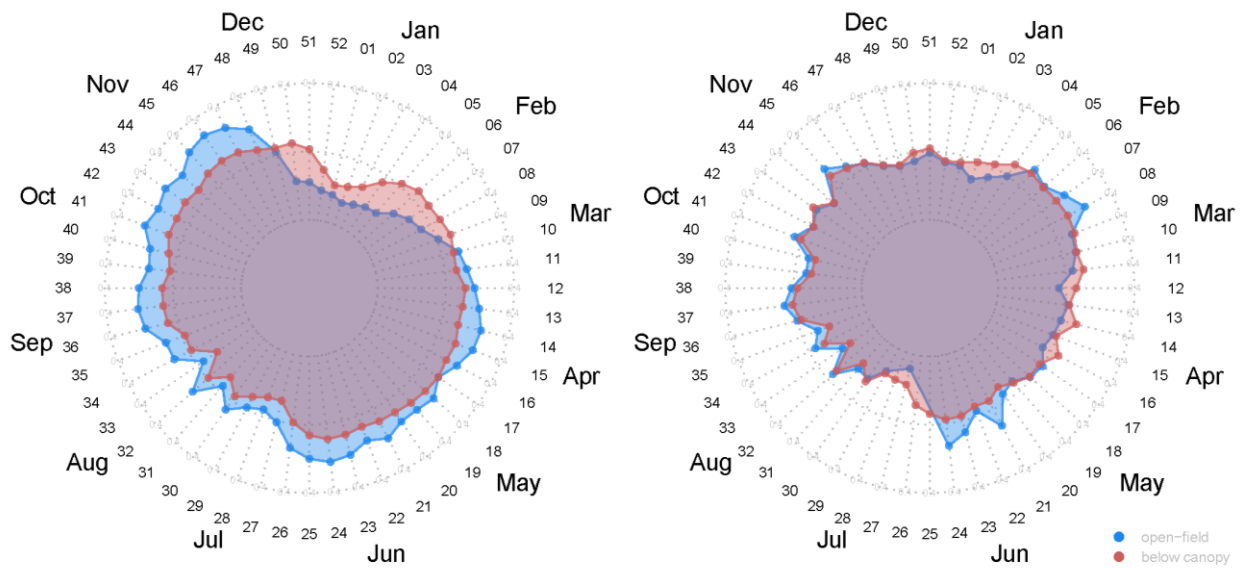
A remarkable difference exists also at the same altitude between the temperatures recorded at the north and south exposures; particularly in March the presence of the snow cover (not yet melted in this month) keep the temperature in the open-field close to 0°C, wherein the south, which alternate periods of snow and non-snow cover, the thermal range occurring in this month bring up and down the average temperatures (Fig. 8). This causes in the south a large thermal amplitude of the average delta temperatures of 8°C which may have a crucial effect on the potential seedling establishment.



**Figure 8.** Comparison of soil average temperature during March 2017 at North and South (further deployed a data logger used as control) high elevation stands. Blue and red lines represent north and south stands at high elevation, respectively.

High altitude north stand showed for almost all the year a very interesting soil moisture pattern which is higher on the open-field, in the prairie, compared to understorey (Fig. 9, and Fig. S8 for average daily soil moisture). Conversely, in the months of December, January and February the moisture content was higher in the open field compared to the covered soil.





**Figure 9.** Average daily (upper panels) and weekly (lower panel) soil moisture recorded in the open-field (blue) and below the forest canopy (red) at the North and South aspects. Black numbers in the radar charts are the week number while grey numbers are the temperature scale ( $\text{m}^3/\text{m}^3$ ).

#### 4.4 Discussions

##### Microclimatic differences between open field and below-canopy conditions

In the Mediterranean mountains, at the southernmost limit of its distribution, the altitudinal range of *Fagus sylvatica* L. spans several hundred meters (Peters 1997) from 900-1,000 up to about 2,140 m a.s.l. (Bonanomi et al. 2018). Along with this altitudinal gradient, trees reduce progressively their size with increasing elevation in response to growth constraints imposed by reduced temperatures (Holtmeier 2009; Körner 2012), hydraulic constraints and/or altered ecosystem properties (Bellingham and Sparrow 2009; Mayor et al. 2017). Thus, the growth habit of *F. sylvatica* progressively shifts from mono- to a multi-stemmed structure, forming in the tree community a canopy layer with live crown base height insertion close to the forest floor at high elevation. The increasing height and pressure of snow cover on the upper side of the stems with increasing elevation, combined with gravity in steep slopes, modify progressively the stem shape as a

gravitropic response (Mouliia and Fournier 2009). The ‘krummholz’ growth habit (referred to the climatically stunted and distorted trees) at our study site, appears as the most obvious phenotypic trait changes related to elevation/temperature (Holtmeier, 2009; Mouliia and Fournier 2009). In such cases, basal lateral branches also layering in the humus may produce adventitious roots and new autonomous secondary stems form dense clonal populations that progress downward the forest floor. It has already been demonstrated that species of the genus *Fagus*, e.g. *F. sylvatica* in Europe (Vacek and Hejzman, 2012) and *F. crenata* in Japan (Homma, 1997), regeneration strategies shift from seed to vegetative reproduction (*sensu* Del Tredici, 2001) as an adaptive response of environmental stresses (mainly temperature) induced by increasing elevation. Modifications in stand density, spatial assemblage and growth habit of tree community could translate in different abilities to capture resources and regulating forest microclimate during the growing season; equally relevant is stem shape modifications which improved the ability of twisted stems to trap and withhold snow against gravity movement during the winter, acting as autogenic engineers (*sensu* Jones et al. 1994) as elevation increases.

### **Effects of exposition on the microclimate pattern of treeline**

The results of this study provide strong support for the notion that forest microclimatic pattern covary with the local macroclimate one and both are strictly shaped by either topographical characteristics and forest structure, where tree canopies buffers near-ground temperatures. The south exposed treeline contrasted with the northern treeline mainly in the diurnal pattern of temperatures, characterized by high values in the middle hours of the day as well as the magnitude of the daily temperature range (*i.e.*, daily maximum temperature-daily minimum temperature), where topographic aspect may also contribute to exacerbate this effect. Canopy structure plays a key role in regulating mostly the offset of average and maximum summer temperatures. Forest thus provide highly heterogeneous thermal environment, where under-canopy is not only cooler on average than surrounding open-field, but negative maximum temperature offset (cooler in forest)

and positive minimum temperature offset (warmer in forest) also imply lower temperature variability below the forest canopy. Such a buffering effect of near-ground temperature was as high as 8.6°C for the maximum temperature (in summer, offset peaking 10°C) and as high as 2.5°C for the average temperature recorded at southern treeline. The average buffering effect that we documented are consistent with the general patterns observed in temperate regions across the globe (*i.e.*, ranging from 1.5°C to 5°C), spanning different forest types and structures (De Frenne et al., 2019; Potter et al., 2001; von Arx et al., 2013). When incoming solar radiation flux increase, temperature generally rises. Consequently, as hypothesized, a great smoothing effect on daily temperature amplitudes of forest canopy was found in summer compared to winter, has also previously reported by Morecroft et al. (1998), Renaud et al. (2011), and Renaud and Rebetez (2009), particularly when considering the offset between maximum and minimum temperatures. At the northern treeline, the buffering effect is much lower than at southern treeline (difference understory-open-field of about 1°C), obviously because of the reduced temperature range. Also, at northern the differences between open-field and below-canopy in mitigating temperature extremes depend on the canopy cover. Infact, the plant area index (PAI), was unexpectedly higher at northern than southern treeline (Table 1), meaning that crown density-related effects likely played a crucial role in smoothing temperature.

The above-reported differences in temperature are biologically significant, as experimental studies have shown that increases in temperature (and consequently air VPD) directly affect the whole plant growth and reproduction (Frey et al., 2003; Lenz et al., 2016; Rita et al., 2014). For instance, Keitel et al. (2003) obtained a strong link between stomatal conductance and air temperature, resulting in a relationship between air temperature and transpiration of beech stands. Analyzing the dynamics of radial stem variance and radial growth of beech stands, van der Maaten et al. (2013) observed that daily parameters mean air temperature, maximum air temperature, and soil water content were found to explain 59% of the variance in day-to-day stem radius variation. Together the above-cited

studies get insight into the role of microclimate temperature on growth and carbon cycles of temperate beech forests.

The temperature offset at the treeline was negatively correlated with the temperature outside forests (*i.e.*, primary and secondary alpine prairies). The offset became -linearly- more negative (that is, lower under-canopy temperatures at treeline) as open-site temperature increased, and more positive (that is, higher under-canopy temperatures at treeline) as open-site temperature decreased. In this context, large differences emerged in the relationship between temperature offset and macroclimate between North and South slopes. That's would mean that for 1°C macroclimate warming/cooling (from the mean value) the maximum difference in microclimate warming/cooling between southern and northern treelines increased. Roughly speaking, the forest canopy treeline at the south-facing slope has a greater cooling power in summer and heating in winter, compared to the north-facing one. It is worthy of note that the maximum offset values recorded for the growing season between below-canopy temperature versus open-field macroclimate exceed 15 °C for the south-facing beech treeline. These very high values far exceed the values for other tree species and across biomes reported by De Frenne et al. (2019), testifying to the high buffering power of the Mediterranean beech stands at this latitudinal and topographical conditions.

Major differences between the two contrasting treelines emerged also in terms of their buffering capacity. The first considerations arising from the Figure 6 is that it is possible to compute the differences ( $\Delta$ ) in terms of buffering capacity of the forest cover between north and south. Indeed as well explained by Davis et al. (2019), this metric is able to capture the combined effect of the decoupling and buffering processes where negative values of the summed-area between fitted lines (*i.e.*, negative difference between the integral south and the integral of fitted north lines) indicate cooler conditions for the southern stand compared to the northern one, and vice versa. The whole buffering capacity of the southern treeline during the growing season (*i.e.*, from May to September) compared to the northern one is 12.9°C when temperature range from 0 to 12.5°C (*i.e.*, left side of the crossing point of Figure 6) and 57.8°C when temperature range from 12.6 to 40°C.

In this regard, the buffering capacity of the canopy might have important implications for the ability of forests to act as microrefugia under changing climate conditions. However, the strong relationship we found with the average summer temperature suggests that buffering capacity also varied strongly over year. That is, the southern treeline was likely to be more decoupled from the free air conditions, and thus climatically stable, than northern treeline and/or open alpine grassland areas. Although such a decoupling effect cannot completely isolate forest climatic conditions from macroclimate fluctuations, it has the potential to partly offset the regional macroclimatic warming experienced in the forest understory due to anthropogenic climate change. For instance, Pepin et al. (2011) have already demonstrated that climate warming is weaker at southern decoupled locations compared with northern exposed locations in the western United States. As such, closed forest canopies might provide a line of defense against the impacts of current and future warming on the ecological processes that influence Mediterranean mountain forest ecosystems (for example, tree regeneration, demography and community reshuffling, litter decomposition, and soil water and nutrient cycling). Plant–water relations are especially sensitive to changes in climate extremes, particularly heat waves and consequent increases in VPD that increase atmospheric demand for plant transpiration. As offsetting was strongest for maximum temperatures, we might expect extreme events in the Mediterranean basin such as heat waves to be more strongly attenuated than gradual temperature changes. The canopy-temperature interaction phenomena also become particularly important during late spring frosts, which may severely affect the photochemical efficiency of young leaves, hereby influencing the seedlings and shoots development for this sensitive species (Allevato et al., 2019; Nolè et al., 2018). In the Mediterranean area, the risk of frost damage is promoted, among other, by a meteorological scenario characterized by diurnal and nocturnal clear skies with large temperature variability. In these situations, a dense canopy cover has well demonstrated to have a beneficial influence in sheltering/favoring seedlings establishment as well as increasing the survival probability after frosty nights (Gray and Spies, 1997; von Arx et al., 2013).

Soil temperature is considered to be the second most important factor regulating tree growth at its upper limit both at global and local scales (Müller et al. 2016a), and, although several authors demonstrated species-dependence effects of soil temperature in terms of photosynthesis, respiration, transpiration, and growth, this parameter is often overlooked in common plant ecophysiological measurements. Our results showed that significant interactions between soil temperature and forest stand characteristics, mainly because of transmittance modulate by the canopy, has an important control over the soil temperature beneath the stand as previously detailed for the treeline ecotone in Nepal (Müller et al., 2016b). The denser the canopy cover (i.e., northern treeline stand), the smaller the soil temperature fluctuations and the later the maximum and minimum soil temperatures tend to occur. Although with less diurnal variability, our results showed that the average soil temperature is strongly coupled with the air one (see Supplementary Table S5 and S6), with a strong cooling effect provided by canopies in summer. Coherently to our findings, this effect has been empirically estimated of about 4-5 °C (difference compared to the open-field) also for the grassland communities in summer up to 80-100 cm soil depth by Liechty et al. (1992). The effect of reduced soil temperatures (i.e., below 7 °C) in decreasing photosynthesis and transpiration is probably linked to an increase in water viscosity, while a reduction in growth could be due to a decrease in the supply of hormones coupled with a rise in ABA production. This has been demonstrated by Hurst (1998), who experimentally showed that cooled soil restricted the water uptake, drop to around a quarter the transpiration rate, and decreased roots growth and the foliage mass of beeches. Besides the direct effect on plants, Grimmond et al. (2000) pointed out that the soil temperature is decisive also for litter decomposition and soil respiration.

Growth limitation in several Mediterranean tree species has been also ascribed to low soil moisture content during summer drought while high productivity is associated with high soil moisture in cool - wet summers (Oberhuber et al. 2015). At warmer treeline, the survival and growth of young tree seedlings, mostly at the initial life stage, favorable temperature as well as soil moisture are crucial

determinants, especially until the root system is sufficiently developed and other factors such as light conditions and nutrient availability become limiting.

At our treelines, the soil moisture and average temperature are partly coupled. However, the effect of soil moisture and temperature on plant growth rate are most often complex and interdependent, since tree water deficits (i.e., transpirational loss from leaves exceeds water uptake) is affected primarily by atmospheric VPD (e.g., Beedlow et al. 2013 for Douglas-fir). The peculiar pattern of soil moisture at the northern treeline (i.e., higher in open-field compared to under-canopy) may have two non-mutually exclusive explanations. First, the northern treeline stand with a dense canopy that would transpire more water and therefore deplete soil moisture faster than areas having a sparse or no canopy (Aussenac, 2000). But the most plausible explanation could be attributed to the nature of the forest substrate. Indeed, in the open-field, the prairie soil appears more soaked compared to the understorey soil where the humus layers, characteristic of understorey beech forest, absorb from two to four times their weight of water. Forest soil, with its overlaying organic layers, behaves like a vast sponge capable of absorbing much more water per unit area than soil in the open alpine grasslands.

#### **4.5 Conclusions**

Forest canopies buffer climate extremes and promote microclimates that may function as refugia for understory species under changing climate. In this study, we posited that forest microclimatic buffering is sensitive to local water balance and canopy cover, and we measured this effect during one year across a climate gradient in a treeline European beech forest in Southern Italy. We found that the microclimatic environment experienced by trees at their distribution limit is both temporally- and spatially-dependent. Specifically, our findings indicate that local landscape structure, as delineated by topographic variability, play an essential role in driving microclimatic pattern through gradients of elevation and aspect. Such a buffering effect of near-ground

temperature was as high as 8°C for the maximum temperature (in summer, offset peaking 10°C) and as high as 2°C for the average temperature recorded at southern low elevation. The temperature offset of forests was negatively correlated with the macroclimate temperature outside forests; in particular, the offset became -linearly- more negative (that is, lower temperatures in forests) as macroclimate temperature increased, and more positive (that is, higher temperatures in forests) as macroclimate temperature decreased. The strong relationship we found to average summer temperature suggests that buffering capacity also varied strongly over time. That is southern forested stands was likely to be climatically more decoupled from the free air conditions, and thus stable, than northern stands and/or open areas. Although such a decoupling effect cannot completely isolate interior climatic conditions from regional exterior climatic fluctuations, it has the potential to partly offset the regional climatic warming experienced in the forest understory due to anthropogenic climate change.

#### **4.6 References**

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## 5. General Conclusion

In this study we provided a scientific contribution to the knowledge on the dynamics of growth and distribution of *F. sylvatica* in the Apennines, notably at the altitudinal limits. Along with the relation to the numerous changes over the centuries that these ecosystems have undergone, this study contributes also to better predict the future behavior of these ecotone.

Even if the temperature is the primary factor controlling treeline occurrence worldwide (Harsch, Hulme, McGlone and Duncan 2009), topography, geomorphological processes, and anthropogenic disturbance can play a significant role at local and regional scale (Holtmeier and Broll 2005; Macias-Fauria and Johnson 2013). Our approach involving three spatial resolutions, namely regional, landscape and local scale, shed light on the treeline elevation dynamics and the related processes involved in. The regional scale study, carried out on fifteen Apennine mountain chains revealed that treeline elevation is, on average, several hundred meters depressed in all the mountain groups analysed. A pervasive anthropogenic effect has been found across all the Apennines, with a strong impact in northern (i.e. Apuan Alps), central (Gran Sasso, Velino-Sirente, Sibillini) as well as in southern Apennines (i.e. Pollino). In some mountain chains, anthropogenic impact effects are evident, especially for the south aspect treeline, while in some cases low temperatures and low rainfall have played a key role. In fact, on the south-aspect slopes, the treeline is much more depressed than the north, the hypothesis of this result is summarized as a combination of different factors including the grazing and lack of water in the high-altitude grasslands beyond the treeline. (Bonanomi et al 2020). The consequence of this limit is the difficulty of restocking the beech in those areas now abandoned by managed grazing (Bonanomi et al 2020).

The study at the landscape scale, demonstrated that *F. sylvatica* advances in altitude as a result of the facilitation effect. The elevation progression of the treeline is due to the presence of shrubs, that promotes facilitating mechanisms (nurse effect) conducive to the seedling recruitment of the beech. The nurse species promote the microclimate for *F. sylvatica* in the first years of life. The presence of shrubs is an indispensable condition for both recruitment and establishment of beech above the upper limit of closed forest, independently by the shrub species and elevation. The nature of the facilitative mechanisms (e.g. climate buffering, seed trapping, wind protection, physical protection from grazing) and the relative roles of topographic features (e.g. elevation, slope, and aspect) must be further investigated.

At local scale we stated that *F. sylvatica* acts as engineer of its ecosystem, being the canopy able to change the underlying micro-environment via their own structures. Microclimatic conditions are strictly related to either topographical characteristics or forest structure, where forest canopy buffers near-ground temperatures. Such a buffering effect of near-ground temperature was as high as 8°C

for the maximum temperature (in summer, offset peaking 10°C) and as high as 2°C for the average temperature recorded at southern low elevation.

In this context, don't consider legacy of anthropogenic effects, could result in unrealistic prediction of treeline dynamic response to environmental change. These results confirm the importance of human activities in shaping the treeline ecotone of the Apennines and predicts an increasing trend if the global warming occurs. A trend for which some hypothesis' claim might intensify tree drought stress, which is already inducing tree decline in sensitive populations (Piovesan et al. 2008; Di Filippo et al. 2010).

Indeed, the history of forests in the Mediterranean area is a history of forest fragmentation and degradation. The spread of agricultural practices and animal grazing, fires, and the need of wood for railway sleepers have all reduced the amount of forest cover. This has resulted in progressively open and degraded woods and most notably in the mountainous areas, bare land with eroded slopes (Thirgood, 1981). In particular, in the Apennines regions, anthropogenic land use, has had a profound effect on forests in most cases, outweighed by far the effects of macroecological constraints (Brown et al., 2013). For this reason, in this study we cannot assert there an effect on *F. sylvatica* from climate change. Some authors (e. g. Good's, 1931) support that the genus *Fagus* has obeyed the theory of tolerance, continuously changing in distribution rather than evolving with new adaptations to changes in the climate. Actually, looking at the *F. sylvatica* with regard to its various approaches of distribution, we can say that beech actually looks for ways to resettle in high altitude areas as well as areas that it has already occupied in the past, where the ecological constraints is not present. In this case, identifying the best strategy of forest management is very important as it should be that improves the complexity and structural composition of the forest (Puettmann et al. 2009). Complexity is understood as the degree of diversity in the response to environmental changes (Elmqvist et al. 2003). The response diversity is a vital contributor to ecosystem resilience (Elmqvist et al., 2003). Good forest management must be based on scientific approaches and building on forecasts of the forest structure and composition (Vacchiano et al 2012). In this context the forests, object that this study, are inside protect areas and in national parks, for this reason the silvicultural choice are very important for preserved these forests.

Below 1500 m a.s.l, for some *F. sylvatica* forests from southern Italy, the forests management is, in the final analysis, heavy influenced from some elements that recur constantly and concern: even-aged on a large surface, the spatial variability of the structure of the stand (but also its origin) and the morphological variability of the slope. These elements should be taken in to account when deciding on the most appropriate silvicultural system to be applied. In addition, grazing by wild ungulates should not be overlooked when the most appropriate stand management must be assessed

(Saracino 2012). A potential conservative management should achieve a heterogeneous structure by seed cuttings on a small spatial scale (0.5-1.0 ha). In this case the management of the beech forest at low elevation (<1500 a.s.l.) is based on conservation criteria, without overlooking those of protection of the side (Saracino 2012).

Regarding to management at altitudinal limit, in exposed timberlines, forest sometimes develops at the leading edge of the intact forest timberline (Billings and Mark 1957, Arno and Hammerly 1990). This timberline is probably generated by an heavy snow deposition just behind the leading row of trees that generates a treeless snow glade with severely distorted tree forms. A greater density of ecotonal trees (in all forms) will act as an advancing snow fence and cause the heavy snow deposition lines (snow glade) to shift upward in elevation. Thus, the increased seedling or sapling abundance leads to a protection of mountain side from erosion and avalanche.

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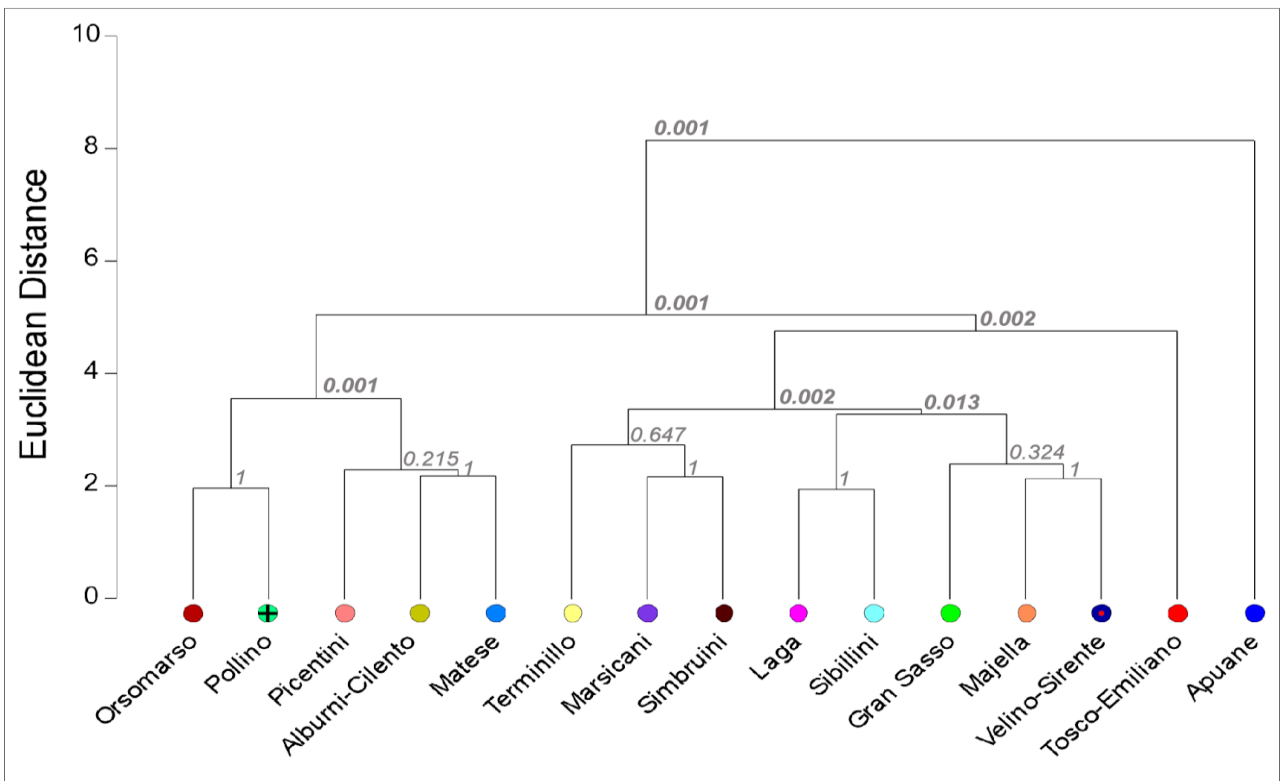
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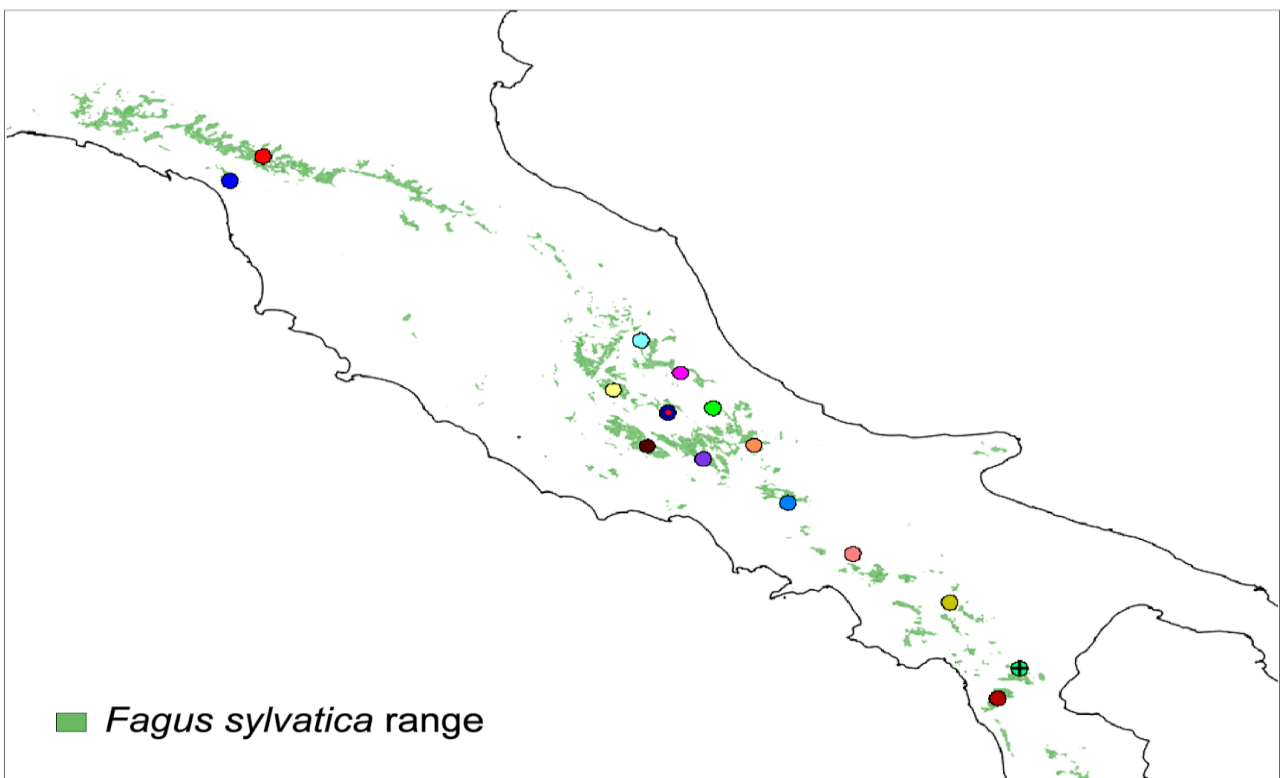
*Annex1: Supplementary material*

**Climatic and anthropogenic factors explain the variability of *Fagus sylvatica* treeline elevation in fifteen mountain groups across the Apennines.**

A



B



**Fig. S1** Selected fifteen Apennine mountain groups. Panel A: hierarchical ordination of the Apennine mountain groups according to Euclidean distance calculated on geographical, demographic and climatic variables. Grey numbers in correspondence of the nodes report p value, in bold significant differences. Panel B: geographical location of the mountain groups along the Apennine *Fagus sylvatica* range.

**Supplementary Table S1:** list of the 224 mountain peaks, distributed across the Apennines, where treeline boundaries were digitized, with mountain group, peak elevation, geographical coordinates, average peak elevation and substrates.

#	Mountain group	Mountain peak	Peak elevation (m a.s.l.)	Latitude N	Longitude E	Average peak elevation (m a.s.l.)	Substrates
1		Altissimo	1589	44.052425	10.234233		
2		Corchia	1677	44.035189	10.294072		
3		Grondilice	1809	44.121342	10.191878		
4		Pania Croce	1858	44.042325	10.345919		
5		Pisanino	1946	44.133089	10.214517		
6		Pizzo D'Uccello	1781	44.138667	10.183472	1791	Limestone
7		Punta Carina (Cavallo)	1895	44.108756	10.237358		
8		Sagro	1752	44.112494	10.158725		
9		Sella	1739	44.0858	10.243142		
10	Apuane	Sumbra	1769	44.077714	10.284531		
11		Tambura	1891	44.034492	10.324197		
12		Alpe Sigola (Bra Da Ba)	1642	44.235506	10.574742		
13		Alto	1904	44.321861	10.183422		
14		Alto 1 (Acuto)	1758	44.004617	10.162039		
15		Bocco	1770	44.346653	10.096986		
16		Brusa	1796	44.376303	10.040022		
17		Campolino	1848	44.106467	10.646933		
18		Cantiere	1617	44.271525	10.634369		
19		Canuti	1743	44.351158	10.109794		
20		Caval Bianco	1824	44.297606	10.296331		
21		Cimone	2165	44.19395	10.701931		
22		Cisa	1701	44.316106	10.404764		
23		Corno alle Scale	1945	44.113944	10.824472	1830	Flysch
24		Curtiglia	1785	44.384294	10.020542		
25		Cusna	2120	44.288056	10.391961		
26		Forbici	1835	44.225347	10.438225		
27		Giovo	1991	44.131994	10.577158		
28		Giovo 1 ( Nuda)	1775	44.160986	10.579056		
29		Giovo 2 (Omo)	1851	44.142811	10.553094		
30		Libro 2 (Cima Tauffi)	1799	44.156506	10.744497		
31		Libro Aperto	1937	44.157047	10.712939		
32	Tosco-Emiliano	Marmagna	1852	44.396931	9.996636		
33		Civago	1740	44.230886	10.465575		
34		Gennaio	1814	44.101489	10.845569		
35		Gomito	1892	44.131117	10.640531		

36	Lancio	1625	44.173758	10.773697		
37	Prado	2054	44.24975	10.407167		
38	Orsaro	1831	44.407825	9.991281		
39	Pellegrino	1675	44.197486	10.489497		
40	Poggio Malandrini	1662	44.087314	10.848361		
41	Prampa	1698	44.324906	10.414836		
42	Romecchio	1702	44.156564	10.525994		
43	Rondinaio	1964	44.114842	10.594794		
44	Sillano	1874	44.269406	10.350578		
45	Sillara	1861	44.367581	10.062872		
46	Spicchio	1669	44.182233	10.517114		
47	Spigolino	1827	44.129089	10.784519		
48	Succiso	2017	44.332958	10.195881		
49	Tre Potenze	1940	44.122017	10.623092		
50	Vecchio	1982	44.235303	10.413464		
51	Ventasso	1727	44.371417	10.284883		
52	Amandola	1706	42.969397	13.264883		
53	Argentella	2200	42.859281	13.244372		
54	Cardosa	1818	42.886394	13.128258		
55	Cima Vallelunga	2221	42.892053	13.241986		
56	Fusconi	1796	42.818269	13.178689		
57	Guaidone	1647	42.782375	13.213339		
58	Lieto	1944	42.842022	13.174764		
59	Macchiata	1751	42.760086	13.244219		
60	Bove	2169	42.918278	13.202675		
61	Porche	2233	42.893406	13.219644		
62	Priora	2332	42.932292	13.240764		
63	Sassotetto	1624	43.005272	13.230681	2009	Limestone
64	Serra	1744	42.742647	13.177944		
65	Palazzo Borghese	2145	42.871981	13.227322		
66	Patino	1886	42.829531	13.154383		
67	Pizzo Berro	2259	42.926942	13.222067		
68	Prata	1745	42.843219	13.142047		
69	Redentore	2449	42.825967	13.253619		
70	Rotondo	2102	42.963675	13.195767		
71	Sibilla	2173	42.900964	13.266389		
72	Torrone	2117	42.844333	13.274633		
73	Tre Vescovi	2092	42.9516	13.216569		
74	Val di fibbia	1577	43.005558	13.161969		
75	Vettore	2476	42.823556	13.276242		

76		Cesarotta	1863	42.696219	13.376172		
77		Cima Lepri	2445	42.653022	13.368597		
78		Laghetta	2369	42.604425	13.389289		
79		Le Vene	2020	42.688158	13.341128		
80		Macera Della Morte	2073	42.69425	13.358339		
81		Monte di Mezzo	2155	42.576322	13.403978	2197	Limestone
82		Gorzano	2458	42.617692	13.396158		
83		Pelone	2057	42.667772	13.380486		
84		Pizzo di Moscio	2411	42.646381	13.398592		
85	Laga	Pizzo di Sevo	2419	42.668761	13.348231		
86		Scalandro	1900	42.716378	13.346975		
87		Cambio	2081	42.51245	13.024975		
88		Cambio 2	1840	42.527233	12.993392		
89		Elefante	2015	42.4656	13.026003		
90		Porcini	1982	42.494178	13.011528		
91		Ritornello	1874	42.4786	13.039581	1973	Limestone
92		Sassetelli	2105	42.484014	12.983917		
93	Terminillo	Terminilletto	2085	42.467394	12.990128		
94		Terminillo	2217	42.473464	12.997386		
95		Terminillo Apex	1560	42.434381	13.014092		
96		Branca Castello	2385	42.447247	13.639078		
97		Camicia	2564	42.439847	13.7182		
98		Cannatina	1790	42.314825	13.812108		
99		Capo Serre	1740	42.374614	13.749811		
100		Collenbri	1610	42.426583	13.413211		
101		Corno grande	2912	42.470419	13.566019	2307	Limestone
102		Corvo	2623	42.480319	13.487961		
103	Gran Sasso	Intertmesoli	2635	42.472669	13.528194		
104		Malecoste	2421	42.463161	13.446611		
105		Prena	2561	42.442347	13.682725		
106		San Franco	2132	42.466644	13.388269		
107		Duchessa	2184	42.190631	13.344856		
108		Magnola	2220	42.141447	13.457167		
109		Tino	1923	42.099989	13.587967		
110	Velino-Sirente	Puzzillo	2177	42.188053	13.382047	2201	Limestone
111		Rotondo1	2064	42.200347	13.480592		
112		Sirente	2349	42.137697	13.6098		
113		Velino	2487	42.148731	13.384089		
114	Majella	Acquaviva	2737	42.101883	14.131139		
115		Amaro	2793	42.087319	14.085547	2218	Limestone
116		Block haus	2070	42.144917	14.111514		

117		Forchetta	2616	42.048631	14.099967		
118		Maje orientale	2197	42.107825	14.164367		
119		Majelletta	2007	42.160328	14.120825		
120		Cavallo 1	2171	42.124567	14.111644		
121		Morrone	2061	42.12065	13.961281		
122		Morrone 2	1705	42.177242	13.887992		
123		Morrone Apex	1905	42.075578	14.003428		
124		Porrara	2137	41.975458	14.094625		
125		Autore	1853	41.956292	13.204933		
126		Monna 1	1929	41.805994	13.371103		
127		Monna Crepacuore	1952	41.835414	13.360964		
128		Passaggio	2064	41.801197	13.474219	1973	Limestone
129		Serra Comune	1855	41.77275	13.521008		
130	Simbruini	Staffi Cotento	2015	41.914858	13.330786		
131		Tarino	1959	41.932725	13.292919		
132		Viglio	2156	41.883222	13.372692		
133		Acero	1670	41.728517	13.804606		
134		Amoro Opi	1862	41.766581	13.879556		
135		Breccioso	1974	41.831972	13.624581		
136		Caprara	1998	41.836436	13.751017		
137		Ceraso	1805	41.802222	13.730964		
138		Colle Olmo	1680	41.761258	13.712994		
139		Colubrica	1698	41.865406	13.567458		
140		Cornacchia	2003	41.796256	13.640636		
141		Genziana 1	2060	41.960744	13.876339		
142		Irto	2222	41.726808	13.918564		
143		Irto 2	2044	41.733203	13.933597		
144		La Sparvera	1998	41.892081	13.936847		
145		La Terratta	2208	41.8871	13.833786	1970	Limestone
146		Longagna	1769	41.906236	13.497378		
147		Manna	1930	41.876283	13.662086		
148		Meta	2242	41.690553	13.936517		
149		Metuccia	2105	41.665583	13.974647		
150		Monte a Mare	2020	41.641472	13.992258		
151		Argatone	2149	41.908008	13.812497		
152		Arzecca	1820	41.811836	14.081211		
153		Arzecca	1820	41.811836	14.081211		
154		Cavallo	1990	41.683539	13.889556		
155	Marsicani	Cocullo	1610	42.010639	13.764356		
156		Godi	2011	41.838664	13.913944		
157		Monte di Scanno	1780	41.874311	13.908825		

158		Genzana	2044	41.933103	13.907714		
159		Greco	2285	41.800897	13.995986		
160		Marsicano	2253	41.802056	13.864922		
161		Mattone	1960	41.808978	13.921731		
162		Mezzana	1791	41.987056	13.768644		
163		Miglio	1711	41.963069	13.774844		
164		Navetta	2060	41.856439	13.856581		
165		Nero	1991	41.719797	13.868822		
166		Palombo	2013	41.843567	13.811289		
167		Rotella	2129	41.924831	14.012114		
168		Rotondo 2	2095	41.871325	13.844792		
169		Petroso	2249	41.741136	13.911633		
170		Pietra Gentile	1979	41.882881	13.789033		
171		Pietre Rosse	1890	41.738664	13.834647		
172		Rocca Altiera	2018	41.706694	13.878486		
173		Rocca Genovese	1940	41.839081	13.707106		
174		San Marcello	2007	41.727181	13.851667		
175		Schiena Cavallo	1962	41.826131	13.736892		
176		Serra Alta	1715	41.758625	13.564892		
177		Serra Re	1790	41.747203	13.758164		
178		Serrone	1927	41.7879	13.703239		
179		Strega	1890	41.780722	13.742369		
180		Tartaro	2191	41.703078	13.927744		
181		Costa maltese	1560	41.453397	14.323797		
182		Costa maltese 2	1550	41.437908	14.295181		
183	Matese	Gallinola	1923	41.435308	14.424925	1781	Limestone
184		Miletto	2050	41.450506	14.372564		
185		Mutria	1823	41.385114	14.521742		
186		Acellica	1660	40.778247	15.003608		
187		Cervialto	1809	40.779358	15.130456		
188		Cervialto 2	1550	40.798814	15.127944		
189		Cervialto 3	1570	40.815011	15.160458		
190		Picciola	1575	40.744742	15.178439	1652	Limestone
191		Polveracchio	1790	40.723253	15.129164		
192		Raja magra	1667	40.787717	15.082014		
193	Picentini	Raja scannella	1527	40.778456	15.062994		
194		San Michele	1567	40.799647	14.843922		
195		Terminio	1806	40.841458	14.937319		
196	Alburni- Cervati	Cervati	1898	40.285	15.484756		
197		Gelbson	1705	40.223383	15.334678	1746	Limestone
198		Mercori	1788	40.290583	15.447658		

199		Motola	1740	40.366642	15.436158		
200		Nuda	1704	40.544442	15.255636		
201		Panormo	1742	40.5352	15.324386		
202		Pedale-Fatella	1710	40.269511	15.449294		
203		Urto	1680	40.546039	15.293294		
204		Capanna	1810	39.907092	16.131606		
205		Colle Paola	1899	39.906758	16.104617		
206		Impisio	1610	39.935844	16.099986		
207		Malevento	1755	39.898831	16.120331		
208		Manfriana	1981	39.870139	16.272706		
209		Pollino	2248	39.906703	16.189158	1942	Limestone
210		Serra delle Ciavole	2130	39.914936	16.219397		
211		Serra del Prete	2181	39.918117	16.157858		
212		Serra di Crispo	2054	39.936594	16.210944		
213		Serra Dolce Dorme	2267	39.895639	16.215181		
214	Pollino	Sparviero	1713	39.919681	16.359519		
215	Pollino	Timpa Lorenzo	1652	39.908928	16.290856		
216		Caccia	1744	39.655497	15.913769		
217		Caramolo	1827	39.796794	16.092311		
218		Magara	1699	39.790658	16.057586		
219		Montea	1785	39.661306	15.941808		
220		Mula	1935	39.704219	15.980997	1764	Limestone
221		Muletta	1699	39.691042	15.988114		
222	Orsomarso	Palanuda	1632	39.814992	16.009211		
223	Orsomarso	Scifariello	1770	39.807644	16.065369		
224	Orsomarso	Scifariello 2	1785	39.797197	16.071125		



# Shrub facilitation promote the treeline advancing of *Fagus sylvatica* across the Apennines (Italy)

Supplementary Table S1

**Table S1.** Main features of the study sites. Paired areas represent two areas in the same study site with shrubland (#s) and with grassland (#g) cover respectively. MJ3s does not have grassland paired area.

Mountain chain	Paired areas	Coordinates	Beech treeline elevation (m a.s.l.)	Vegetation type above treeline	Bedrock type	Types of treelines
Sibillini	Sibillini (SBs)	42°57'2.11"N; 13°11'21.51"E	1641	<i>Juniperus communis</i>	Limestone	Abrupt
	Sibillini (SBg)	42°49'35.77"N; 13°10'27.59"E	1600	Grassland		Abrupt
Laga	Laga (Ls)	42°34'42.84"N; 13°24'45.80"E	1920	<i>Vaccinium myrtillus</i>	Arenaceous-pelitic flysch	Kkrumholz
	Laga (Lg)	42°34'34.15"N; 13°24'57.67"E	1730	Grassland		Abrupt
Gran Sasso	Gran Sasso (GSs)	42°22'18.66"N; 13°45'11.61"E	1753	<i>Juniperus communis</i>	Limestone	Abrupt
	Gran Sasso (GSg)	42°24'30.93"N; 13°46'36.02"E	1700	Grassland		Abrupt
Majella	Majella (MJ1s)	42° 7'58.87"N; 14°6'38.22"E	2010	<i>Pinus mugo</i>		Abrupt
	Majella (MJ3s)	42° 5'41.21"N; 14° 9'18.26"E	1900	<i>Pinus mugo</i>		Abrupt
	Majella (MJ1g)	42° 8'53.11"N; 14° 6'0.38"E	1783	Grassland	Limestone	Abrupt
	Majella (MJ2s)	42° 4'6.03"N; 14° 4'31.80"E	1900	<i>Juniperus communis</i>		Abrupt
	Majella (MJ2g)	42° 9'27.65"N; 14° 6'45.94"E	1800	Grassland		Abrupt
Simbruini	Simbruini (Ss)	41°47'56.86"N; 13°30'1.09"E	1760	<i>Juniperus communis</i>	Limestone	Abrupt
	Simbruini (Sg)	41°48'32.91"N; 13°27'17.30"E	1673	Grassland		Abrupt
Marsicani	Marsicani (MRs)	41°54'8.92"N; 13°49'5.23"E	2082	<i>Juniperus communis</i>	Limestone	Krummholz

	Marsicani (MRg)	41°47'54.93"N; 13°58'9.09"E	2060	Grassland		Abrupt
Pollino	Pollino (Ps)	39°54'2.39"N; 16°11'48.10"E	2020	<i>Juniperus communis</i>	Limestone	Abrupt
	Pollino (Pg)	39°55'9.74"N; 9°21.73"E	16° 2140	Grassland		Krummholz

***Fagus sylvatica* stand structure modulates near-ground climate in a  
Mediterranean treeline**

**Table S1.** Summary statistics of near-ground temperature performed below-canopy (IN) and in the open field (OUT) at North-West and South expositions. Min, minimum value; Max., maximum value; IQR, interquartile range; cv, coefficient of variation. In parenthesis are the average daily values.

	North IN	North OUT	South IN	South OUT
<b>Min.</b>	-10.1 (-8.05)	-9.87 (-8.51)	-8.30 (-5.27)	-7.87 (-4.54)
<b>Median</b>	2.9 (3.81)	4.09 (5.05)	6.70 (7.55)	7.77 (9.42)
<b>Mean</b>	4.72 (4.70)	5.56 (5.55)	7.43 (7.40)	9.11 (9.05)
<b>Max.</b>	29.8 (17.86)	33.29 (18.17)	28.90 (20.28)	39.45 (23.35)
<b>IQR</b>	9.5	9.76	12	13.64
<b>cv</b>	1.3394	1.265	0.9153	0.9944

**Table S2.** Results of random-slope models testing the effect of the temperature outside the forest on temperature offsets for mean (Tmean) temperatures. Est, estimates; CI, confidence interval; p, P-value; sigma-squared ( $\sigma^2$ ), within-group variance; tau-zero-zero ( $\tau_{00}$ ), between-group-variance; N, number of observations; ICC, Intra Class Correlation; R<sup>2</sup>m, marginal R<sup>2</sup>-values (fixed effects only); R<sup>2</sup>c, conditional R<sup>2</sup> values (fixed and random effects).

	South - JJA			North - JJA			South - DJF			North - DJF			South - G.S.			North - G.S.		
	Est.	CI	p	Est.	CI	p	Est.	CI	p	Est.	CI	p	Est.	CI	p	Est.	CI	p
(Intercept)	-2.58	-2.82 -2.35	<0.001	0.01	-0.72 0.74	0.986	-1.18	-1.45 0.91	<0.001	-0.08	-6.47 6.32	0.981	-0.08	-6.47 6.32	0.981	-1.01	-1.39 0.63	<0.001
<b>Random Effects</b>																		
$\sigma^2$	0.35			0.12			0.25			0.03			0.03			0.14		
$\tau_{00}$	14.85 hour:(day:month)			1.89 hour:(day:month)			5.61 hour:(day:month)			0.48 hour:(day:month)			0.48 hour:(day:month)			4.27 hour:(day:month)		
	0.03 day:month			0.99 day:month			0.08 day:month			1.90 day:month			1.90 day:month			0.14 day:month		
	0.02 month			0.38 month			0.05 month			31.89 month			31.89 month			0.18 month		
ICC	0.98			0.97			0.96			1			1			0.97		
N	24 hour			24 hour			24 hour			24 hour			24 hour			24 hour		
	31 day			31 day			31 day			31 day			31 day			31 day		
	3 month			3 month			3 month			3 month			3 month			5 month		
Obs.	4002			4320			4445			4320			4320			6720		
R <sup>2</sup> m/R <sup>2</sup> c	0.000 / 0.977			0.000 / 0.965			0.000 / 0.957			0.000 / 0.999			0.000 / 0.999			0.000 / 0.971		

**Table S3.** Results from linear mixed-effects models with open-field temperatures and daytime (as sin and cos of hours) as predictors and month and day as a nested random effect to take into account the nonindependence of data. Est, estimates; CI, confidence interval; p, P-value; sigma-squared ( $\sigma^2$ ), within-group variance; tau-zero-zero ( $\tau_{00}$ ), between-group-variance; N, number of observations; ICC, Intra Class Correlation; R<sup>2</sup>m, marginal R<sup>2</sup>-values (fixed effects only); R<sup>2</sup>c, conditional R<sup>2</sup> values (fixed and random effects).

	South			North		
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	4.99	4.85 – 5.13	<0.001	3.05	2.95 – 3.16	<0.001
Temp.open	0.56	0.55 – 0.57	<0.001	0.68	0.67 – 0.68	<0.001
hour.sin	0.37	0.31 – 0.42	<0.001	-0.1	-0.16 – 0.04	<0.001
hour.cos	0.04	-0.03 – 0.11	0.238	-0.64	-0.69 – 0.60	<0.001
<b>Random Effects</b>						
$\sigma^2$	0.73			0.71		
$\tau_{00}$	2.58 day:month			1.82 day:month		
	0.90 month			0.25 month		
ICC	0.83			0.75		
N	31 day			31 day		
	3 month			3 month		

Obs.	4002	4445
R2m/R2c	0.762 / 0.959	0.812 / 0.952

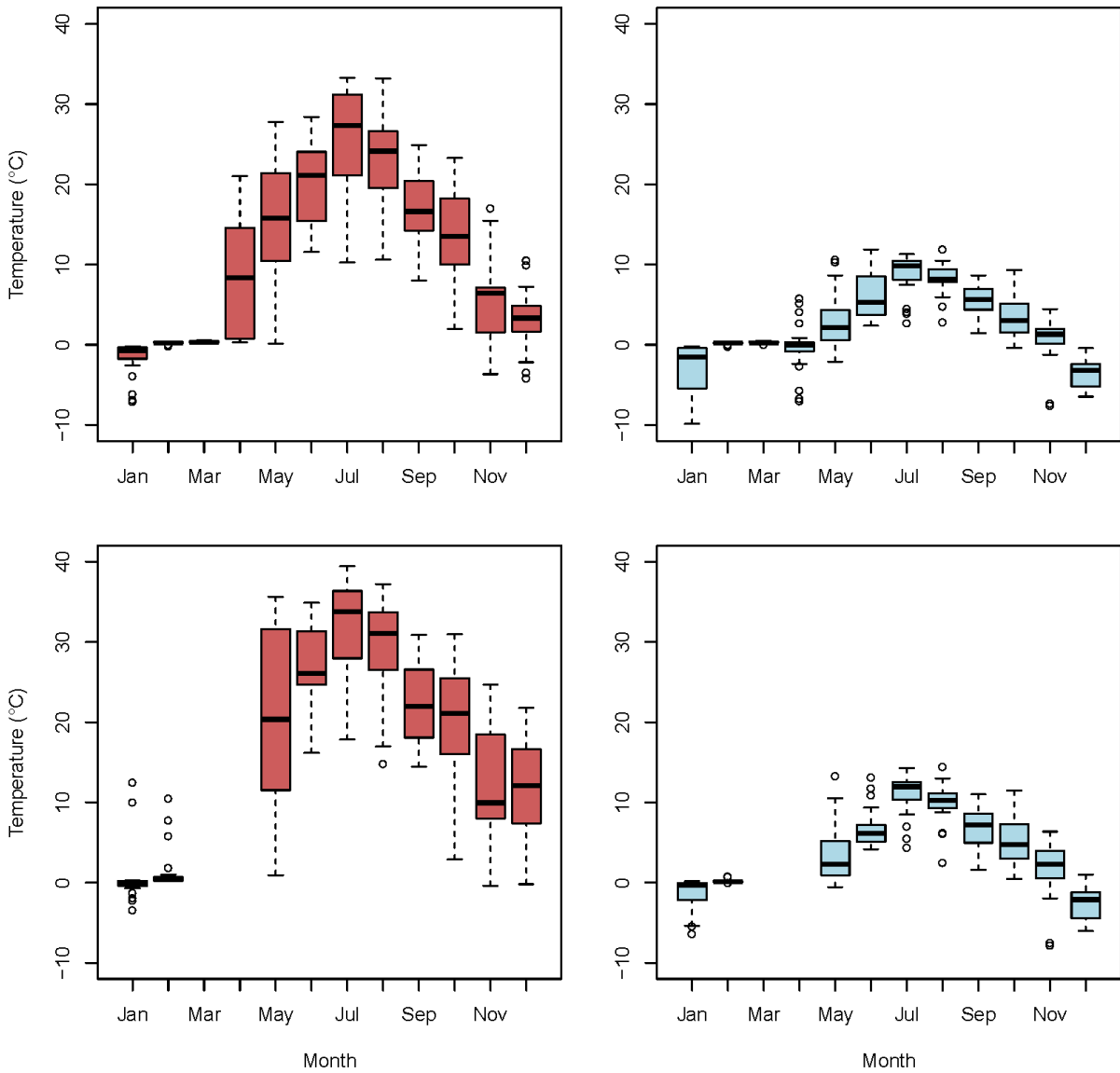
**Table. S4.** Pairs of correlations among measured variables at the northern stand.

	<b>Soil Temp IN</b>	<b>Soil Temp OUT</b>	<b>Soil moisture IN</b>	<b>Soil moisture OUT</b>	<b>Air temperature IN</b>
<b>Soil Temp OUT</b>	0.96				
<b>Soil moisture IN</b>	-0.24	-0.18			
<b>Soil moisture OUT</b>	0.28	0.29	0.72		
<b>Air temperature IN</b>	0.84	0.88	-0.19	0.22	
<b>Air temperature OUT</b>	0.78	0.88	-0.13	0.24	0.94

**Table. S5.** Pairs of correlations among measured variables at the southern stand.

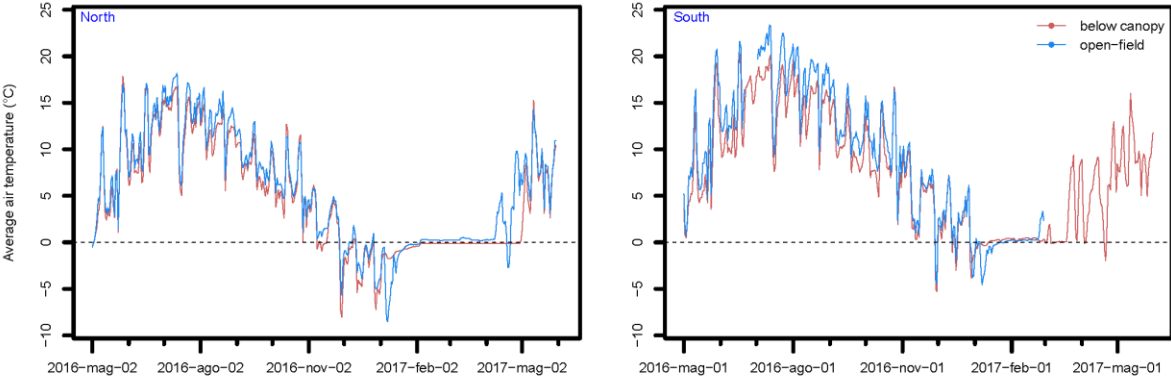
	<b>Soil Temp IN</b>	<b>Soil Temp OUT</b>	<b>Soil moisture IN</b>	<b>Soil moisture OUT</b>	<b>Air temperature IN</b>
<b>Soil Temp OUT</b>	0.96				
<b>Soil moisture IN</b>	-0.7	-0.71			
<b>Soil moisture OUT</b>	-0.48	-0.45	0.81		
<b>Air temperature IN</b>	0.85	0.9	-0.65	-0.42	
<b>Air temperature OUT</b>	0.77	0.85	-0.58	-0.36	0.96

**Fig. S1.** Maximum (red) and minimum (blue) median monthly temperature distributions in the open-field (upper panels) high elevation north stand and low elevation (lower panels) south stand. Each box represents the 75th to 25th percentiles, and the line inside the median; upper and lower marks are the largest to smallest observation values, which are less than or equal to the upper and lower quartile plus 1.5 the length of the interquartile range; circles outside the lower-upper mark range are outliers.

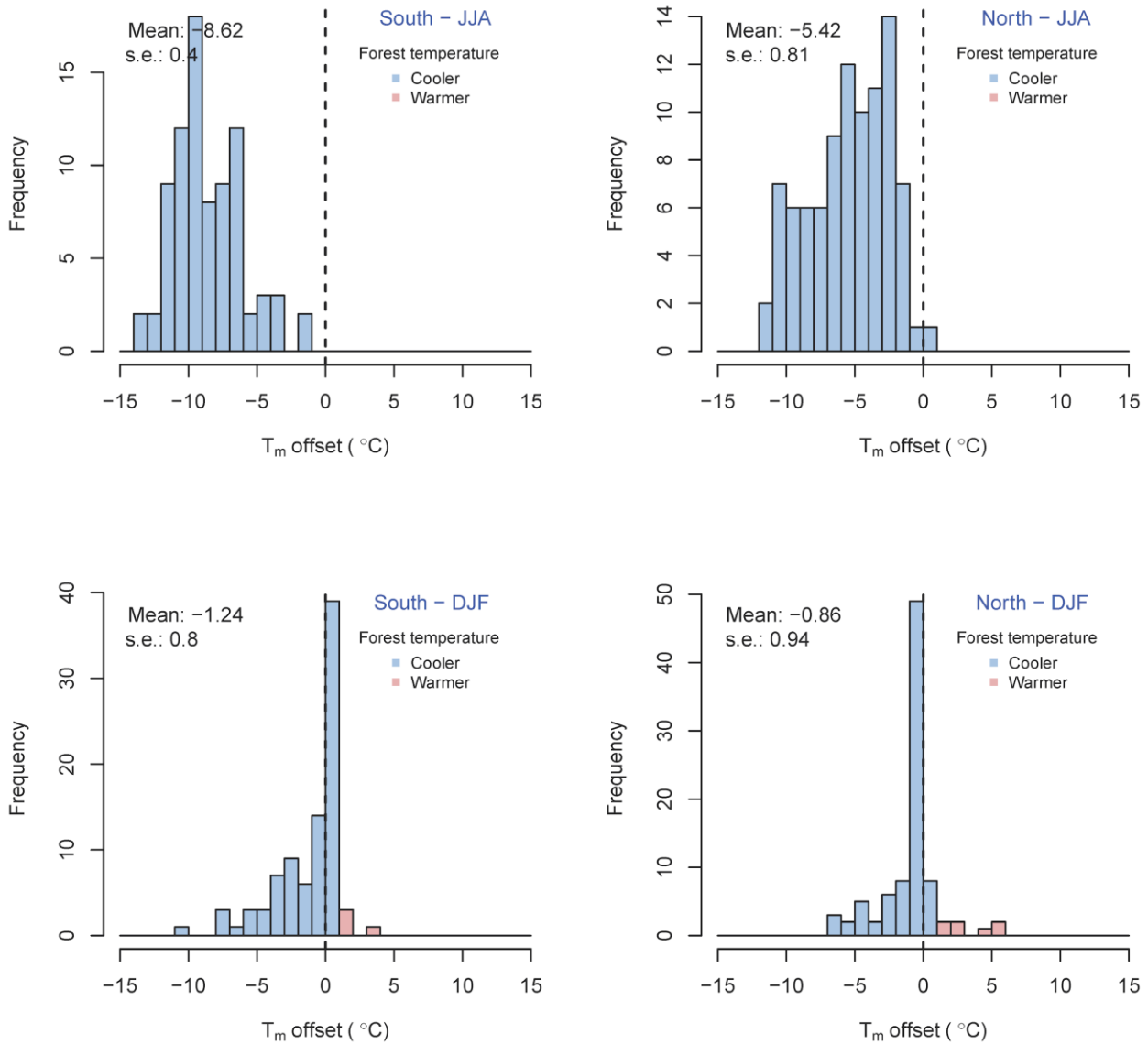




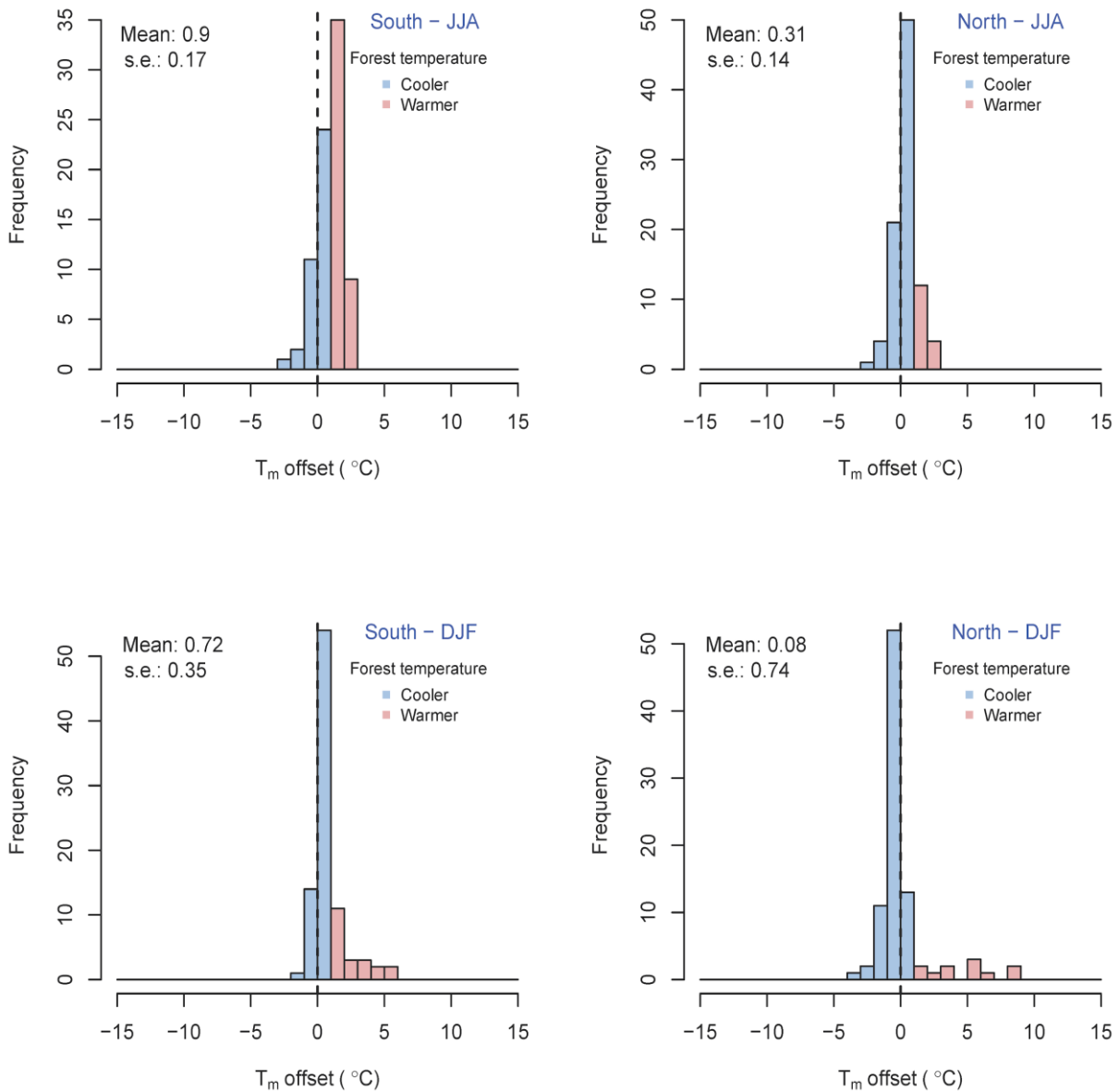
**Fig. S2.** Average daily near ground air temperature ( $^{\circ}\text{C}$ ) recorded in the open-field (blue) and below the forest canopy (red) at North and South aspects.



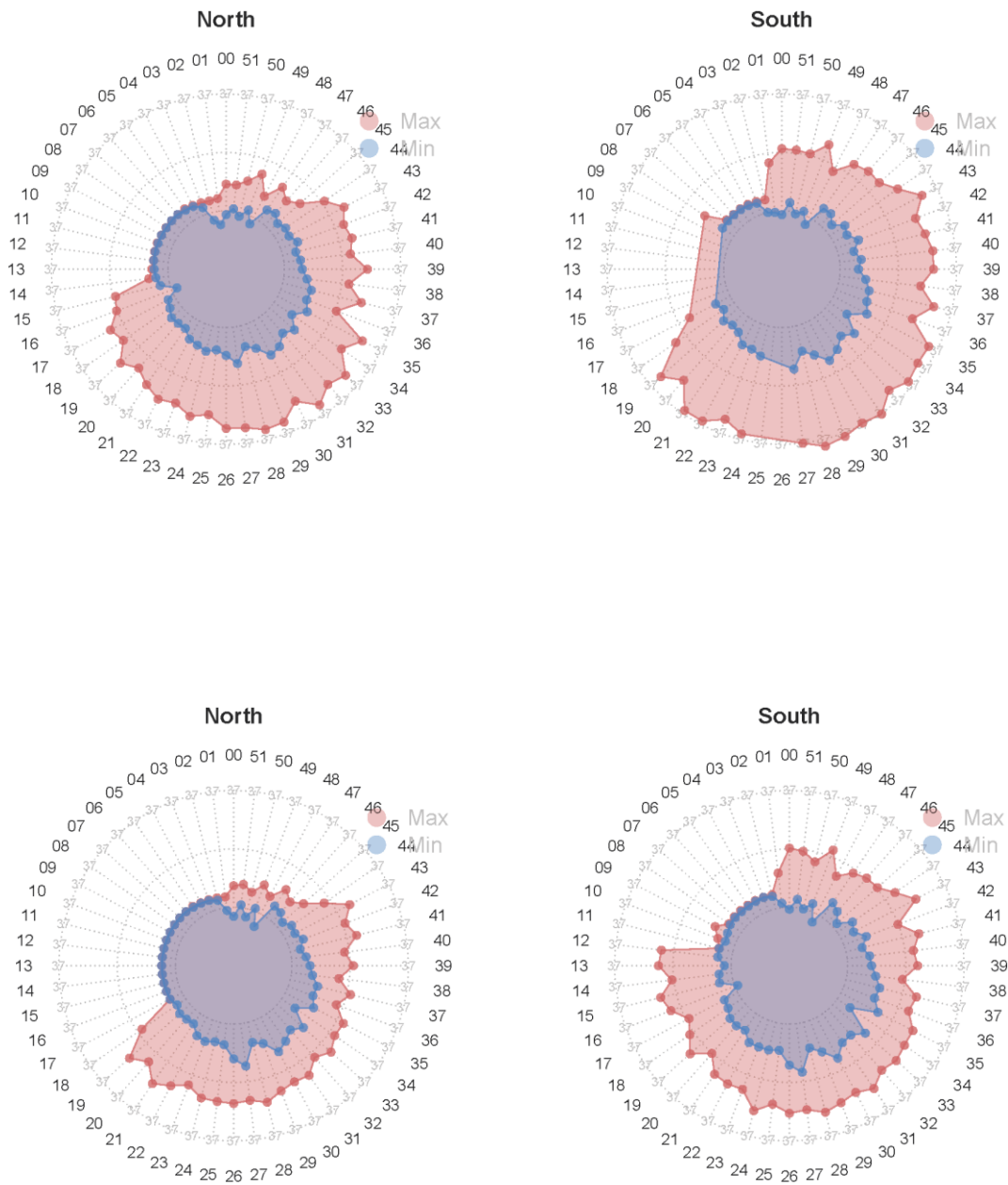
**Fig. S3.** Forests buffer temperatures under canopies. Histograms display the temperature offset values for maximum ( $T_{max}$ ) temperatures during summer (JJA) and winter (DJF). Maximum temperatures are consistently cooler, within forests compared to macroclimate temperatures. Temperature offset means  $\pm$  s.e are based on mixed-effects models with months, days, and hours as



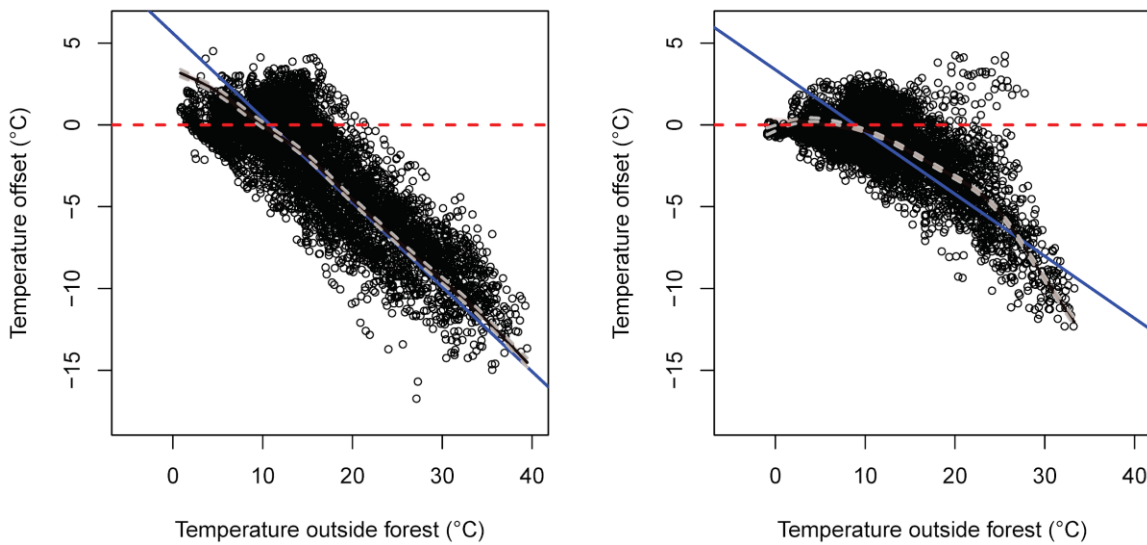
**Fig. S4.** Forests buffer temperatures under canopies. Histograms display the temperature offset values for minimum ( $T_{min}$ ) temperatures during summer (JJA) and winter (DJF). Maximum temperatures are consistently cooler, within forests compared to macroclimate temperatures. Temperature offset means  $\pm$  s.e are based on mixed-effects models with months, days, and hours as nested random-effect term.



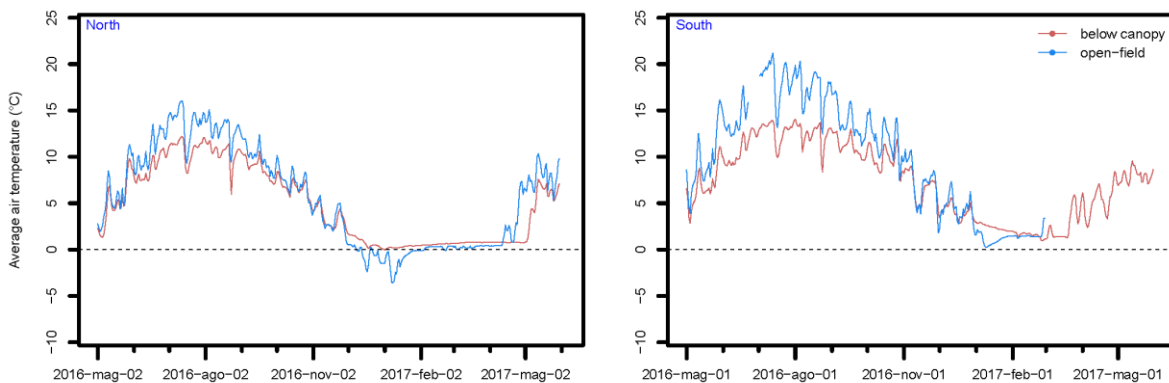
**Fig. S5.** Open field (OUT, top) and inside the forest cover (IN, bottom) weekly absolute maximum (red) and minimum (blue) temperature ( $^{\circ}\text{C}$ ) at North and South aspect.



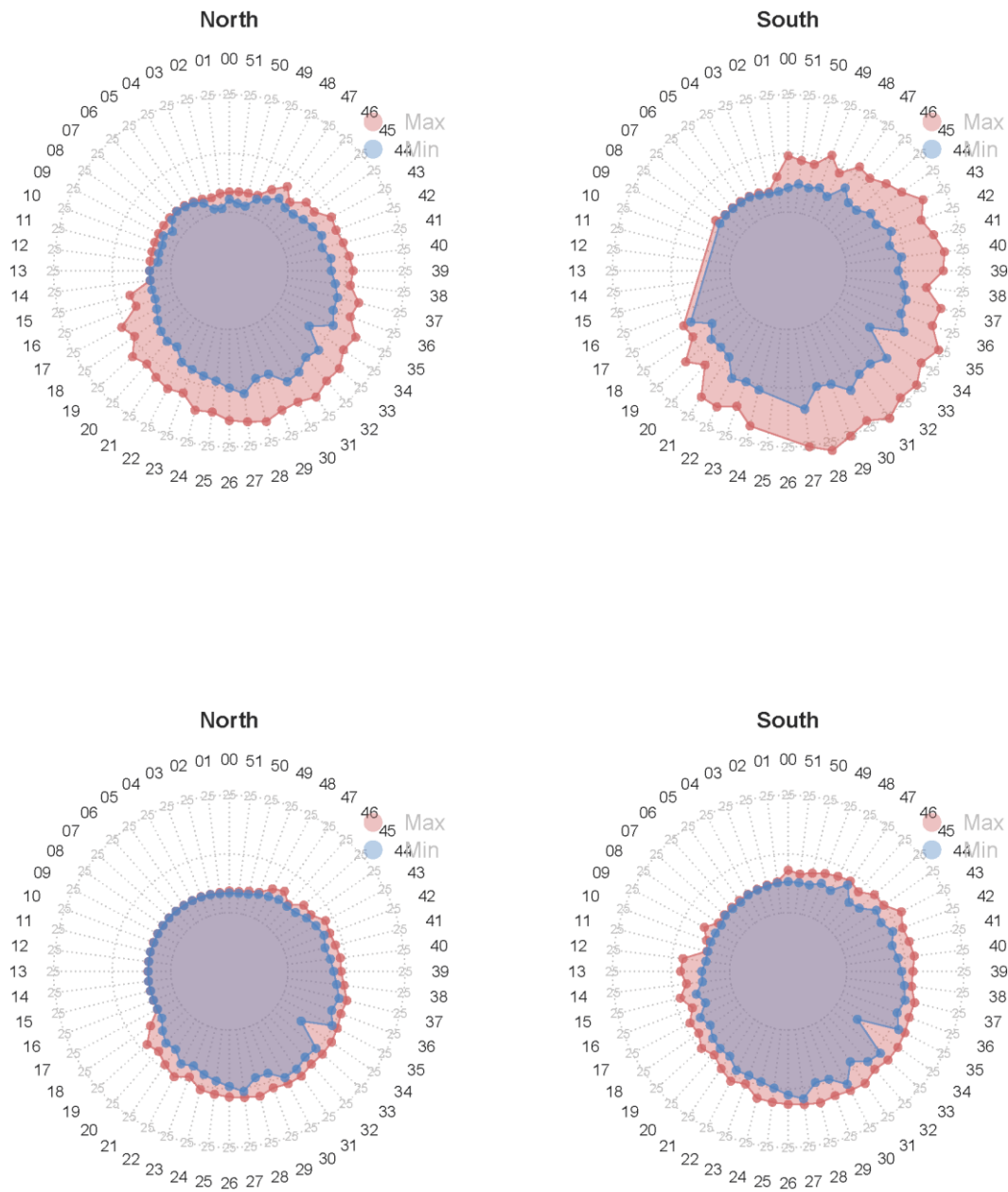
**Fig. S6.** Testing for non-linearity using General Additive Mixed Models (GAMMs). Relationships between the average temperatures outside the forest and the forest temperature offset during the growing season (i.e., from May to September) for south (left panel) and north (right panel) stand, respectively. Solid black lines show the fitted GAMMs with month, day and hour as nested random-effect term (dashed grey lines and grey shaded areas between the dashed lines show the standard error around the predicted values); solid blue lines show the fitted linear mixed-effects models (LMMs) with nested random-effect term; red dashed lines show the null line (temperature offset = 0 °C, or forest temperature equals macroclimate temperature).



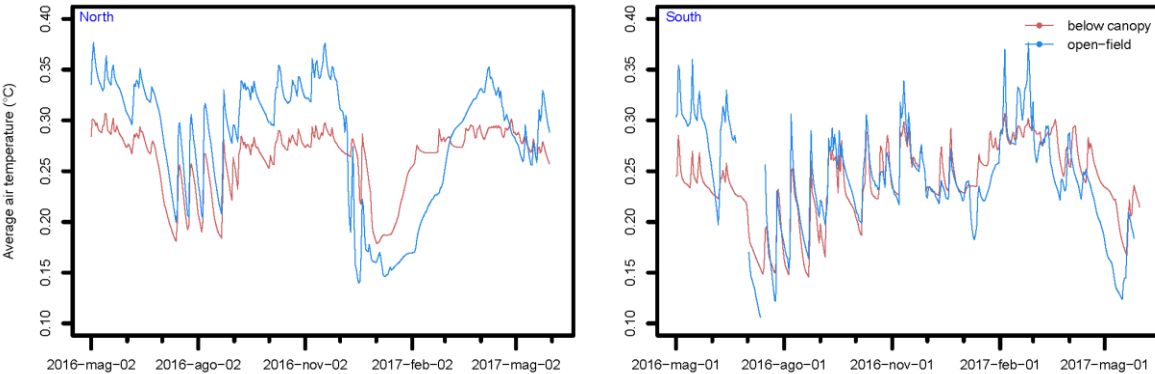
**Fig. S7.** Average daily soil temperature (°C) recorded in the open-field (blue) and below the forest canopy (red) at North-West and South aspects.



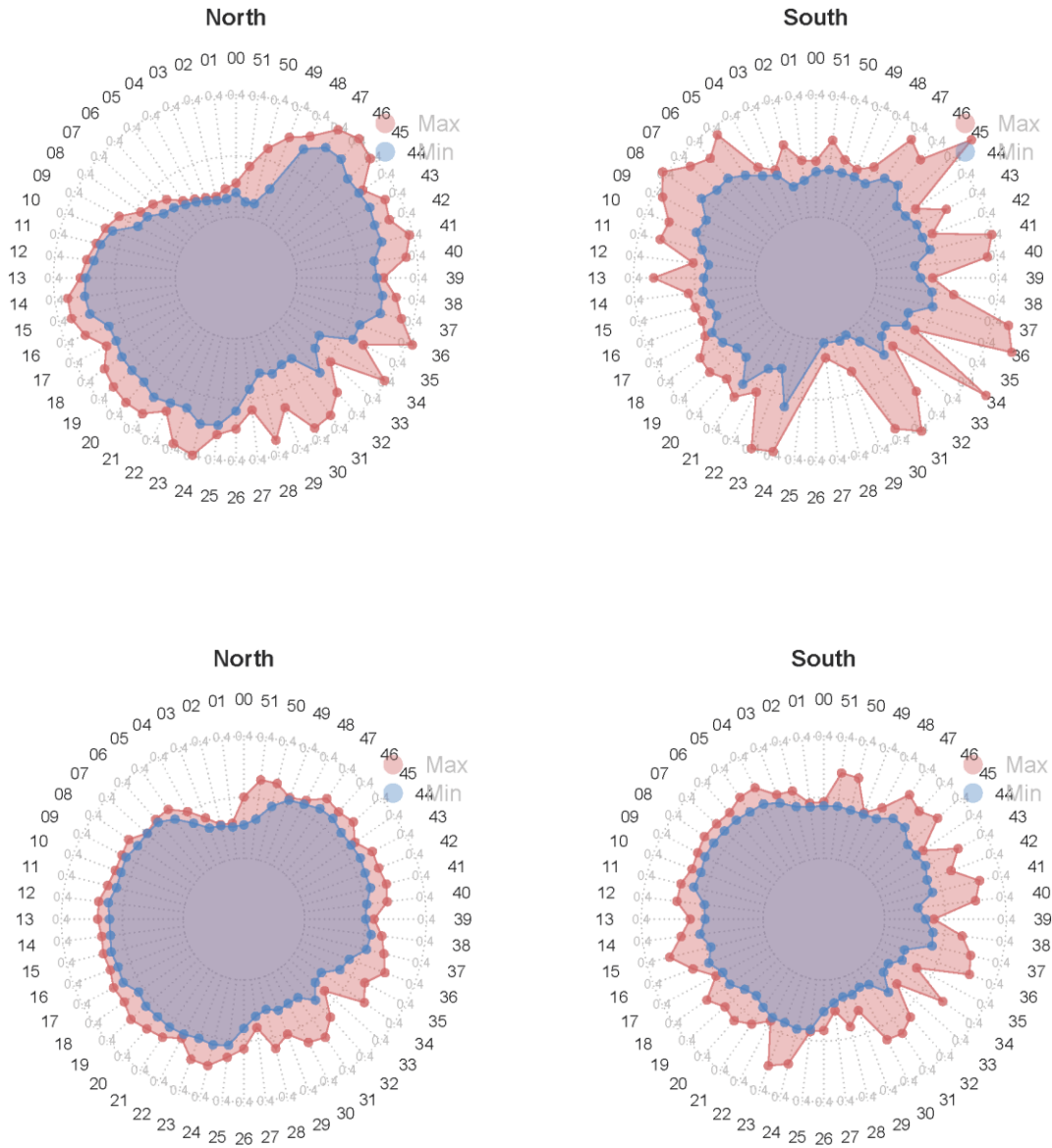
**Fig. S8.** Open field (OUT, top) and inside the forest cover (IN, bottom) weekly absolute maximum (red) and minimum (blue) soil temperature ( $^{\circ}\text{C}$ ) at North and South aspect.



**Fig. S9.** Average daily soil moisture (m<sup>3</sup>/m<sup>3</sup>) recorded in the open-field (blue) and below the forest canopy (red) at North and South aspects.



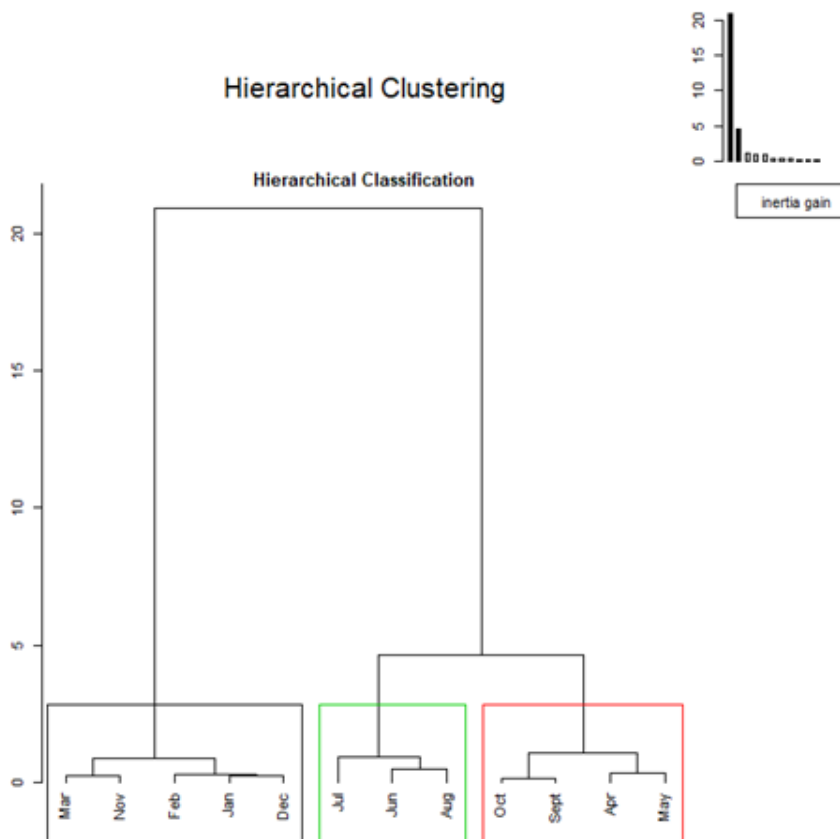
**Fig. S10.** Open field (OUT, top) and inside the forest cover (IN, bottom) weekly absolute maximum (red) and minimum (blue) soil moisture (m<sup>3</sup>/m<sup>3</sup>) at North and South aspect.





**Fig. S11. Principal component methods - hierarchical clustering - partitional clustering for the monthly average air temperature.**

Multiple Factor Analysis (MFA) in the sense of Escofier and Pages (1998) for variables structured by groups, etc. Individuals are considered in a high dimensional Euclidean space and studying the similarities between individuals means studying the shape of the cloud of points. Principal component methods then approximate this cloud of points into an Euclidean subspace of lower dimensions while preserving as much as possible the distances between individuals. Another way to study the similarities between individuals with respect to all the variables is to perform a hierarchical clustering. Hierarchical clustering requires to define a distance and an agglomeration criterion. Many distances are available (Manhattan, Euclidean, etc.) as well as several agglomeration methods (Ward, single, centroid, etc.). The indexed hierarchy is represented by a tree named a dendrogram. A third kind of method is partitional clustering. We performed a hierarchical classification on the principal components of a factorial analysis for the OUT temperature of the mount S Prete.



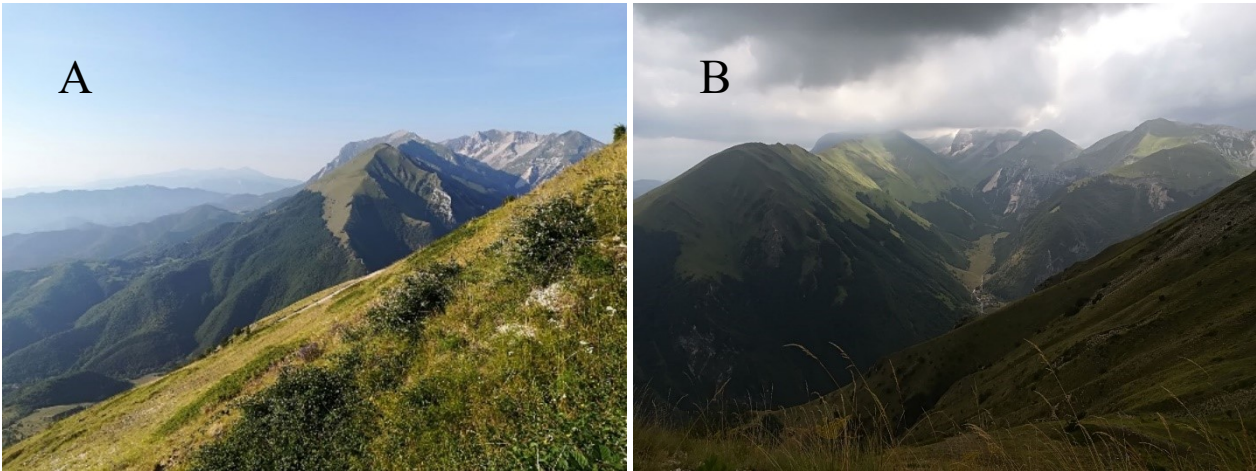
## Annex 2. Image gallery

**Figure 1.** *Fagus sylvatica* Krummholtz treeline in Southern Apennine, Pollino National Park.

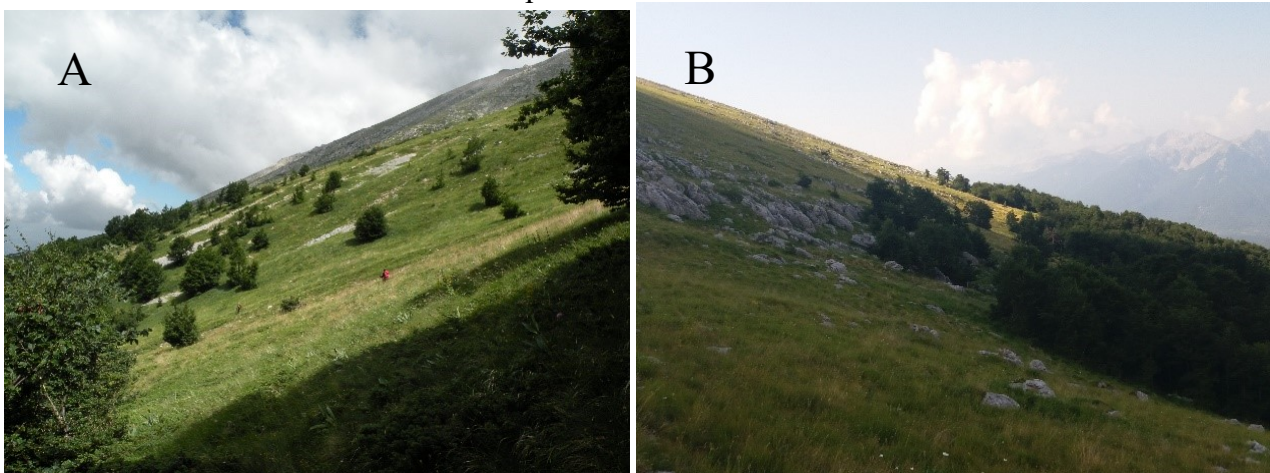
Panel A: July 2016, Mt. Serra del Prete. Highest treeline of Apennines (2.141 m a.s.l.) in the northern slope of the mountain. Panel B: July, 2016, Mt. Serra del Prete. Treeline at the southern slope (1,893 m a.s.l.). Panel C: April, 2016, Mt. Serra del Prete. beech treeline at the northern slope (right side of the picture) and grassland at the southern slope (left side of the picture). See different altitude of melting snow between northern and southern slopes.



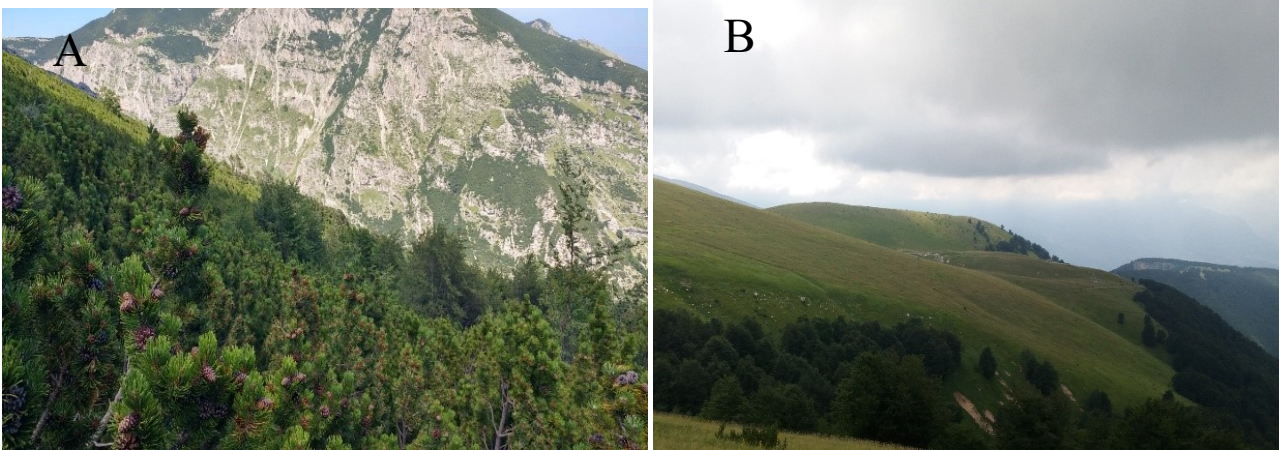
**Figure 2.** *Fagus sylvatica* abrupt treeline in Central Apennine, Sibillini Mts. Panel A: June 2017, Mt. Vettore. Treeline at northern slope (1700 m a.s.l.). Panel B June 2017, Mt. Vettore. Treeline at southern slope (1500 m a.s.l.).



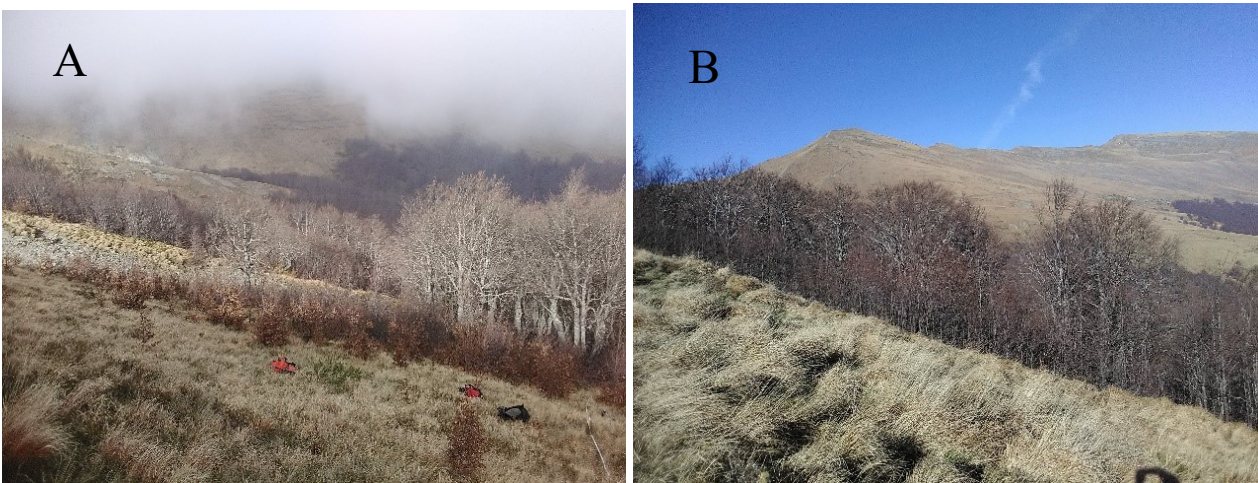
**Figure 3.** *Fagus sylvatica* Krummholtz treeline in Central Apennine, Marsicani Mts. Panel A: July 2017, Mt. Argatone. Treeline (2082 m a.s.l.) and advancing beech trees in the *Juniperus communis* shrubland. Panel B: July 2017, Mt. Greco. Treeline (2060 m a.s.l.) and high elevation grassland. See the absence of beech trees above the present treeline.



**Figure 4.** *Fagus sylvatica* Krummholtz treeline in Central Apennine, Majella Mts. Panel A: July 2017, Mt. Cavallo. Treeline (1900 m a.s.l.) and advancing beech trees in the *Pinus mugo* shrubland. Panel B: July 2017, Block House. Treeline (1820 m a.s.l.) and high elevation grassland. See the absence of beech trees above the present treeline.



**Figure 5.** *Fagus sylvatica* abrupt treeline in Central Apennine, Laga Mts. Panel A: October 2018, Mt. Gorzano. Treeline (1900 m a.s.l.) and advancing beech trees in the *Vaccinium myrtillus* shrubland. Panel B: October 2018, Mt. Gorzano. Treeline (1870 m a.s.l.) and high elevation grassland. See the absence of beech trees above the present treeline.



**Figure 6.** *Fagus sylvatica* treeline in Southern Apennine, Pollino Mts. Panel A: April 2017, Mt. Serra del Prete. Abrupt treeline (1900 m a.s.l.). Panel B: April 2017, Mt. Serra del Prete. Krummholtz treeline (2140 m a.s.l.)



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