



UNIVERSITÀ
POLITECNICA
DELLE MARCHE

Doctoral School in Agriculture, Food and Environmental Sciences

XXX cycle

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Spatio-temporal dynamics at treeline ecotones

Doctoral dissertation

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November 2014 – October 2017

Table of contents

Abstract.....	3
Chapter 1 - Introduction.....	6
Chapter 2 - Effects of natural and anthropogenic drivers on land-cover change and treeline dynamics in the Apennines (Italy).....	7
Chapter 3 - Deconstructing human-shaped treelines: microsite topography and distance to seed source control <i>Pinus nigra</i> colonization of treeless areas in the Italian Apennines.....	25
Chapter 4 - Remaking forests: pine recolonization in Mediterranean anthropogenic treelines.....	45
Chapter 5 - Direct measurement of tree height provides different results on the assessment of LiDAR accuracy.....	65
Chapter 6 - General conclusions.....	78
Chapter 7 – References.....	80

Abstract

This research is aimed to apply a multi-scale approach to the analysis of the spatial-temporal dynamics of forest tree species at anthropogenic treeline ecotones in Southern Europe, within the context of land-use and climate changes.

Firstly, we explored the position and species composition of the treelines in the Apennines, the second largest mountain range in Italy. We searched how climate, topography and human impact affected land cover changes, elevation of treelines and dominant tree species composition at multiple spatial scales. Multiscale approach is an excellent tool to detect the recent dynamics of Mediterranean anthropogenic treelines. At the regional scale (n=776 municipalities covering 43 000 km²), we assessed the relationship between human demographic processes and forest cover dynamics for the 1990-2012 period using Corine Land Cover maps and national census datasets. At the landscape scale (n=18 landscape units of 16 km² each), we tested the effects of site topography on forest cover changes between 1954 and 2012. At the local scale (n=5484 sampling points), we extracted the location and species composition of the current treeline (year 2012) using semi-automatic segmentation methods. We quantified the association of climatic, topographic and anthropogenic variables with the position of upper treelines in the Apennines. At regional scale, demography and land cover changes provide evidence of widespread land abandonment and forest expansion, with a human population decrease of 3% between 1991 and 2011. Within the same time interval, there was an increase in shrubland (+7%) and forest extension (mixed +4%, conifers +2%, broadleaf +1%) and a decrease in pastures (-9%). At the landscape scale, secondary succession occurred particularly at sites more exposed to solar radiation and a previous heavier human footprint followed by a widespread abandonment: forests expanded more on south-western (+109%) than on north-eastern slopes (+19%). At local scale, the mean treeline altitude was 1755 m a.s.l. *Fagus sylvatica* L. was the most widespread species (94%), with forests growing at elevations lower than predicted by climate conditions alone, suggesting a widespread and significant past human influence on the treeline position. The altitudinal transition from broadleaf to conifer species does not generally occur here, as it would be expected from a global ecological model. Moreover, we also found *Pinus nigra* Arn. plantations and *Pinus mugo* Turra shrublands in the central Apennines and *Pinus heldreichii* H.Christ in the southern Apennines. Overall, the elevations of the current treelines are negatively related to population density, road proximity and SW exposures, especially among *Pinus nigra* stands. Anthropogenic treelines of the Apennines will react differently than natural climatic treelines to global environmental changes. Models of treeline response to global change in the Mediterranean area should account for land-use history.

Secondly, we investigated the recent dynamics of human-shaped treelines, which are a common feature in mountain landscapes across Europe and particularly in secularly managed Mediterranean high-elevation areas. The abandonment of traditional land use, and especially the reduction in grazing pressure at high elevations, triggered secondary succession in treeless grassland areas, and in some cases favoured the upward shift of anthropogenic treelines. We explored this process in four anthropogenic treeline ecotone sites in the Central Apennines (Italy) populated by European black pine (*Pinus nigra* Arn.). The upward treeline shift was controlled by microsite topography and the proximity to plantations acting as seed source. We found a 50% probability of producing cones in trees with basal diameters of 15–25 cm, heights of 2–5 m and ages of 20–25 years. The role played by climate on tree growth and recruitment processes seems to be secondary, or it could be masked by man induced processes. The presence of cone bearing trees at the treeline, mainly growing on debris-rich and steep slope sites, indicate that the recruitment process is likely to increase in the future, leading to patchy tree patterns at different elevations. The observed high growth and encroachment rates would indicate that general growth dynamics are speeding up, including the tree colonization of treeless areas. These succession processes could cause a significant long-term decline in plant diversity in species-rich grasslands. Nonetheless, tree encroachment could increase forest protection against landslides and avalanches in the context of global change.

The following step was to assess the occurrence of similar dynamic processes in other human-shaped treelines hosting native pine species, like the Monte Pollino (Southern Apennines) the Dinaric Alps (Montenegro and Albania) and the Pyrenees (Spain). The thesis includes a very preliminary draft of the manuscript to be submitted shortly to an indexed international journal (e.g. *Global Ecology and Biogeography*). The field surveys were concluded during summer 2017 and several analyses are already run. We compared the recolonization process of four different pine species (*Pinus heldreichii*, *Pinus peuce*, *Pinus sylvestris* and *Pinus uncinata*) at nine anthropogenic treeline ecotones. Our challenge is to define conceptual models to forecast treelines expansion based on their spatio-temporal patterns and processes (e.g. type of regeneration niches, size-age structures, spatial distribution, individual tree growth and cone production).

The last chapter of the thesis is a new technology application for the detection of tree heights and of treeline position and dynamics at landscape scale. Airborne laser scanning-based (ALS) and traditional field-based survey methods for tree heights estimation in forest stand are assessed by using one hundred felled trees as reference dataset. The comparison between remote sensing and field-based methods were applied to four circular permanent plots located in the western Italian Alps. Remote sensing, traditional field-based and direct measurement of felled trees methods were compared by using summary statistics, linear regression models and variation partitioning. When dealing with large areas, the use of remote sensing techniques allows reducing some constraints, obtaining spatially continuous data over large study areas cost efficiently. Our results show that tree height estimates by Light

Detection and Ranging (LiDAR) data approximated to real heights of felled trees. We observed that traditional field-based survey can be less accurate than laser scanner in estimating tree heights and this was particularly valid for tall trees with conical shaped crowns. Advanced remote sensing technologies such as LiDAR offer significant potential to map individual tree crowns, monitoring the location of the treeline position and potential shifts, without difficulties of cost and technical challenges. Moreover, these tools allow collecting data for large study areas and in mountainous lands where rugged terrain can limit access to sampling areas.

This dissertation is a compilation of 3 published original articles (Chapters 2-3-5), 1 article in progress (Chapters 4) and some bridging chapters. Each research chapter stands alone, containing its own introduction, materials and methods, results, discussion, conclusions and appendices. Specifically, chapter 2 is the result of collaboration with researchers at the University of Nevada (Reno-USA). This study has been revised and accepted for online publication on *Journal of Vegetation Science* (12-Dec-2017). The research chapter 3 was published on *Forest Ecology and Management* (15-Dec-2017) with the collaboration of researchers from the Instituto Pirenaico de Ecología (Spain) and University of Cambridge (UK). Chapter 4 is an ongoing research that we are planning to submit to a peer-reviewed journal as soon as possible, with the collaboration of researchers from Instituto Pirenaico de Ecología (Spain), Agricultural University of Tirana (Albania) and University of Montenegro. Finally, chapter 5 is a research study published on *Forests* (23-Dec-2016) with the collaboration of researchers from University of Torino and University of Padova.

CHAPTER 1

Introduction

Treeline ecotones are a research target in vegetation science for their dynamic responses to global change, as growth, recruitment and mortality in these marginal populations respond both to climatic variability (Daniels and Veblen 2004, Camarero and Gutiérrez 2004) and to anthropogenic disturbances (Batllori and Gutiérrez 2008, Harsch and Bader 2011, Woods 2014). Generally, treeline elevation varies with latitude, a surrogate of air temperature, which acts as the main limiting factor at global scales (Körner 1998; 2012). However, the relationship between treeline elevation and air temperature is often not linear since numerous natural and anthropogenic limiting factors can mask or confound the climatic signal (Hofgaard 1997; Cudlín et al., 2017). For these reasons, treelines could be classified as climatic, edaphic/orographic and anthropogenic, depending on the dominant limiting factors shaping treeline structure and response to changing environmental conditions (Holtmeier & Broll 2005). Land-use changes are long-term broad-scale disturbances and should be considered as major drivers of treeline formation in human-disturbed mountain areas (Foster et al. 1998) and their effects can persist long after the abandonment of human activities (Camarero et al. 2017, Gimmi et al. 2008).

Numerous studies on European treelines have concluded that recent tree establishment above upper treeline results primarily from reduced human pressure (Gehrig-Fasel et al., 2007; Motta et al. 2006; Treml et al., 2016) because of a progressive decline in the profitability of mountain agriculture (Gotsch et al. 2004, Leuch 2005). In southern Europe, the rapid industrialization of the mid-20th century triggered deep socio-economic shifts, including a massive rural exodus toward cities and the decline of traditional practices in mountains based on small-scale agriculture, pastoralism and forest resource utilization (Blondel and Aronson, 1999). Understanding the synergic influences of climate, topography and human pressure is essential for predicting trajectories of change in alpine treelines. Importantly, human shaped treelines respond differently to climate warming than undisturbed treelines, providing useful information for climate sensitivity modelling (Batllori et al. 2010). Treeline ecotone change will have far-reaching implications for biodiversity, plant and animal communities, and for the relative effects of microtopography on site conditions and ecosystem services, like protection from avalanches and reduction of soil erosion (Wielgolaski et al., 2017).

CHAPTER 2

Effects of natural and anthropogenic drivers on land-cover change and treeline dynamics in the Apennines (Italy)

This chapter has been revised and accepted for online publication on Dec. 12th 2017:

Vitali A.¹, Urbinati C.¹, Weisberg Peter J.², Urza A.², Garbarino M.³, 2017. Effects of natural and anthropogenic drivers on land-cover change and treeline dynamics in the Apennines (Italy). *Journal of Vegetation Science*. [DOI: 10.1111/jvs.12598](https://doi.org/10.1111/jvs.12598)

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ABSTRACT

Questions

How do climate, topography and human impact affect land cover changes, elevation of treelines and dominant tree species composition at multiple spatial scales?

Location

Apennine Mountains, Italy.

Methods

At the regional scale (n=776 municipalities covering 43 000 km²), we assessed the relationship between human demographic processes and forest cover dynamics for the 1990-2012 period using Corine Land Cover maps and a national census dataset. At the landscape scale (n=18 landscape units of 16 km² each), we tested the effects of site topography on forest cover changes between 1954 and 2012. At the local scale (n=5484 sampling points), we extracted the location and species composition of the current treeline (year 2012) using semi-automatic segmentation methods. We quantified the association of climatic, topographic and anthropogenic variables with the position of upper treelines in the Apennines.

Results

Regional scale: human population in the Apennines decreased by 3% between 1991 and 2011. During the same time period, there was an increase in the extent of shrublands (+7%) and forests (mixed +4%, conifers +2%, broadleaf +1%) and a decrease in the extent of pastures (-9%). Landscape scale: forests expanded more on southwest (+109%) than on northeast slopes (+19%). Local scale: the mean treeline altitude was 1755 m a.s.l. *Fagus sylvatica* L. was the most widespread species (94%), but we also found *Pinus nigra* Arn. plantations and *Pinus mugo* Turra shrublands in the central Apennines and *Pinus heldreichii* H.Christ in the southern Apennines. Overall, the elevations of the current treelines are negatively related to population density, road proximity and southwest exposures, especially among *Pinus nigra* stands.

Conclusions

At the regional scale, demographic and land cover changes provide evidence of widespread land abandonment and forest expansion. At the landscape scale, secondary succession occurred particularly at sites with more solar radiation (SW slopes) and a previous heavier human footprint followed by a widespread abandonment. Treelines of the dominant tree species (*Fagus sylvatica*) were found at elevations lower than would be predicted based on climate conditions alone, suggesting a widespread and strong role of past human influence on the location of treelines. The altitudinal transition from broadleaf to conifer species does not generally occur here, as would be expected from a global ecological model. Anthropogenic treelines of the Apennines will react differently than natural climatic treelines to global environmental changes. Models of treeline response to global change in the Mediterranean area should account for land-use history.

INTRODUCTION

Treeline ecotones are of particular interest in vegetation science for their dynamic responses to global change, as growth, recruitment and mortality in these marginal populations respond both to climatic variability (Daniels and Veblen 2004, Camarero and Gutiérrez 2004) and to anthropogenic disturbances (Batllori and Gutiérrez 2008, Woods 2014). Treeline elevation varies with latitude, a surrogate of air temperature, which acts as the main limiting factor at global scales (Körner 1998; 2012). However, the relationship between treeline elevation and air temperature is often not linear since numerous natural and anthropogenic limiting factors can mask the climatic signal (Hofgaard 1997). For these reasons, treelines can be globally classified as climatic, edaphic/orographic and anthropogenic, depending on the dominant limiting factors shaping treeline structure and response to changing environmental conditions (Holtmeier & Broll 2005).

In several Eurasian mountain ranges that have been settled since prehistoric times, treelines have been largely affected by human influences including forest fires, pastoral use, and the need for wood and charcoal fuels for ore-mining (Schickhoff et al. 2015; Malanson et al. 2011; Holtmeier & Broll 2005). Under natural conditions, treelines in the Northern hemisphere are usually positioned at higher elevations on south-facing slopes, but anthropogenic disturbances have frequently reversed this pattern since utilization pressure on southern aspects is disproportionately higher (Schickhoff 2005). In European mountains, climatic treelines today are rare and limited to rocky, steep slopes that have been less accessible to human activities (Dirnböck et al. 2003). Thus, current treelines are largely the product of past and current anthropogenic uses and geomorphic factors (Leonelli et al. 2011).

Numerous studies on European treelines have concluded that recent tree establishment above upper treeline results primarily from reduced human pressure (Gehrig-Fasel et al., 2007; Motta et al. 2006; Treml et al., 2016) because of a progressive decline in the profitability of mountain agriculture (Gotsch et al. 2004, Leuch 2005). In the Apennines, land abandonment occurred later and was related to property shifts and urbanization processes in the lowland, favoring the natural secondary succession (Torta 2004; Caballero et al. 2009; Pelorosso et al. 2009, Bracchetti et al. 2012; Vacchiano et al. 2017). Shifting agricultural economies have caused an increasing exodus from mountain and rural areas in general (Chauchard et al., 2007; Didier 2001; Motta and Garbarino 2003), causing widespread spontaneous reforestation (MacDonald et al., 2000; Conti and Fagarazzi, 2005; Gellrich et al., 2007). Nonetheless, recruitment of tree cohorts above the current treelines is likely to occur only if climatic and edaphic conditions are favorable and if land uses are suitable for their establishment and range expansion (Ott et al. 1997; Weisberg et al. 2013). Within this context, understanding the interacting influences of climate, topography and human pressure is essential for predicting trajectories of change for alpine treelines. Importantly, human shaped treelines respond differently to climate warming than undisturbed treelines, providing useful information for climate sensitivity modelling (Batllori et al. 2010).

Factors controlling treeline structure and dynamics are strongly scale dependent (Malanson et al., 2007), and treeline elevation varies at a range of scales in response to multiple biotic and abiotic factors (Jobbágy & Jackson 2000; Case & Duncan 2014). In this study, we adopted a multiscale approach to study the spatial-temporal dynamics of the anthropogenic treelines of the Apennines. We hypothesized that: (1) forest cover dynamics at the regional scale correlate with human demographic processes; (2) the dominant exposure of the Apennines (northeast vs. southwest) is a major driver of high-elevation forest cover change at landscape scales; (3) climate, topography and human pressure influence current treeline position and species composition at local scales.

METHODS

Study Area

The Apennines, the second largest mountain range of Italy, extend NW-SE and host several peaks higher than 2000 m a.s.l. Since post-Würmian times (11 700 years ago), the high elevation forests were first largely cleared for hunting of wild herbivores and were later transformed into wood pastures or grasslands (Dibari et al., 2015; Piermattei et al., 2014). The accessibility of the mountain passes, combined with the seasonal transhumance between upland and lowland pastures occurring until a few decades ago, caused a generalized elevation lowering and a significant structural alteration of the upper treeline ecotones. In the absence of human impact, the climate conditions of the Apennine region would have allowed forests to reach much higher elevations. Based on global treeline-climate relationships (Körner, 1998), climatic treelines within the latitudinal range of the Apennines should reach approximately 2500 m a.s.l.

The Apennine 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 snowfall events above 1000 m a.s.l. (Vacchiano et al., 2017). The montane zone (800-2000 m a.s.l.) is largely dominated by *Fagus sylvatica*, locally mixed with *Abies alba*. *Fagus sylvatica* (European beech) is one of the most important and widespread broadleaf tree species in Europe, maintaining high growth rates until late maturity. It is a hardy, shade tolerant species and not particularly soil-sensitive, but its optimal growth is in humid soils situated on calcareous or volcanic parent material (Houston Durrant et al. 2016). In Italy, *Fagus sylvatica* forests are more widespread on northern slopes and under conditions of high relative humidity (Nocentini 2009).

Coniferous forests are limited to a few sites, especially in the central and southern Apennines. These include natural and rare populations of *Pinus mugo* (Palombo et al., 2013) and *Pinus heldreichii* (Todaro et al. 2007), but most coniferous forests are *Pinus nigra* stands planted for erosion control on steep slopes (Piermattei et al. 2013). Mixed deciduous forests of *Quercus cerris*, *Ostrya carpinifolia*, *Acer* spp., and *Castanea sativa* dominate the sub-montane zone (400-800 m a.s.l.). Xeric oak forests of *Quercus pubescens* and *Quercus ilex* dominate the lower zone (< 400 m a.s.l.) and steep rocky slopes respectively. The Apennines are also

rich in mountain grasslands, shaped over millennia by livestock grazing and transhumance, but still providing species-rich ecosystems especially on fertile limestone soils (Catorci et al. 2012).

DATA COLLECTION AND ANALYSIS

Upper treeline structure and dynamics were assessed at three spatial scales: i) at a regional scale across the entire Apennine chain; ii) at a landscape scale with 18 sites of 16 km² each; and iii) at a local scale with 5484 sampling points at 500-m distance along the current treeline (Figure 1).

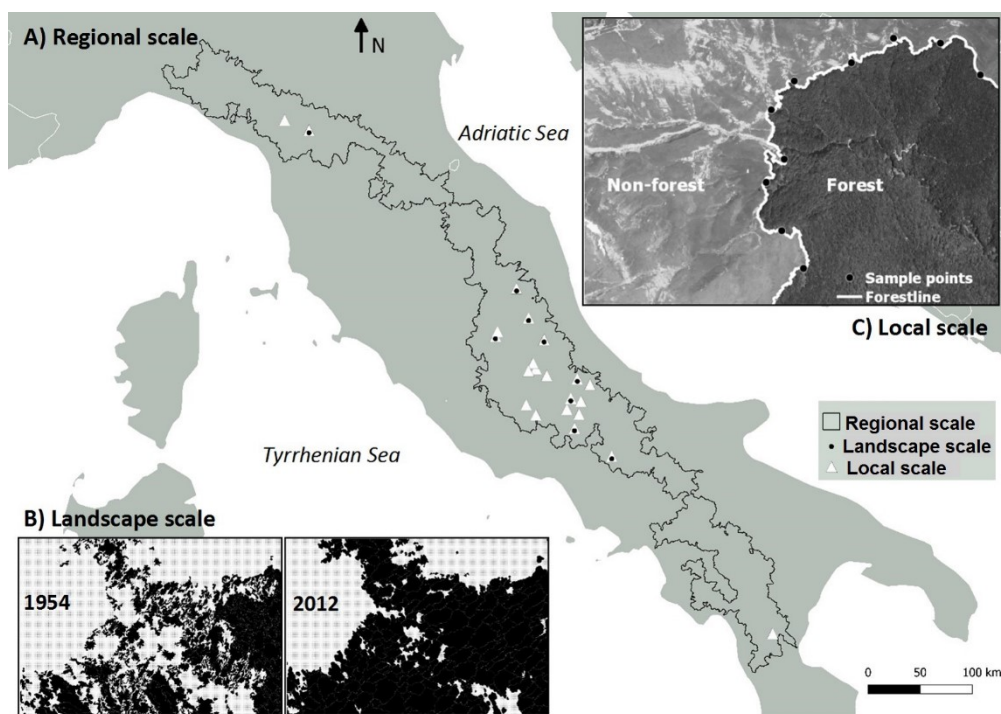


Figure 1. A) Black contour line: the regional scale study area along the Apennines; Black dots: the nine landscape scale study sites; White triangles: the 22 local scale sampled segments; B) example of sample design procedure for the landscape scale analysis (forest cover and metrics changes); C) example of the local scale analysis (treeline detection and sample points).

Regional scale: human population and land cover changes (1990 – 2012)

At the regional scale, the study area was composed of 776 “mountain municipalities” (*sensu* ISTAT, Italian Statistic head office classification), excluding those geographically separated from the main mountain range (Figure 1A). Within this 43 000-km² area, we assessed population density and land cover changes. We extracted human population data for the 1991-2011 period from national censuses (ISTAT 1999, 2011) and geo-referenced them using mountain municipalities’ administrative boundaries as basic units. We produced a map of demographic change by calculating the change in population density for each municipality between 1991 and 2011. For the land cover change analysis, we produced matrices of Land

Cover Change (LCC) obtained by comparing CORINE Land Cover (CLC Level 3) maps from 1990 (CLC1990) and 2012 (CLC2012) with 100 m of resolution. We obtained land cover changes at the regional scale by merging the 44 classes of the original CORINE maps to generate a reduced set of land cover classes, excluding water and non-vegetated classes for the following analysis. We developed a transition matrix for the whole region by calculating changes in areal extent for selected land cover classes: broadleaf forests, conifer forests, mixed forests, shrublands and transitional woodlands, pastures, agriculture lands, orchards and artificial areas. We focused mainly on the transitions between forested and non-forested cover classes. We calculated the proportional change for each cover class to describe individual class dynamics. We computed the relative weight of each category as the percentage of the total changed area. We performed a correlation analysis between population and forest changes at the municipality level and we compared human density change classes (threshold = $\pm 20\%$ of population) to forest cover gain and loss.

Landscape scale: forest cover changes at high elevation (1954 – 2012)

For landscape-scale analyses, we selected nine major mountain peaks with a minimum elevation of 2000 m a.s.l. (see Table S1 in Supplementary Materials). For each peak, we selected two landscapes stratified according to predominant slope exposure, northeastern (NE) vs. southwestern (SW), for a total of 18 landscapes analyzed throughout the study area (Figure 1A). To assess land cover changes (LCC) at high elevation, we used aerial images from 1954 (IGMI - GAI database: Italian Military Geographic Institute – Aerial Italian Group flight) and 2012 (orthoimages from AGEA database: Agency of Supplies in Agriculture). Historical aerial photographs were scanned and orthorectified at 1-m resolution using PCI Geomatica (version 10.2, PCI Geomatics Enterprises Inc., Richmond Hill, ON). The aerial photographs were processed with the software eCognition Developer 64 (version 8.9, Trimble Navigation) through automatic segmentation (scale parameter = 100, color parameter = 0.5) and a manual classification (Definiens 2004). We classified each landscape into two land cover classes: forest (>50% crown cover) and non-forest cover (Figure 1B). The 36 resulting maps (i.e. 18 landscapes x 2 years) with a cell size of 1 meter were then enhanced in a GIS environment in order to reduce the effect of differing input image quality, and to achieve a minimum mapping unit of 100 m² (Garbarino et al. 2011). We also used a 3x3-majority filter to reduce the “salt and pepper” effect.

The landscape pattern analysis was limited to broadleaf forests to focus on natural dynamics and ecological succession, excluding the recently established coniferous plantations (mainly *Pinus nigra* stands). We excluded other sites with some peculiarities (e.g. presence of *Pinus mugo* or *Pinus heldreichii*) in order to standardize the dataset and to compare all landscapes together. Therefore all sites of landscape analysis are located in central Apennines plus one in northern Apennines. An accuracy assessment was performed on each map resulting in the K statistic ranging from 0.68 (77% overall accuracy) for 1954 to 0.74 (84% overall accuracy) for 2012. As control data, we randomized 100 points in a GIS environment for each

landscape and classified them visually using the same land cover classes adopted in the automatic segmentation (Garbarino et al. 2013). We analyzed the percentage change in relative cover for broadleaf forests at higher elevations (>1500 m a.s.l.) between 1954 and 2012. We obtained forest class metrics (cover, mean patch area, patch density, mean shape index) from raster images using the FRAGSTATS 4 statistical package (McGarigal et al., 2012). We categorized the 18 landscapes based on their prevailing exposure (9 northeast vs. 9 southwest) and we analyzed each exposure separately. We applied a Mann-Whitney test to compare the medians of these two prevailing exposures.

Local scale: current treeline position and natural and anthropogenic constraints

The local-scale analysis included 22 Apennine mountain peaks with elevations exceeding 2000 m a.s.l. (Table S1). Using each of the peaks as centroids, we enlarged the study area to include neighboring land with a minimum elevation of 1500 m a.s.l., including any neighboring mountain peaks \geq 2000 m a.s.l. Current treelines were mapped using object-oriented image segmentation from satellite images (Bing Maps, Microsoft Corp., year 2011-2012) available from the Open Layer Plugin of QGIS (version 2.18, QGIS Development Team, 2016). We used the same semi-automatic procedure applied for the landscape analysis. The resulting forest cover polygons were dissolved and transformed into polylines indicating the upper limit of the treeline forest. In the rare case of diffuse treelines (0.18% of total), we connected the uppermost neighboring forest patches (Körner & Paulsen 2004).

We established 5484 sampling points (1 per 500 m) along the resulting treelines in a GIS environment (Case & Duncan 2014) (Figure 1C). In order to quantify the risk of overestimation for misclassification associated with shadows, or underestimation due to variable tree crown spectra, we adopted an accuracy/validation assessment method. We based the validation procedure on a random extraction of 55 sampling points (1%) and we visually assessed the percentage of well-classified points using the aerial imagery. We correctly identified 76% of the points as occurring at treeline, with 16% overestimation and 8% underestimation error. The average horizontal distance between inaccurate points and the correct treeline position was <5 m. We considered this a sufficient precision threshold because the geographic data sources used are raster files with a spatial resolution of \geq 30 m.

For all sampling points, we used the “value to points” GIS tool to derive nine predictor variables describing the potential influences of topography, climate, soil, vegetation and human proxy variables (Table 1). Topographic features were obtained from the digital elevation model (ELEV) of ASTER GDEM2, having a geometric resolution of 30 m (Tachikawa et al. 2011). We derived northeastness index (NE) and slope (SLO) maps from digital elevation models. We derived sand proportion in the soil texture (SAND) from the ISRIC SoilGrid map (Hengl et al. 2014). We extracted spatially distributed climate variables (PREC and TEMP) from the WorldClim database (1 km resolution), representing the 1950-2000 climate conditions (Hijmans et al. 2005). Given the difficulty of obtaining high-quality data on past land use, we used the proximity to the closest road (ROAD) as a proxy for past anthropogenic impact

(Garbarino et al. 2009; Dainese et al. 2017). Population density (POP) at the municipality level (year of census: 2011) was selected as an indirect measure of current anthropogenic impact (Weisberg et al. 2013). We derived the dominant treeline species by photo-interpretation of aerial images, using local vegetation maps as reference (Table S1). In order to identify broad geographic and climatic trends, we plotted the mean elevations of treelines, annual precipitation and annual mean temperature as functions of latitude. We applied simple linear regression models to quantify effect sizes of each predictor (β -value of linear models). We derived mean treeline elevations directly from sample points and extracted climatic variables for an elevation range of 1700-1800 m a.s.l., to reduce any confounding influences from adiabatic and orographic effects. Data were summarized for each selected mountain peak along the Apennines. We conducted a Principal Component Analysis (PCA), using the statistical package PcOrd v6 (McCune and Mefford, 1999), to explore the correlation structure of the eight predictor variables (Table 1, excluding VEG) and to identify key factors underlying position, landscape pattern, and forest tree species composition of the Apennine treelines. We overlaid treeline species composition (VEG variable) as centroids and convex hull polygons on the ordination biplot of 5484 sampling points to illustrate the mean environmental characteristic of the species groups. The statistical significance of the ordination analysis was tested using a Monte Carlo permutation method based on 10 000 runs with randomized data.

Table 1. Local scale analysis: variables used for treeline sample points.

Category	Code	Variable Description	Unit	Source	Scale/pixel size
Topography	ELE	Elevation a.s.l.	m	Aster GdemV2	30 m x 30 m
	V				
	NE	Northeastness Index	-	Aster GdemV2	30 m x 30 m
	SLO	Slope angle	°	Aster GdemV2	30 m x 30 m
Climate	TEM	Annual mean temperature	°C	Worldclim	1 km x 1 km
	P				
	PRE	Annual precipitation	mm	Worldclim	1 km x 1 km
Soil	C	Sand proportion in the soil texture	%	ISRIC SoilGrid	1 km x 1 km
	SAN				
Human infrastructure	ROA	Proximity to the closest road	m	OpenStreetMap	vector
	D				
Vegetation	POP	Current population density	inhabitants/k m ²	ISTAT database	vector
	VEG	Dominant treeline species	-	Thematic maps	vector

RESULTS

Regional scale

Human population decreased by 3.4% during the 1991-2011 period in the 776 “mountain municipalities”, with a stronger reduction in the southeastern and northern regions of the Apennines (Figure S1 in Supplementary Materials). On average across municipalities, there was a reduction of 2.8 inhabitants/km² (SD \pm 11.2). However, there was no correlation between population change and forest cover change at the municipality level (Pearson’s $r = 0.009$), from which we infer that the gain and loss of forest cover within municipalities was not associated with a corresponding trend in recent human population change. The analysis of land cover change at the regional scale showed that forests covered approximately 50% of the Apennine land area in both 1990 and 2012. We observed an increase of 4% (4141 ha) for mixed forests, 2% (1191 ha) for coniferous forests and 1% (11 119 ha) for broadleaf forests. In the same period, there was a 9% decrease of pastures (45 613 ha) and a 7% increase of shrublands (18 626 ha). Expressing the changes within each category relative to the total area subjected to land-cover change (100% = 104 804 ha), pastures experienced the greatest relative variation (44%), followed by shrublands (18%), broadleaf forests (11%), mixed forests (4%) and coniferous forests (1%). The residual change (23%) can be attributed to other merged classes. Transitions that most closely describe the succession to forest vegetation types include those from pastures to shrublands (9.05%) and from shrublands to broadleaf forests (13.75%). Other minor reforestation processes (Table S2 in Supplementary Materials) were from artificial lands (0.46%), agriculture (1.21%), orchards (0.40%), and pastures (1.68%) to broadleaf forests. Transitions to coniferous and mixed stands also originated from shrublands (0.54% and 0.62% respectively) and pastures (0.12% and 0.10% respectively).

Landscape scale

At the landscape scale, high elevation broadleaf forest dynamics were related to exposure. There was a significant difference (Mann-Whitney $U = 8$, p -value < 0.005) between forest cover change on the northeast (NE) and southwest (SW) aspects of the mountain range: on average, forests expanded more on SW (+109%) than on NE (+19%) slopes (Figure S2 in Supplementary Materials). The other class metrics were not statistically significant at a critical alpha value of 0.05: mean patch area ($U = 33$; $p=0.55$) increased more on SW slopes (+96%) than NE (+61%); patch density ($U = 0.34$; $p=0.61$) increased on SW slopes (+42%) but decreased on NE slopes (-20%); and mean Shape Index ($U = 37$; $p=0.80$) increased more on SW slopes (+19%) than on NE slopes (+15%).

Local scale

The mean elevation of the upper treelines observed in our study area was 1755 m a.s.l. (SD \pm 133 m). Treeline elevations exceed 2000 m a.s.l. in many sites, especially at Mt. Pollino (mean 1942 m a.s.l., SD \pm

91) and in the Majella Mts. (mean 1854 m a.s.l., SD \pm 220). The lowest mean treeline location is in the Sibillini Mts. (1600 m a.s.l., SD \pm 73). From north to south, the mean annual temperature of treeline increases ($\beta = 9.2$, $p < 0.05$), the mean elevation increases ($\beta = 2.2$, $p < 0.05$) and precipitation decreases ($\beta = -3.1$, $p < 0.05$; Figure 2). Across the study area, the mean annual temperature is 5.7 °C (SD \pm 1). The cumulative annual mean precipitation ranges from 879 mm (Sibillini Mts.) to 753 mm (Matese Mts.).

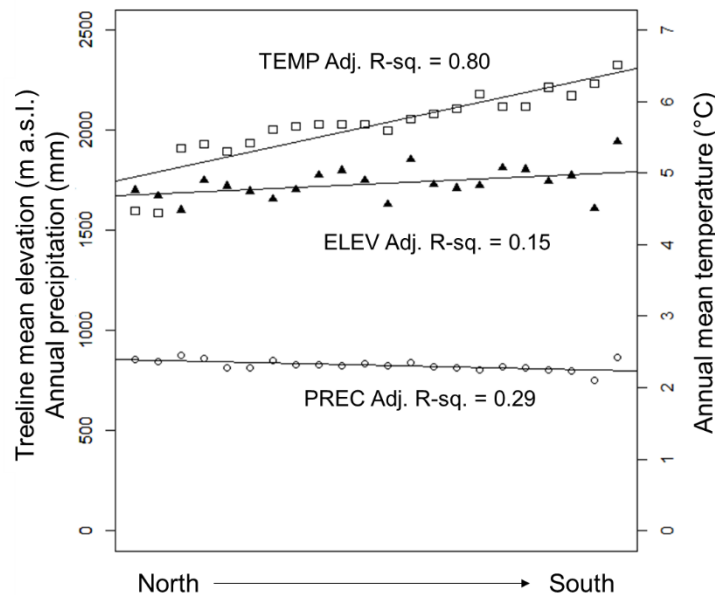


Figure 2. Mean annual temperature (white squares), annual precipitation (white dots) and treeline elevation (black triangles) along the latitudinal range of the Apennines from North (left) to South (right).

Fagus sylvatica (Fs) is the dominant tree species in 94% of all treeline samples and at some sites is the only tree species present. The central position of the species' centroid in ordination space and the size of its convex hull confirms its wide distribution unrelated to a specific variable (Figure 3). Plantations of *Pinus nigra* ssp. *nigra* Arn. comprise 2.3% of forest limits, with a maximum relative abundance (13%) of this species recorded in the central Apennines (Gran Sasso Mts.). *Pinus mugo* Turra (3.2%) dwarf shrublands are the dominant communities only at the highest elevations (up to > 2500 m a.s.l.) of the Majella and Meta-Petroso Mts. In the southern Apennines, *Pinus heldreichii* H.Christ var. *leucodermis* comprises a small proportion of the uppermost forests (0.1% of sampled points), forming 3% of treelines in the Mt. Pollino mountain group. Human population density was negatively associated with the NE index and elevation of the treeline site (Figure 3). Moreover, the highest treelines are at greater distances from roads. *Pinus nigra* (Pn) stands were associated with lower elevation sites (1659 m a.s.l. SD \pm 89 m), closer proximity to roads and on SW slopes. *Pinus mugo* (Pm) reached the highest elevations (2084 m a.s.l. SD \pm 185 m), where the lowest mean annual temperatures occur. The *Pinus heldreichii* (Ph) centroid and convex hull polygon represent the very clustered and limited presence of this species at Mt. Pollino, related to high

precipitation and low temperatures (2037 m a.s.l. $SD \pm 38$ m). . Treelines formed by plantations of *Picea abies* (L.) Karst occurred only at Mt. Cimone (0.3%), in the northern Apennines.

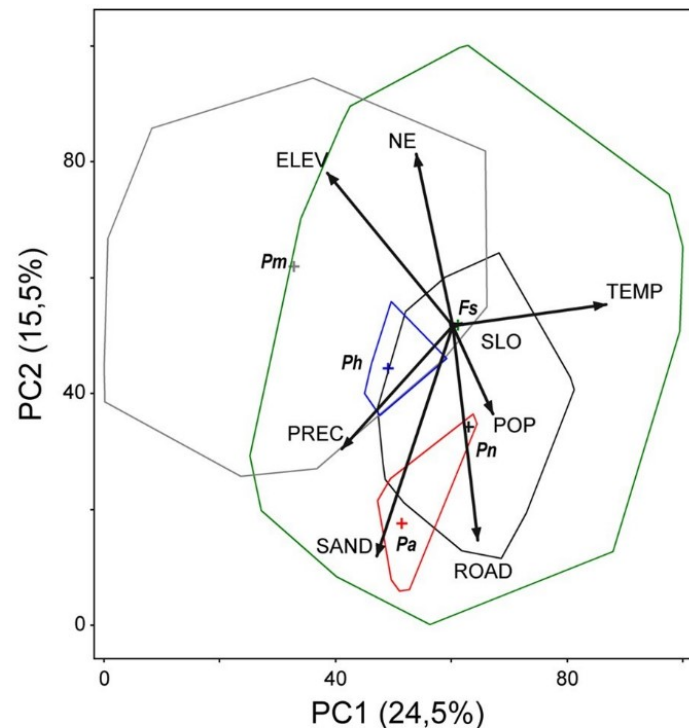


Figure 3. Biplot from Principal Components Analysis of 5484 sampled points with tree species distribution polygons and centroids (cross): Fs=*Fagus sylvatica* (green), Pn=*Pinus nigra* (black), Pa=*Picea abies* (red), Pm=*Pinus mugo* (grey), Pl=*Pinus heldreichii* (blue). Linear vectors are correlations ($p < 0.01$) of eight variables with PCA axes: TEMP: mean annual temperature; PREC: annual cumulative precipitation; ELEV: elevation; NE: northeastness index; SAND: proportion of sand in the soil texture; ROAD: proximity to the closest road; POP: human population density.

DISCUSSION

Forest cover expansion and human population decrease

Agro-pastoral practices over past millennia have greatly modified Mediterranean mountain-forest landscapes (Chauchard et al. 2007). Forest clearing has given way to forest expansion processes since the 19th century, following the progressive abandonment of pastures and croplands. This occurred first in marginal areas and mountain regions (Navarro & Pereira 2012), followed by a more widespread post-World War II rural depopulation process (MacDonald et al. 2000). In our regional study area of 776 Apennine municipalities, population decreased by 3.4% between 1991 and 2011, with the most rapid declines in the southeastern and northern sectors. In Europe, the rural population decreased by 17% from 1961 to 2010 (FAOSTAT 2010). In Italy, the overall population increased on average by 3.3% from 1960 to 1990; but the median change within municipalities was a population loss of 5.7% and most of

the administrative units featuring a population decrease are located in the Apennines, in the Alps and in the mountainous regions of Sicily and Sardinia (Falcucci et al. 2007). Demographic changes often trigger forest cover expansion in inhabited regions, but this process is not straightforward. In our study area, recent changes in forest cover were not statistically correlated to recent population dynamics within the same municipalities. Possible reasons are: i) down-valley migrations within the same municipality, ii) shifts of workers between job sectors (e.g. gain and loss of agricultural workers); iii) a lag in vegetation responses to demographic changes.

Spontaneous reforestation is a widespread process in Europe. Previous studies in the Apennines have found an increase in forest cover, excluding coniferous plantations, of 131%, (Assini et al. 2015), 45% (Bracchetti et al. 2012) and 48% (Rocchini et al. 2006), and a decrease of grassland cover of 67%, 57% and 71% respectively. However, these studies differed in categorical definitions, time period length, type of landscape and study area extent and thus are challenging to compare directly. In our study, the increase in forest cover accounted for 1% of broadleaf forest area and 4% of mixed woodland area, for a total increase of 15 260 ha. Our finding of limited land-cover change is due to the shorter time period analyzed (22 years) and, more importantly, to the much larger size of the study area (4.3 million hectares), that included a larger variety of land-cover classes and a more diversified human presence. Importantly, the time span for our study did not include the effects of the most relevant socio-economic migrations that occurred in the 1960's, after the fall of "mezzadria", a medieval agricultural management system that was used in central Italy. Natural reforestation is a complex, transient process dependent on previous land cover, and tree encroachment is usually faster in former pastures (Chauchard et al. 2007). In our study, 45 613 ha of pastures (9%) became shrublands. Many of these shrublands are likely to transition into forests in the near future, as shrub species commonly facilitate tree establishment near and above treeline (Weisberg et al. 2013). This process is already occurring, given that 14% of shrublands have converted to forests over the 22-year period studied. Other recent studies confirm this highly dynamic character of shrubland communities in Mediterranean mountains (Gartzia et al. 2014).

Forest cover changes and topography

The influence of land-use changes on new forest dynamics is evident in most southern European mountain ranges that historically experienced long-term anthropogenic pressure, followed by a subsequent reduction or total cessation of intensive land use (Albert et al., 2008; Ameztegui et al., 2015). In the Apennines, anthropogenic pressure has historically taken the form of intensive grazing on high-elevation pastures and short-rotation coppicing in forests. The relatively recent decline of such traditional practices has progressively changed the mosaic structure of mountain landscapes. The observed increase of high-elevation forest cover (> 1500 m a.s.l.), due to gap-filling and upward tree expansion, was significantly greater on SW slopes that have experienced more intensive land uses in the past. The more rapid forest cover change on SW slopes is also consistent with climatic influences. On these warmer

slopes, the upper forest limit is at lower elevations providing a more extended gradient for natural recolonization. In addition, the NE slopes, particularly on the Adriatic side, are steeper and cooler, possibly reducing the expansion rate of forest woody species (Gellrich et al. 2007; Gartzia et al. 2014). Our findings from the Apennines are consistent with recent Alpine studies (Garbarino et al., 2013; Tasser et al., 2007). In general, SW exposures in the northern hemisphere are warmer and expected to host forests at higher elevation than northern slopes (Danby and Hik 2007). Downslope expansion of alpine pastures, treeline elevation depression and forest clear-cuts are all common human-induced features on southern aspects of mountain regions in the Tropics (Miehe and Miehe, 2000). In the Himalayan region, south-facing slopes are more severely disturbed, particularly due to cattle grazing (Miehe et al. 1998; Schickhoff 2005; Schickhoff et al., 2015). In the central Pyrenees, rates of woody plant encroachment and forest productivity correlate positively with westerly aspects, due to the harsher climate conditions on north-facing slopes (Poyatos et al., 2003; Gartzia et al., 2014).

Effects of climate, topography and human pressure on treeline position

In the northern hemisphere, when comparing lower latitude sites with higher latitude sites at the same elevation, the former receive on average more radiant energy per unit area and tend to be warmer than the latter, causing a negative relationship between treeline elevation and latitude (Case & Duncan 2014). According to an empirical climatic relationship between treeline elevation and latitude (Hermes, 1955; Körner, 1998), we expect a decrease of 130 m in treeline elevation for each latitudinal degree along the entire temperate-subtropical transition zone (30°-50°N). Along the 4.4° of latitudinal range in the Apennines, we would expect a difference of 572 m in treeline elevation between the extreme northern and southern limits. However, we found a difference of only 243 m between the mean value at Mt. Cusna-Prado in the north (1699 m a.s.l.) and at Mt. Pollino in the south (1942 m a.s.l.). The mean elevation of the uppermost forest limit in the Apennines is 1755 m a.s.l. (SD \pm 133 m), 900 m lower than what would be expected based on global climatic relationships between temperature and treeline position (Körner 2007). Most Apennine mountain peaks do not overpass 2000 m a.s.l., indeed in the absence of edaphic limiting factors, they could be completely covered by forests. This suggests a widespread anthropogenic impact along the entire range, which caused lower treelines and substantial changes in their structure and composition. Multivariate statistics showed that topographic variables and human pressure were important drivers of treeline positioning. The highest treelines are located far from roads, particularly on NE exposures, and in municipalities with lower population density. On NE exposures, the presence of unfavorable soils for cattle grazing and steeper, colder conditions likely protected the treeline forests from past over-exploitation and left the treeline ecotone in a semi-natural condition. Monitoring tree regeneration dynamics above the current treelines could confirm what we have observed at the landscape scale: a more rapid expansion where the severity of human disturbance was historically higher. In mountains with prevalent agro-pastoral abandonment, forest migration associated with climate warming

may lead to increased contrast in the forest-alpine ecotone between areas with and without intensive land use (Weisberg et al. 2013). Variables representing slope steepness and climate explained a relatively small portion of the variation of treeline position, considering that the ordination explained 39% of the total variation in the data.

Effects of climate, topography and human pressure on treeline species composition

Globally, human pressure has acted as a selective process, modifying the density and distribution of woody species according to their life history traits and commercial value. For example, in the Swiss Alps, some species were disadvantaged by intense burning and browsing; some were purposely cultivated for increased demand of food supply (e.g. *Castanea sativa*) and for other uses like charcoal and litter (e.g. *Fagus sylvatica* and deciduous *Quercus* spp.; Conedera et al. 2017). In the Apennines, human impact, geomorphology and environmental conditions likely acted concurrently to define tree species distributions in high elevation forests. *Fagus sylvatica* is by far the dominant species of the Apennine treelines (94%), forming the typical abrupt transition from forest to grasslands at the upper treeline ecotone. Today the main ecosystem services of these forests are slope protection and biodiversity conservation, but until the 1960's they provided wood, charcoal production and wood pastures. Although all treeline forms may be affected by land use, abrupt treelines are most frequently associated with past human impact (Harsch & Bader 2011). Similar spatial patterns occur in beech forests of the Carpathians (Weisberg et al. 2013), *Pohlylepis* communities in South America (Kessler 2002), and *Nothofagus* forests of New Zealand (Cullen et al. 2001).

Apennine treelines with *Fagus sylvatica*, together with temperate southern hemisphere *Nothofagus* treelines and Pacific Island treelines with *Metrosideros* species, all represent taxa-specific rather than tree life-form boundaries (Körner & Paulsen 2004). Prostrate *Pinus mugo* treelines (3% of all sampled data) located at high elevations (> 2500 m a.s.l.) at Mt. Majella and Mt. Meta-Petroso in central Italy were associated with the lowest mean annual temperature and the highest mean value of the northeastness index. Some of the treelines found at the lowest elevations (mean 1659 m a.s.l.) are *Pinus nigra* plantations (2% of all sampled data). They occur mainly in the central Apennines and exclusively on limestone slopes. These forests were planted for slope erosion control after deforestation and intensive grazing (Barbero et al. 1998). Natural *Pinus nigra* stands are usually located within the optimal altitudinal range of 800-1500 m. However, *Pinus nigra* can grow on extremely dry sites and recent studies in the central Apennines showed that microsite topography and distance to seed source control *Pinus nigra* colonization of treeless areas (Piermattei et al. 2016; Vitali et al. 2017). Although its past distribution in Europe is difficult to reconstruct, more localized studies suggest that large populations of *Pinus nigra* (together with *Juniperus* spp.) were already present during the late Pleistocene and the Holocene in areas of the northwestern Mediterranean basin (Barbero et al. 1998; Roiron et al. 2013) and in the central Apennines during the post-Würmian period (Coltorti et al., 1998), supporting the hypothesis of an upper treeline ecotone above

the closed *Fagus sylvatica* forest made of open pine woodlands and dwarf junipers (Marchetti 1936; Stanisci 1997).

CONCLUSION

Land cover changes due to demographic variations of local populations have occurred during recent decades across Europe, especially in mountainous areas (Navarro & Pereira 2012). Spontaneous reforestation is a widespread process in mountain landscapes that were subjected to long-term anthropogenic pressure (Ameztegui et al., 2015; Gehrig-Fasel et al., 2007). In the Apennines, rural population decrease and forest cover increase are ongoing processes. Our results suggest that human impact is the major control on Apennine treelines, by lowering treeline elevation and constraining species composition (one dominant tree species). Moreover, the sites most severely impacted by historical human activities, on southwest aspects, have also experienced the greatest recent land cover changes.

Within the context of continuous land-use changes in the Apennines, we would expect that the widespread *Fagus* treelines would slowly shift upslope in the future, if future conditions will provide higher rainfall rates associated with increased growing season length and atmospheric CO₂ concentration. Otherwise, the negative influence of increasing temperatures may cause a retreat of *Fagus sylvatica* distribution in southern Europe (Jump et al. 2006; Sabaté et al. 2002). In general, deciduous species marking the upper tree limit in the Apennines appear to have ample opportunity to expand to climatically favorable sites at higher elevations, and more research on the constraints to *Fagus sylvatica* regeneration at high elevation is needed (Harsch et al. 2012). In contrast, the faster successional processes of *Pinus* spp. are expected to result in more rapid responses within these ecotones.

As anthropogenic treelines will respond differently than natural climatic ones to agents of global environmental change, models of treeline responses to global change need to account for land-use history. More treeline studies are needed that integrate the interacting effects of both natural and anthropogenic drivers on treeline position and structure, fostering interpretation of potential climate change responses in the context of historical and ongoing land-use change.

SUPPLEMENTARY MATERIALS

Table S1. Study sites at local and landscape scales. Lat/Long coordinates are defined for mountain ranges location.

Local scale mountain range	Latitude WGS84 [°]	Longitude WGS84 [°]	Mean treeline elevation (\pm SD) [m a.s.l.]	Local scale area > 1500 m a.s.l. [km ²]	Landscape scale mountain peaks	Landscape scale area [km ²]	Vegetation maps source
Mt. Prado - Mt. Cusna	44.27	10.40	1699 (\pm 47)	31			Carta aree forestali Regione Emilia-Romagna Inventario Forestale Regione Toscana
Mt. Cimone	44.19	10.70	1670 (\pm 62)	15	CI NE (Mt. Cimone) - CI SW (Mt. Cimone)	16 - 16	Carta aree forestali Regione Emilia-Romagna
Monti Sibillini	42.89	13.24	1600 (\pm 73)	99	SI NE (Mt. Bove) – SI SW (Mt. Vettore)		Carta Forestale Regione Marche Carta Forestale Regione Umbria
Monti della Laga	42.64	13.38	1749 (\pm 69)	107	GO NE (Mt.Gorzano) – GO SW (Mt.Gorzano)	16 - 16	Carta Forestale Regione Abruzzo Carta Forestale Regione Marche Carta Forestale Regione Lazio
Reatini (Mt. Cambio)	42.51	13.02	1719 (\pm 84)	11			Carta Forestale Regione Lazio
Reatini (Mt. Terminillo)	42.47	13.00	1693 (\pm 83)	27	TE NE (Mt. Terminillo) - TE SW (Mt. Terminillo)	16 - 16	Carta Forestale Regione Lazio
Gran Sasso	42.45	13.57	1655 (\pm 96)	171	GS NE (Mt. Portella) - GS SW (Mt. Portella)	16 - 16	Carta Forestale Regione Abruzzo
Mt. Ocre-Mt. Cagno	42.25	13.45	1703 (\pm 105)	35			Carta Forestale Regione Abruzzo
Mt. Sirente-Mt. Velino (Mt. Rotondo)	42.20	13.48	1774 (\pm 96)	9			Carta Forestale Regione Abruzzo
Mt. Sirente-Mt. Velino (Mt. Velino)	42.18	13.39	1799 (\pm 90)	131			Carta Forestale Regione Abruzzo
Mt. Sirente-Mt. Velino (Mt. Sirente)	42.14	13.61	1750 (\pm 91)	41			Carta Forestale Regione Abruzzo
Mt. Morrone	42.12	13.97	1627 (\pm 73)	11	MO NE (Mt. Morrone) - MO SW (Mt. Morrone)	16 - 16	Carta Forestale Regione Abruzzo
Majella	42.07	14.11	1854 (\pm 220)	146			Carta Forestale Regione Abruzzo
Mt. Genzana	41.95	13.89	1728 (\pm 98)	27	GE NE (Mt. Genzana) - GE SW (Mt. Genzana)	16 - 16	Carta Forestale Regione Abruzzo
Mt. Rotella	41.93	14.01	1710 (\pm 88)	13			Carta Forestale Regione Abruzzo
Monti Càntari (Mt.Viglio)	41.89	13.37	1723 (\pm 75)	15			Carta Forestale Regione Abruzzo Carta Forestale Regione Lazio
Monti Marsicani (Mt.Marsicano)	41.85	13.85	1812 (\pm 101)	81			Carta Forestale Regione Abruzzo
Monti Marsicani (Mt.Greco)	41.81	13.99	1803 (\pm 107)	76			Carta Forestale Regione Abruzzo
Monti Simbruini	41.80	13.49	1743 (\pm 89)	14			Carta Forestale Regione Abruzzo Carta Forestale Regione Lazio
Monti della Meta	41.69	13.94	1772 (\pm 100)	89	MM NE (Mt. Mare) - MM SW (Mt. Mare)	16 - 16	Carta Forestale Regione Abruzzo Carta Forestale Regione Molise Carta Forestale Regione Lazio
Monti del Matese	41.45	14.37	1607 (\pm 53)	10	MA NE (Mt. Miletto) - MA SW (Mt. Miletto)	16 - 16	Carta Forestale Regione Molise
Pollino	39.91	16.19	1942 (\pm 91)	55			Carta Forestale Regione Basilicata Carta di Uso del Territorio Regione Calabria

Table S2. Transition matrix of relative change (%) of land cover classes to shrubs and forests at the regional scale (CLC 1990-2012).

	2012			
	Broadleaf forest	Coniferous forest	Mixed forest	Shrubland
Artificial	0.46	0.03	0.01	0.36
Agriculture	1.21	0.04	0.04	1.65
Orchards	0.40	0.00	0.05	0.98
Pasture	1.68	0.12	0.10	9.05
Shrubland	13.75	0.54	0.62	74.04

1990

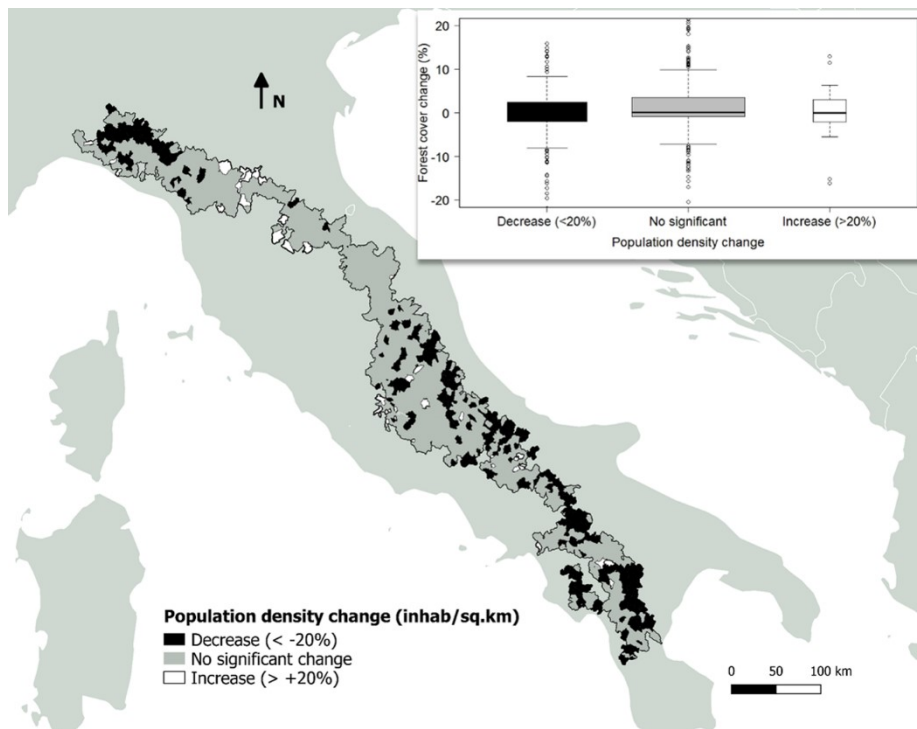


Figure S1. Population density change (inhabitants per square kilometer) expressed in percentage for the period 1991-2011. White and black areas indicate municipalities with positive and negative relevant changes. Grey municipalities are those without significant change in population density ($-20\% < X < +20\%$). The box-plot shows forest cover change across the three population categories.

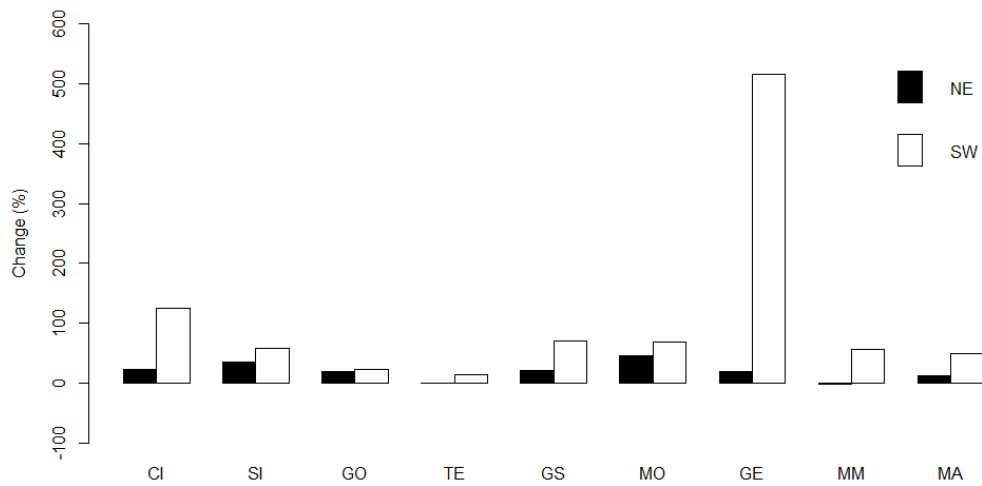


Figure S2. Percent of relative broadleaf forest cover changes (1954-2012) above the elevation threshold of 1500 m a.s.l. by the two main exposures. Mountain peak codes on the X-axis are listed from North (left) to South (right): CI= Mt. Cimone, GE= Mt. Genzana, GO= Mt. Gorzano, GS= Mt. Gran Sasso, MA= Mt. Matese, MM= Mt. Mare, MO= Mt. Morrone, SI= Mts. Sibillini, TE=Mt. Terminillo.

CHAPTER 3

Deconstructing human-shaped treelines: microsite topography and distance to seed source control *Pinus nigra* colonization of treeless areas in the Italian Apennines

This chapter has been revised and published:

Vitali A.¹, Camarero J.J.², Garbarino M.³, Piermattei A.^{4,1}, Urbinati C.¹. 2017. Deconstructing human-shaped treelines: microsite topography and distance to seed source control *Pinus nigra* colonization of treeless areas in the Italian Apennines. *Forest Ecology and Management* 406: 37-45. <http://dx.doi.org/10.1016/j.foreco.2017.10.004>

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ABSTRACT

Human-shaped treelines are a common feature in mountain landscapes across Europe, and particularly in secularly managed Mediterranean high-elevation areas. The abandonment of traditional land use, and especially the reduction in grazing pressure at high elevations, triggered secondary succession in treeless grassland areas, and favored the upward shift of anthropogenic treelines in some cases. We investigated this process in four anthropogenic treeline ecotone sites in the Central Apennines, Italy, populated by European black pine (*Pinus nigra* Arn.). The upward treeline shift was controlled by microsite topography and the proximity to plantations acting as seed source. We found a 50% probability of producing cones in trees with basal diameters of 15–25 cm, heights of 2–5 m and ages of 20–25 years. The role played by climate on growth and the recruitment processes seems to be secondary, or could be masked by human-shaped processes. The presence of reproductive age trees at the treeline, mainly growing on debris-rich and steep slope sites, could indicate that the recruitment process will increase in future, leading to patchy tree patterns at different elevations. The high growth and encroachment rates observed at these human-shaped treelines would indicate that general growth dynamics are speeding up, including the tree colonization of treeless areas. These succession processes could cause a significant long-term decline in plant diversity in species-rich grasslands. Nonetheless, tree encroachment could increase forest protection against landslides and avalanches in the context of global change.

INTRODUCTION

Alpine treeline ecotones are sensitive indicators when assessing the ecological effects of two global-change components on forests, namely climate warming and land-use modification (Harsch and Bader 2011). The greater sensitivity of these high altitude tree populations to temperature variability confirms that growth and tree recruitment in these marginal populations respond to climate variation (Daniels and Veblen 2004, Camarero and Gutiérrez 2004). However, climate warming is only one aspect of global change that may affect the location of treelines (Holtmeier and Broll 2005). If traditional human activities near the treeline are common (Körner 2012), the forest-grassland ecotones are usually affected by changes in the anthropogenic disturbance regimes (, Batllori and Gutiérrez 2008, Woods 2014).

Anthropogenic treelines develop under severe human impact that alters site conditions, such as forest clearing, fire or livestock grazing (Holtmeier and Broll 2005). Moreover, land-use shifts can severely influence treeline physiognomy masking or reversing the response of treelines to climate warming (Harsch and Bader 2011, Woods 2014). Although land use is more frequently associated with an abrupt transition from forested to treeless areas, different treeline types and structures may be the result of various past human influences (Batllori and Gutiérrez 2008, Harsch and Bader 2011). Land-use changes are long-term broad-scale disturbances and should be considered as major drivers of treeline formation in human-disturbed mountain areas (Foster et al. 1998). Their effects on treeline dynamics can persist long after the abandonment of human activities (Camarero et al. 2017, Gimmi et al. 2008).

During the past century, European mountains experienced rapid and extensive changes in land-cover and landscape patterns which facilitated woody plant invasions in formerly grass-dominated ecosystems and also upward shifts in treelines (Hofgaard 1997, Chauchard et al. 2007, Gehrig-Fasel et al. 2007, Ameztegui et al. 2010, Treml et al. 2016). In southern Europe, the rapid industrialization of the mid-20th century triggered deep socio-economic shifts, including a massive rural exodus toward cities and the decline of traditional practices in mountains that had been based on small-scale agriculture, pastoralism and forest resource utilization (Blondel and Aronson, 1999). In the northern Mediterranean Basin, traditional land uses (grazing, forest and forest-floor exploitation) in mountain areas became unsustainable during the 20th century and rapidly abandoned (Debussche et al., 1999). Land abandonment and/or the reduction of grazing pressure were often followed by national forest plantation programs which increased the surface area of mountain forests and, in some cases, fostered tree invasion in old-field pasture lands (Chauchard et al. 2007).

The Apennines are a mountainous range extending for 1200 km NW-SE across Italy with numerous peaks higher than 2000 m a.s.l. (maximum elevation Mt. Corno Grande 2912 m a.s.l.). The vegetation zones of the Apennines have been severely shaped by climate change and millenary human activities, and now are mainly covered by deciduous forests and woodlands. European beech (*Fagus sylvatica* L.) is the

main species of the mountainous zone ranging from 800-900 m to 1700-1800 m and forming the treeline at most sites (Vitali et al. 2017. Submitted). In Paleo and Neolithic times, high-elevation Apennine forests (1900-2200 m a.s.l.) were extensively cleared for hunting of wild herbivores and were transformed into wood pastures or grasslands (Piermattei et al. 2014). In the central Apennines, the decrease of agro pastoral exploitation and the migration of rural populations toward urban areas increased during the last 60 years (Falcucci et al. 2007). These changes, together with climate warming, enhanced tree encroachment and forest expansion at high elevations (Dibari et al. 2015). European black pine (*Pinus nigra* Arn.) was extensively used in mountain plantations during the 20th century reforestation programs for landslide and erosion control due to its pioneering character and fast land cover capacity (Isajev et al. 2004, Piermattei et al. 2016). Black pine revealed a natural inclination to expand on treeless areas above the closed forest limit exclusively on the limestone soils of central Apennines, reaching unexpectedly high elevations (> 2000 m a.s.l.) and suggesting the formation of new and higher treeline ecotones (Piermattei et al. 2012, 2014, 2016).

Black pine was more dynamic and expanded upslope more rapidly than most of the other woody species (*Juniperus* species, *Rhamnus alpina*, *Fagus sylvatica*) in the central Apennines. This process could rearrange anthropogenic treelines and timberlines (*sensu* Körner 2012) ecotones above secularly disturbed mountain forests. This upslope spread of black pine could be regarded as an “advance guard” of a conifer-dominated anthropogenic treeline (Piermattei et al. 2012). The black pine upward expansion started 30-40 years ago and its spatial distribution at higher elevations generally appeared random with no evident patterns (Piermattei et al. 2012) or even over-dispersed along the slope (Piermattei et al. 2016). The radial growth of planted black pine is particularly sensitive to maximum temperatures and water availability during the growing season forming numerous intra-annual density fluctuations (IADF) (Piermattei et al. 2014). In a recent study in the central Apennines the spatial pattern of black pine encroachment revealed that its expansion pattern is independent of site location and local disturbance histories (Piermattei et al. 2016). This process of secondary succession is considered to be complex and depends on several factors such as masting occurrence, seed availability and dispersal, suitability of regeneration niches (*sensu* Grubb 1977), growth rates and tree establishment (Piermattei et al. 2012, 2016). Some of these variables are linked to tree growth rates, and could be enhanced by the observed temperature increase (Camarero et al. 2017). Nevertheless, site micro-topography is a major factor in treeline dynamics since concave and wind-sheltered lee slopes can promote the formation of thick and long-lasting snowpack, affecting tree establishment (Hagedorn et al. 2014, Kullman and Öberg 2009).

We investigated a recent process leading to a treeline upshift, testing the predicting role of microsite topography and the distance of individual trees from neighboring black pine plantations acting as seed sources. We tested whether trees that had encroached at the higher elevations in the late 20th century acted as a secondary source of regeneration. We also investigated how tree size and age could influence

cone production which would facilitate in turn the ascent of new individuals and the treeline (Piermattei et al. 2016). We used tree height rather than tree diameter because height is the variable that defines treeline position and determines the tree uncoupling from soil microclimate conditions (Körner 2012). Finally, we compared the microhabitat type closely around the seedlings or saplings (classes defined by tree height), assuming that saplings ground vegetation is influenced by vegetation dynamics under the influence of established trees.

In particular with this study, we searched for answers to the following questions: (i) are there differences between seedlings and saplings vegetation ground-cover?; (ii) what are the main abiotic variables affecting tree growth in these treeline populations?; (iii) is there a minimum reproductive age threshold for newly encroached pines?; and (iv) does microsite topography and/or the presence of cone-producing trees allow tree encroachment to be successfully predicted? We hypothesized that microsite topography and distance to seed sources were the main factors influencing the black pine colonization process at high elevation, and that this expansion process could be spatially aggregated.

MATERIALS AND METHODS

Study sites

We sampled four mountain treeline ecotones situated in the central Apennines (Italy). Sites were located in the Marche (Mt. Bove, hereafter BOV site) and Abruzzo regions (Mt. Ocre, OCR; Mt. Morrone, MOR; Mt. Genzana, GEN), where black pine encroachment is widespread (Tables 1 and 2; supporting information, Figure A1). We selected the sampling sites after examining and interpreting aerial photographs and then carried out field visits. Selected sites fulfilled three requirements: i) the presence of a timberline located over 1500 m; ii) the existence of mountain peaks with elevation higher than 2000 m a.s.l. and iii) the potentiality of the upward shift up to the mountain peak without geomorphological constrains. Field data was collected between 2013 and 2015 within altitudinal transects (width 50 m and variable length) running from the timberline up to the uppermost black pine tree (Figure 1). All sampled area surfaces range from 2.25 to 4.50 ha (Table 1). We regarded the timberline as the upper limit of a closed canopy forest (tree cover > 50 %), either broadleaf natural forest or conifer plantation, and the treeline as the highest elevation where we found trees with height > 2 m. All study sites were included in different types of protected areas: BOV is located in the Sibillini Mountains National Park, OCR in the Mount Ocre-Acquazzone State Forest, MOR in the Majella National Park, and GEN in the Natural Reserve of Mts. Genzana and Alto Gizio.

Site	Latitude (N°)	Longitude (E°)	Timberline elevation (m a.s.l.)	Treeline elevation (m a.s.l.)	Slope aspect	Mean slope angle (%)	Surveyed surface area (ha)
BOV	42° 54'	13° 11'	1715	1809	SW	49	3.60
OCR	42° 15'	13° 27'	1635	1708	NE	54	2.25
MOR	42° 06'	13° 57'	1542	1900	SW	32	4.50
GEN	41° 56'	13° 53'	1705	2016	SW	30	4.50

Table 1. Main features of the study sites. *Timberline* is the upper limit of a closed canopy forest (tree cover > 50 %). *Treeline* is the altitude of the upper sampled tree with a height ≥ 2 m. The growing season length was set from May to September.



Figure 1. Upward encroachment of European black pine (*Pinus nigra*) trees at Mt. Bove site (BOV). A pine plantation acting as seed source is visible on the left. .

Livestock grazing, especially by sheep, cows, and more recently horses, was the most important human-induced pressure at all four sites. Grazing intensity has decreased significantly over the last 40 years in the study region (Santilocchi and D'Ottavio, 2005). Past uncontrolled intensive grazing caused widespread slope erosion that required extensive pine plantations between the 1950s and 1970s. Today, less disturbed treeline ecotones are formed by forests and woodlands of European beech (*Fagus sylvatica* L.) along the Apennines, and by species-rich dry grasslands dominated by *Sesleria*, *Bromus* and *Festuca*

species (Halada et al. 2011). All study areas are mainly located on calcareous bedrock. They share a temperate oceanic climate (Rivas-Martinez et al. 2004) with a Mediterranean influence characterized by summer drought downwards and the main precipitation peaks in spring and autumn. Summer precipitation is not a limiting factor for treeline shift since it increases upwards as in other mountain chains (Körner 2012). Snowfall is more common and abundant in late winter to early spring, especially from February to the end of March (De Bellis et al. 2010). The mean growing season (May to September) temperatures at the four sites are 11-13 °C (SD \pm 3 °C), with extreme mean values ranging from 7° to 16 °C.

Field sampling

We mapped 429 *Pinus nigra* trees that had encroached above the timberline with a Trimble Pro 6H GPS antenna (Trimble Inc., Sunnyvale, USA). A post-processing differential correction through Pathfinder Office 4.2 software was performed with a 0.5-m estimated accuracy. We measured basal stem diameter, total height and counted the number of cones for each individual pine (Table 2). To characterize the regeneration niche of seedlings and saplings, we quantified the percentage cover of microhabitat types (rock, debris, grass and shrub) within a circular plot with a 0.5 m radius around each pine stem. The age of all the trees with a basal stem diameter \geq 4 cm was determined after the extraction of one basal increment core. For trees with a basal stem diameter < 4 cm we counted the number of annual internodes (terminal bud scars) along the main stem to estimate their age (Camarero and Gutiérrez 1999). We classified trees as seedlings (tree height < 2 m) and saplings (height \geq 2 m), respectively.

Site	No. trees	Tree density (N° ha ⁻¹)	No. sampled cores	Trees with cones (%)	Seedlings / saplings (%)	Mean basal diameter \pm SD (cm)	Mean height \pm SD (m)	Mean age \pm SD (years)
BOV	228	63	71	4	87 / 13	6 \pm 7	1.09 \pm 1.36	10 \pm 5
OCR	39	17	23	26	77 / 23	9 \pm 7	1.41 \pm 1.23	16 \pm 6
MOR	113	25	84	23	54 / 46	11 \pm 6	1.81 \pm 1.03	16 \pm 5
GEN	49	11	35	24	67 / 33	11 \pm 9	2.08 \pm 2.42	17 \pm 8

Table 2. Main structural variables of the sampled black pine (*Pinus nigra*) trees that had encroached the four study sites. Seedlings are trees with height \leq 2 m; saplings are trees with height \geq 2 m.

We estimated the competition index for each sampled tree by calculating a distance-dependent competition index at the individual scale, taking into account the number and size of the neighboring competitors and their distance to the focal tree (Hegyi, 1974). We calculated the competition index as the sum of the diameter quotients obtained for all the neighboring trees located within a 2-m radius from the

focal tree, divided by the distance between focal trees and neighborhoods. We corrected edge effects by omitting trees with distances from the plot limits of lower than 2 m from the calculation.

Topographic, climatic and microsite ground-cover data

Topographic variables were extracted from the 10-m-resolution DEM for the Italian territory (Tarquini et al. 2012) for each pixel covering the mapped altitudinal transects. Specifically, we calculated: i) the slope; ii) the north-eastness index with values ranging between -1 (sunniest exposure) and $+1$ (shadiest exposure) and iii) the plan curvature index perpendicular to the maximum slope and ranging from -1 (concave) to $+1$ (convex). Mean monthly temperatures for the period 1950-2015 were obtained using the procedure reported in Carturan et al. (2016) and in Brunetti et al. (2012). In the field, we assessed the seedling and saplings ground-cover, according to four cover types: grass, shrub, debris, and bare rock. We compared these ground-cover proportions in each site, to detect significant differences, considering that saplings can have a higher influence on the ground vegetation than seedlings, during their growing process.

Growth data

We collected 213 basal cores from trees located at four treeline ecotones (Table 2). Cores were mounted and glued on wooden supports, and then thoroughly polished with progressively finer sandpaper until the tree rings were clearly visible. We used the semi-automatic LINTAB system and WinTSAP (Rinntech, Heidelberg, Germany) to measure tree-ring width at 0.01 mm precision. Most of the ring-width series were too short (< 30 years), and did not allow for a robust statistical verification but only visual crossdating. Tree-ring widths were converted into basal area increments (BAI) since this variable reflects growth changes more accurately (Biondi and Qeadan, 2008).

Statistical analyses

We used χ^2 tests to compare seedlings and saplings microsites at each site. We used Generalized Linear Models (GLM) to predict the probability of cone production as a function of several relevant variables (stem diameter, tree height and age). The goodness of fit of the GLM models was assessed using McFadden's pseudo- R^2 values (Venables and Ripley 2002).

We fitted linear mixed-effect models (LME) to radial growth data at each site considering pine trees as random factors. We applied the autoregressive process (AR(1)) which describes the in-tree correlation structure of radial growth which was quantified as basal area increment. We considered the following as fixed factors in the LMEs: basal diameter, year, elevation, ground curvature, competition index and mean spring monthly temperatures (March April and May) that can play a crucial role at the beginning of the growing season. We ranked all the potential models according to the Akaike Information Criterion (AIC)

and then selected the most parsimonious models showing the lowest AIC value (Burnham and Anderson, 2002). We also used the Akaike weights (W_i) of each model to measure the conditional probability of the candidate model assuming it was the best one. We assessed the fit of the models by graphical examination of the residual and fitted values (Zuur et al. 2010).

Finally, we fitted negative binomial GLMs to predict the number of pines (the density of pines in 100 m² subplots) as a function of four topographic variables (elevation difference from plantation, slope, north-eastness and curvature indices). These models were ranked according to their AIC values and we selected the best ones (Burnham and Anderson, 2002). Then we applied the Akaike weights (W_i) to each model (Zuur et al., 2010).

All statistical analyses were run using the R package (R Core Team 2016). Model selection was performed using the MuMIn package (Barton, 2013). The 'lme' function of the *nlme* package was used to fit the LMEs (Pinheiro et al., 2016). The 'glm.nb' function of the *mass* package was used to fit the GLMs (Venables and Ripley 2002).

RESULTS

Size and age of treeline trees

Mean timberline elevation was 1650 m and ranged between 1542 m (MOR) and 1715 m a.s.l. (BOV), whilst the mean treeline elevation was 1858 m and ranged between 1708 m (OCR) and 2016 m (GEN) (Table 1). Black pine colonization across the treeline ecotone was scattered since tree density showed a wide range of values, from 11 to 63 trees ha⁻¹ (Table 2). On average, these recruited pines corresponded to 71% and 29% of seedlings and saplings, respectively. Overall, the average tree size was small, with lower values at the BOV site and higher values at the GEN site. The mean basal diameter was 9 cm, the mean height was 1.60 m, and the mean age was 15 years (Table 2). Most sampled trees had basal diameters of lower than 15 cm and heights of lower than 2 m (Figure 2). On average, trees took 10-15 years to reach a height of 2 m (Supporting Information, Figure A2). Modal age values varied between 5 and 20 years. The oldest trees suggested that colonization started at least 30 years ago (1985–1990).

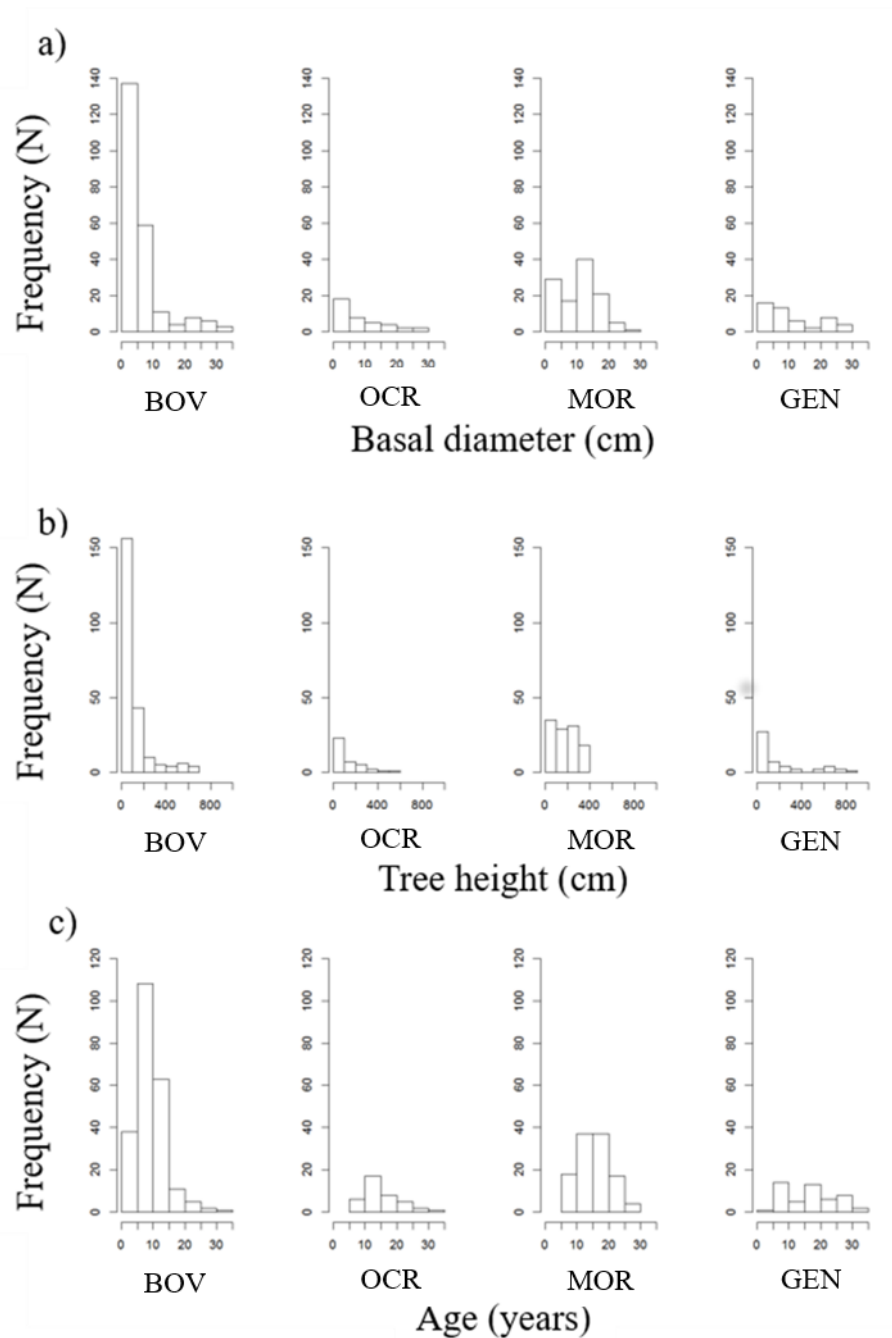


Figure 2. Frequency distribution of basal diameter (a), tree height (b) and estimated age (c) of the treeline black pines (*Pinus nigra*) sampled at each of the four study sites.

Treeline structure and regeneration niche

Tree density decreased with altitude and distance from the pine plantations at most of the sites (Figure 3), but tree height and age did not. A negative correlation of tree height with altitude was observed only at BOV ($r = -0.22$, $p < 0.05$). On the other hand, there were significant and positive correlation values between altitude and tree height and age at the MOR site (both variables $r = 0.36$ $p < 0.05$). Generally, the pine encroachment pattern across the treeline ecotones was not spatially structured in cohorts, but some clustered patterns were detected at 200 m intervals. These spots with higher tree density occur

usually with increasing slope and consequently debris cover. Whereas in moderate slopes the grass-cover treeless areas increased.

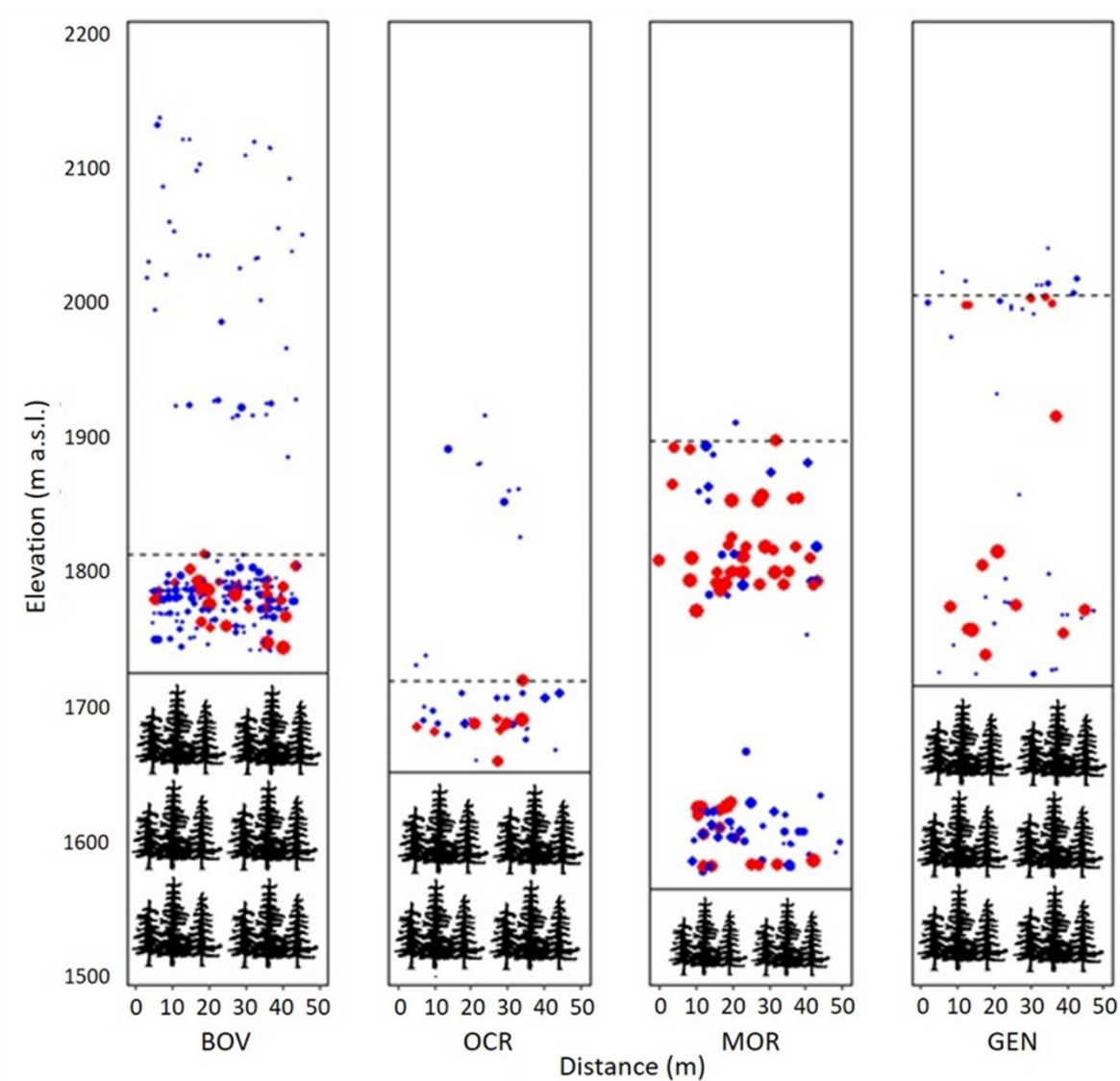


Figure 3. Mapped point patterns of black pine individuals at the four Apennines treeline ecotones (see Tables 1 and 2 for site characteristics). Blue dots are seedlings (tree height < 2 m) and red dots are saplings (height \geq 2 m). The dot scale size is proportional to the tree height. Solid and dashed lines correspond to the current timberline and treeline positions, respectively (*sensu* Körner 2012).

The negative binomial GLMs fitted to tree density showed that this variable decreased as the elevation and distance to the pine plantation increased at all sites but at GEN (Table 3). A steeper slope was also positively linked to tree encroachment at the BOV and MOR sites, whilst a higher north-eastness index (cooler conditions) was negatively related to tree density at the BOV and GEN sites.

Site	Parameters	W_i
BOV	- 8.48 Pla + 4.96 Slo - 2.41 NE	0.44
OCR	- 4.29 Pla °°	0.34
MOR	+ 2.89 Slo - 1.88 Pla	0.26
GEN	- 2.37 NE	0.26

Table 3. Summary of the negative binomial generalized linear models fitted to black pine density as a function of topographic variables (elevation, slope, north-eastness index). The last column shows the relative Akaike weights (W_i). Variable abbreviations: Pla, elevation difference from pine plantation; Slo, slope; NE, north-eastness index; °°, not-significant parameters

We detected significant differences in ground cover types of seedlings and saplings at all sites ($\chi^2 = 13.41 - 22.10, p < 0.01$ in all cases), except for the OCR site ($\chi^2 = 3.95, p = 0.27$). Most mapped seedlings were found on debris microsites, whereas most saplings were found on grass microsites (Figure 4). The most relevant difference between seedlings and saplings microsites was the very lower proportion of debris cover in saplings sites.

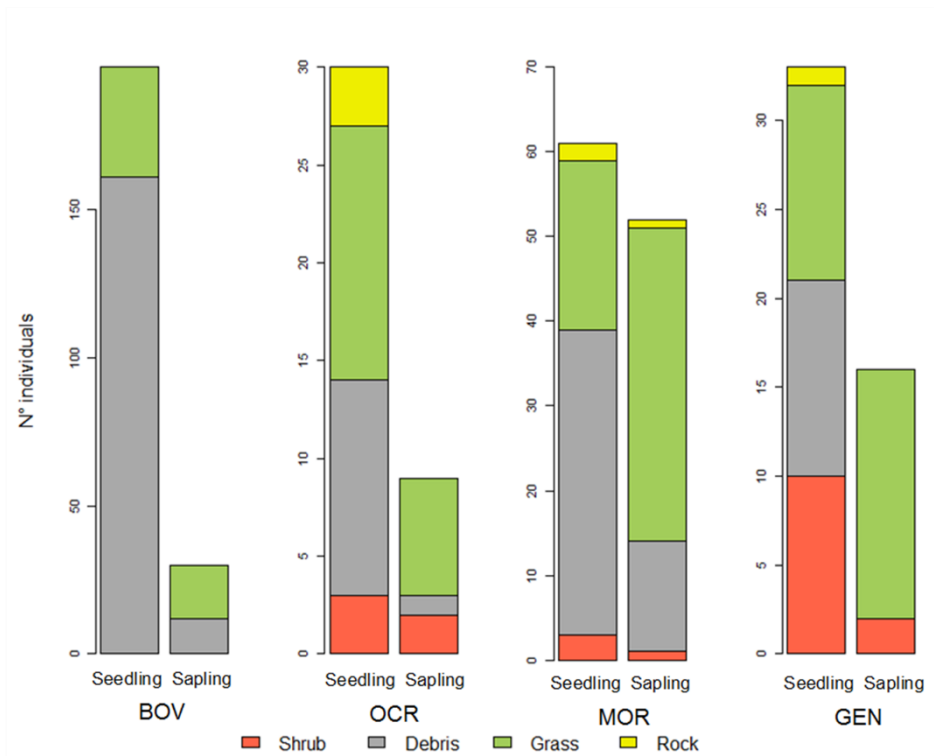


Figure 4. Number of black pine recruits sampled at each treeline ecotone (BOV, OCR, MOR and GEN sites) and classified as a function of their height (seedling and sapling; see Figure 3) and microsite types (shrub, debris, grass and rock).

Growth trends

Basal-area increment (BAI) data showed high recent growth rates (5-10 cm² yr⁻¹), and narrow rings were formed one year later in response to the warm-dry summer conditions observed in 2003, 2007 and 2011 (Supporting Information, Figure A3). LMEs fitted to BAI data showed that tree age and basal diameter were the most important predictors of growth, whereas elevation and mean spring temperatures played a minor role (Table 4). Neither the curvature nor the competition indices were selected as growth predictors in any of the best-fitted models.

Site	Parameters	W_i
BOV	18.66 Age + 3.45 Diam + 2.86 Tm	0.77
OCR	7.60 Age + 3.45 Diam + 2.86 Tm	0.79
MOR	14.99 Age + 9.73 Diam	0.78
GEN	12.95 Diam + 9.82 Age + 3.73 Tm	0.80

Table 4. Summary of the linear mixed-effect models of tree growth (basal area increment) fitted as a function of site, topographic variables (elevation and curvature index), tree variables (age, basal diameter, and competition index), and climate variables. All regression intercepts are significant. The last column shows the relative Akaike weights (W_i). Variable abbreviations: Age, age of tree; Diam, basal diameter; Tm, mean spring temperature (March, April and May). Variables not included in the best-fitted models: Elev, elevation; Ci, Competition index; Curv, Curvature index.

Production of cones by treeline trees

At each site, 19% of trees produced cones (Table 2). All sites showed common tree size and age characteristics when they reached a 50% probability of producing cones: 15–25 cm of basal diameter, 2–5 m of tree height, and 15–25 years in age (Supporting Information, Figure A4). The GLMs of cone production showed higher pseudo- R^2 values with basal diameter ($R^2 = 0.38$ – 0.55) or height ($R^2 = 0.37$ – 0.75) as predictors rather than using age ($R^2 = 0.12$ – 0.47) (Table 5).

Site	Degrees of freedom	McFadden's pseudo- R^2		
		Basal diameter	Height	Age
BOV	226	0.47	0.37	0.32
OCR	37	0.49	0.59	0.12
MOR	111	0.38	0.34	0.16
GEN	47	0.55	0.75	0.47

Table 5. Results of the Generalized Linear Models (GLMs) applied for the prediction of cone production by black pine at the four study sites (BOV, OCR, MOR and GEN) as a function of tree basal diameter, height and age.

DISCUSSION

We described the natural ascent of human-shaped treelines in the central Apennines. Black pine is expanding upwards in formerly treeless areas, particularly on steep slopes and where seed availability depends on downslope pine plantations. The irregular structures found at all sites could also be affected by un-stationary mortality caused by climate extreme events, e.g. frosts, winter drought (Camarero et al. 2015, Barros et al. 2017), or other factors such as pathogens or mass wasting processes (e.g. rock fall, debris flow, land slide). We observed a patchy pattern (Figure 4) of treeline shift driven by both changes in microtopography and availability of suitable regeneration sites for black pine. Our results show that most tree seedlings were located on debris ground-cover and steeper slopes, avoiding grass competition. The relative lower number of trees on flat and grass-cover areas could be a consequence of herbs competition and snow accumulation on late winter, particularly in convex areas (Tremblay and Chuman 2005). However, recruits that overcome grass competition on less steep sites grew successfully, as confirmed by the abundance of saplings on those sites. Indeed, debris microsites on steeper slopes most frequently hosted pine seedlings (Figure 3), and tree encroachment was also favored at shorter distances from the pine plantations (Table 4). Herbaceous vegetation, which is often dominant at many treeline ecotones, exerts an important and mostly limiting impact on the establishment of tree seedlings (Loranger et al. 2017). Studies on Scots pine (*Pinus sylvestris*) encroachment in Mediterranean mountain grasslands showed that the physical barrier created by the herbaceous layer could hamper pine regeneration and limit potential forest expansion (Castro et al. 2002). Bare soil or very sparse vegetation are favourable substrates for pine recruitment (Loranger et al. 2017). Sites with prevailing shrub cover and rocky outcrops were considered safe for establishment and development of black pine (Piermattei et al. 2016) and for mountain pine (*Pinus uncinata*) recruitments (Camarero and Gutiérrez 2007, Batllori et al. 2009). Abrupt treeline physiognomy and a decreasing number of new trees (but no changes in height or age) as elevation increases are typical features of anthropogenic treelines (Batllori and Gutiérrez 2008). These results compare well with other treelines that have been studied in the central Apennines, where the density of newly established trees decreased with elevation (Piermattei et al. 2016).

The general patchy pattern of the pine distribution observed at about every 200 linear meters does not imply the formation of spatially segregated even-aged cohorts. We found different age and size classes grouped together on the same preferred locations. We did not find any statistical correlation between elevation and tree age or height, except for the positive values at the MOR site, where older and taller trees are located at the highest elevations (Figure 2).

We observed that tree density decreased with elevation due to the increasing distance of upslope encroached trees from pine plantations. This fits with a general theory where the shorter the distance to old trees (the plantations in our case), the higher the reforestation rate (Tasser et al. 2007, Stueve et al.

2011). The higher availability of seeds is the main driver of pine colonization since it helps propagules ascend higher, and potentially favors the establishment of new pine individuals. Moreover, the results based on the negative binomial GLMs showed a positive slope influence on tree density at least at the BOV and MOR sites (Table 3). Similar recruitment patterns were found in the Southern United States where increased density was found to relate to slope and proximity to the forest (Coop and Givnish 2007).

Our tree growth models showed the dominant role played by tree age and size in determining growth rates (BAI) at the treeline, whereas spring temperatures had secondary importance. Elevation, curvature and the competition index were not included in the best-fitted growth models (Table 4). Tree density was relatively low in the study sites, likely excluding the competition effect from the best models. The newly established pines are not growth-limited at high elevations indicating that they have not reached the uppermost climatic threshold for tree growth. We did not assess the role of wind disturbance and radiation stress on seedling abundance or tree growth even though they can be additional abiotic constraints at the treeline (McIntire et al. 2016). Linking changes of grazing intensity and individual tree growth is a big challenge since such historical pastoral records are often lacking at local to regional scales, but their availability would allow more precise testing of the impact of land-use changes on forest growth at high elevation and treeline dynamics.

The fecundity of Mediterranean pines like black pines is particularly important considering that they are significant pioneering and/or invasive species across many world regions (Richardson and Rejmánek 2004). Our results showed that tree height or stem diameter were better predictors of cone production than tree age (Table 5), and that similar thresholds for becoming reproductive individuals occurred at all sites: ca. 15 cm of basal diameter, ca. 2 m of height and about 15 years of age (Supporting Information, Figure A4). This agrees with Isajev et al. (2004) indicating that black pine maturity is reached at 15 years old. We did not assess either seed production or seed viability which can be relevant variables in the understanding of treeline encroachment since slow-growing treeline standing trees or krummholz may form cones, but with few or no viable seeds (Camarero et al. 2017). Generally, trees release many more seeds when conditions are dry and windy, potentially increasing the proportion of long-distance dispersal events (Coutts et al. 2012). A comparison showed that non-native black pine populations had a higher net reproductive rate and higher effective dispersal than native Scots pine, leading to a rapid expansion of black pine into grasslands (Debain et al., 2007). If recently encroached trees overcome bottlenecks related to seed viability, the future of these anthropogenic treeline ecotones will depend on the future dynamics of successful high-density tree groups or clustered islands. These trees growing on debris-rich and steep slope sites may become new seed sources and catalyze the recruitment process, increasing the annual seed production at closer distances.

The establishment of trees into treeless, high-elevation areas could become widespread in many European mountains where there has been a consistent decline in human land-use and traditional agro-pastoral practices (MacDonald et al. 2000, Chauchard et al. 2007, Gellrich et al. 2007), combined with the absence of relevant geomorphological constraints (Leonelli et al. 2011). These tree encroachment and forest re-growth processes may have relevant impacts on ecosystem processes, influencing biogeochemical cycles, carbon sequestration and cycling, soil properties and ecohydrological processes (Rundel et al. 2014). These successional processes could lead to biodiversity problems since they can cause significant long-term declines in plant diversity in species-rich calcareous grasslands (Dullinger et al. 2003). On the other hand, tree encroachment could improve protection against landslides and avalanches (Holtmeier and Broll 2005). We need a better characterization and understanding of these encroachment processes to predict the pace and pattern of human-shaped treeline rebuilding.

CONCLUSIONS

We investigated the patterns and processes of the recent encroachment of black pine cohorts taking place at various anthropogenic treelines in the Central Apennines due to the abandonment of traditional land-uses. Treeline encroachment was mainly driven by microsite topography and the presence of nearby seed sources (pine plantations). Overall, the high growth rates found at high elevation and the rapid and often clustered encroachment patterns indicate that these human-shaped treelines can also respond quickly to the future global change.

SUPPORTING INFORMATION

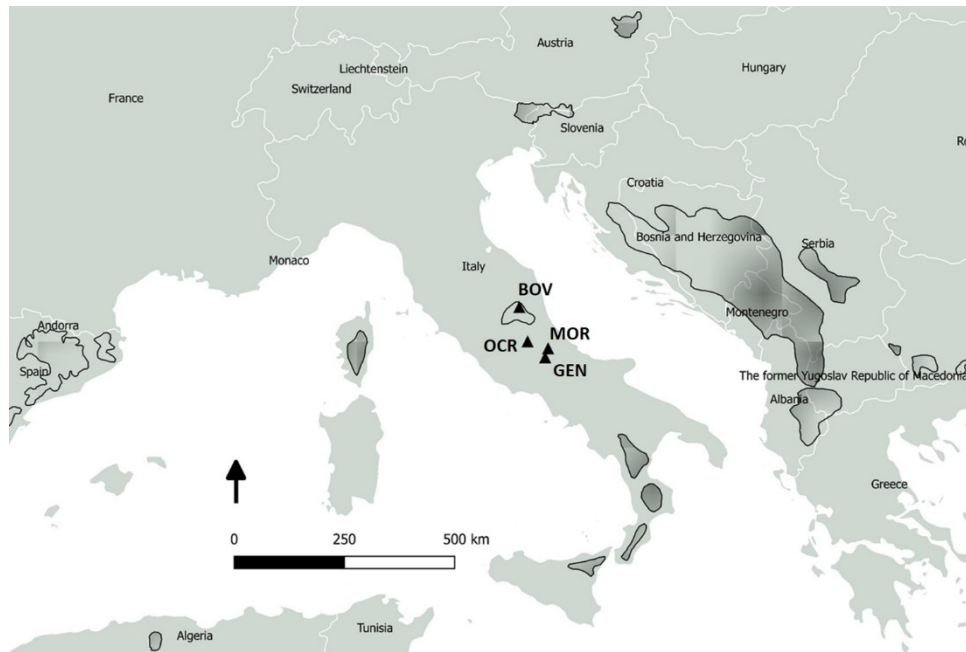


Figure A1. Natural distribution range of European black pine (*Pinus nigra* and sub-species) in the circum-mediterranean areas (black contours); locations of the four study treeline sites at the central Apennines, Italy (black triangles).

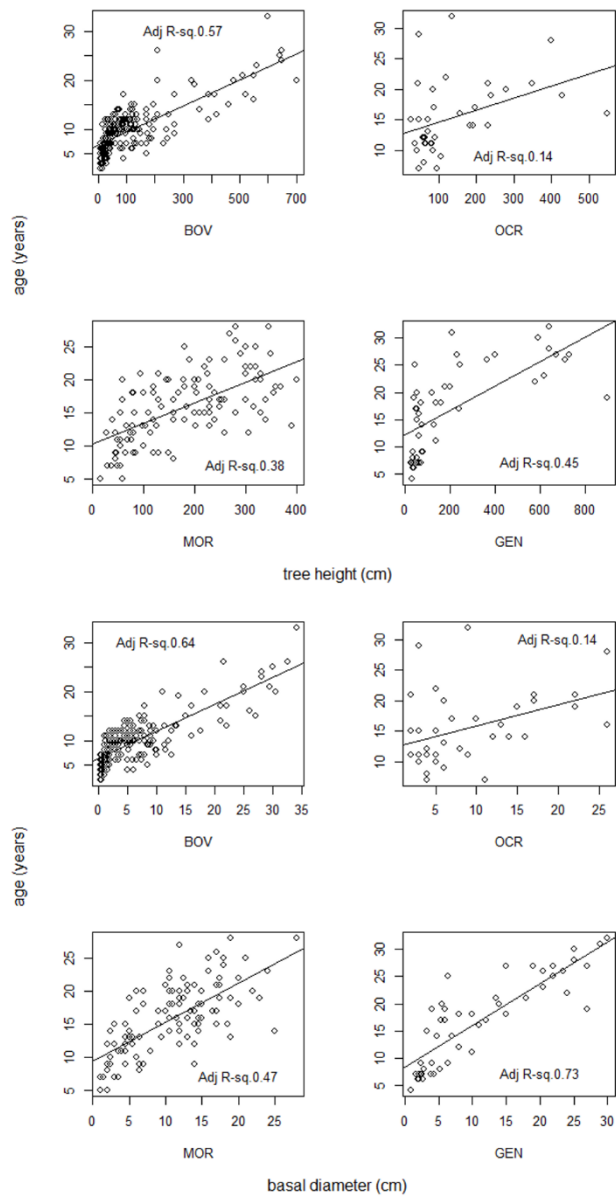


Figure A2. Adjusted R^2 values and linear regressions calculated for models of tree age as a function of basal diameter and tree height in the four black pine treeline sites.

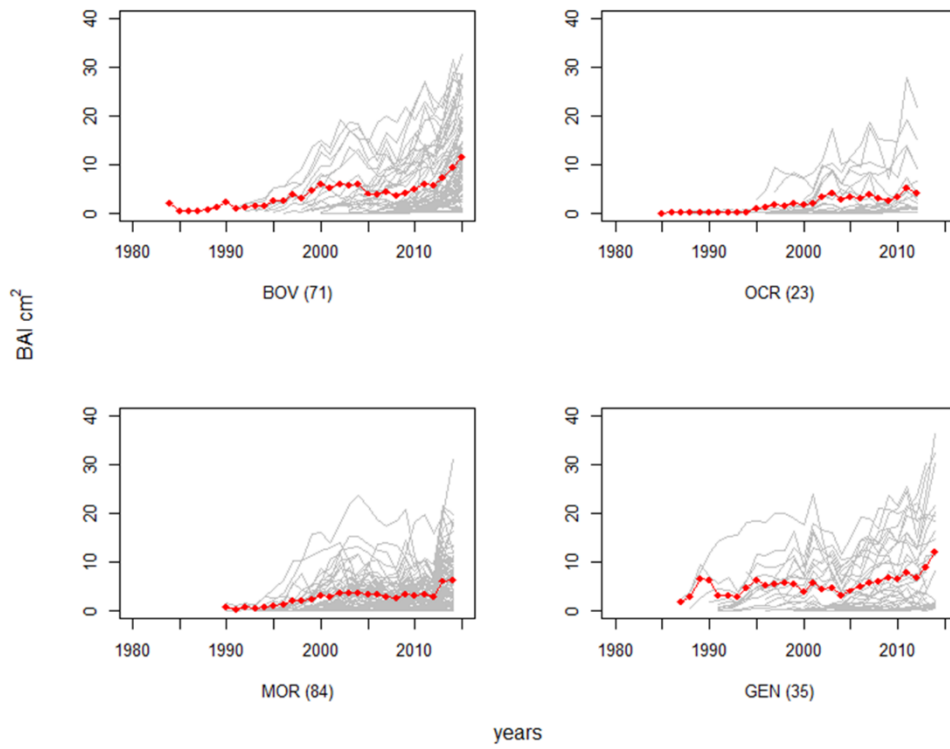


Figure A3. Radial-growth trends of black pine (*Pinus nigra*) at the four treeline sites expressed as basal area increment (BAI). Grey lines are individual series and red lines are the means of each. The numbers in brackets on the x-axis label are the number of analyzed cores at each site.

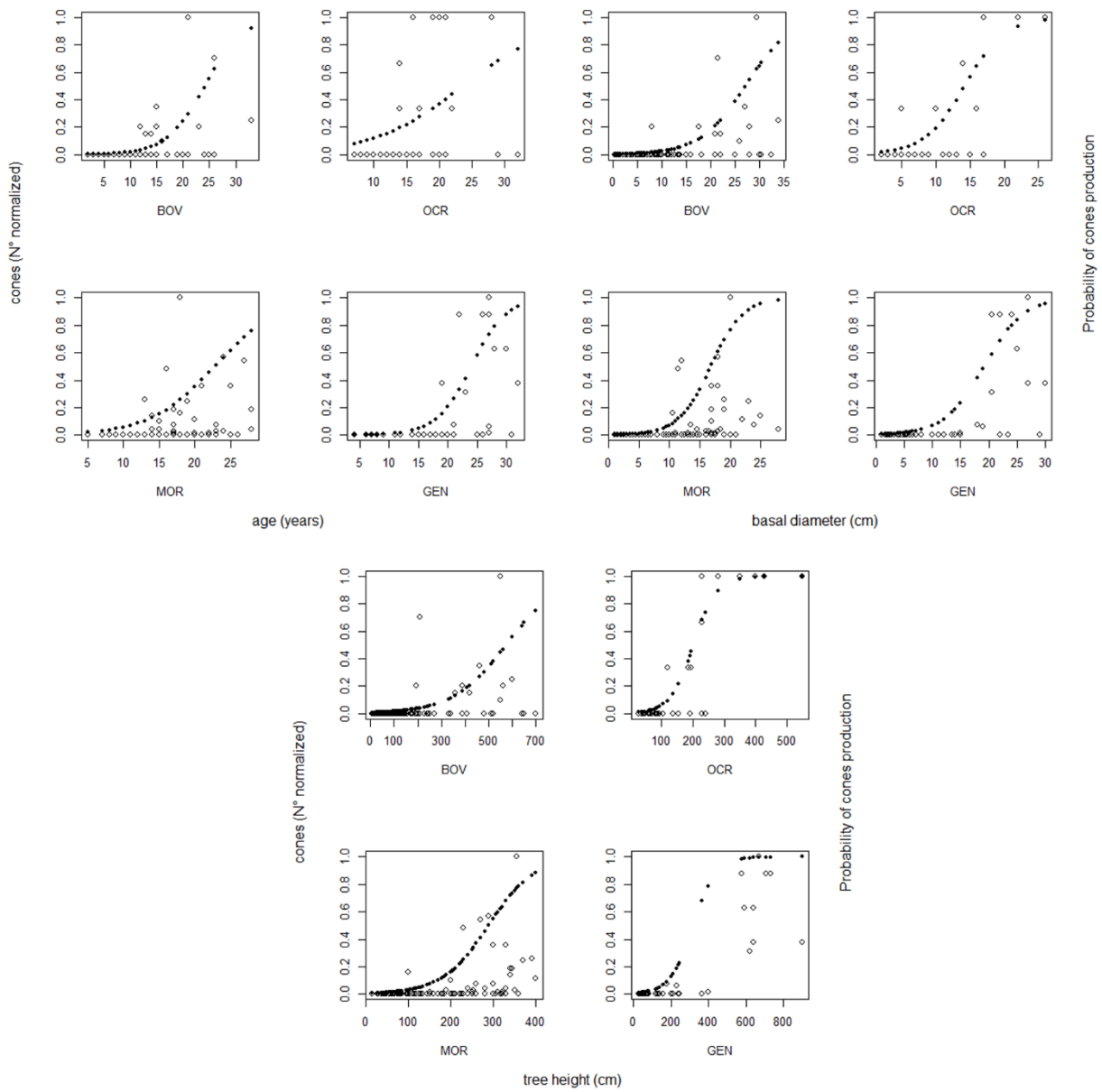


Figure A4. Generalized Linear Models (GLMs, black symbols) fitted to cone numbers (normalized values) to predict the probability of cone production in treeline black pine trees as a function of tree age, basal diameter and height.

CHAPTER 4

Remaking forests: pine recolonization in Mediterranean anthropogenic treelines

A printable version of this chapter will be prepared and submitted to an international journal

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INTRODUCTION

Treelines could be classified as climatic, edaphic/orographic and anthropogenic, depending on the dominant limiting factors shaping treeline structure and response to changing environmental conditions (Holtmeier & Broll 2005). Human-shaped treelines are a common feature in mountain landscapes across Europe, and particularly in secularly managed Mediterranean high-elevation areas. Traditional land uses (grazing, forest and forest-floor exploitation) in mountain areas became unsustainable during the 20th century and rapidly abandoned (Debussche et al., 1999). The reduction in grazing pressure at high elevations, triggered secondary succession in treeless grassland areas, and favoured the upward shift of anthropogenic treelines.

We compared several *Pinus* spp. recolonization patterns in Mediterranean anthropogenic treelines in the context of land-use and climate changes. We selected four native pine species with non-dwarf form naturally present at the treeline ecotones in southern Europe: *Pinus heldreichii*, *Pinus peuce*, *Pinus sylvestris* and *Pinus uncinata*. We concluded the field surveys on summer 2017 (see Figure 1a and Figure 1b for picture examples of the studied dynamics). Preliminary, mostly descriptive analyses are presented here and will be improved during the next weeks with some model-approaches to better describe the treeline ecotone dynamics (e.g. seed-dispersal models for all investigated species).

A more thorough characterization and understanding of the occurring encroachment processes is needed to predict pace and pattern of these upshifting human-shaped treelines. Overall, the preliminary results indicate that these treelines are responding quickly to the ongoing global change (land use and climate).

MATERIALS AND METHODS

Study sites

We sampled nine anthropogenic treelines located in the Mediterranean basin: 1 in southern Italy, 4 at the border between Albania and Montenegro (Dinaric Alps) and 4 in northern Spain (Pyrenees and Iberian mountain system). The Italian site was located in the Basilicata region (Mt. Pollino, hereafter POL site) where Bosnian pine (*Pinus heldreichii*) is at its easternmost range limits and its encroachment is widespread above the timberline *Fagus sylvatica* forests. The Balkan sites were selected for the native and widespread presence of *Pinus heldreichii* and *Pinus peuce* (respectively in Mt. Komovi and M. Prokletije). The Spanish sites correspond to the easternmost limits of *Pinus sylvestris* (Mt. Picos de Urbi3n) and *Pinus uncinata* (Mt. Pico de la Magdalena) distribution ranges (Figure 1b).

We selected the sampling sites after examining and interpreting aerial photographs and conducting field visits. Selected sites fulfilled three requirements: i) a timberline located over 1500 m; ii) mountain peaks'

elevation higher than 2000 m a.s.l. and iii) potential for and upward shift free from geomorphic constrains. Field data were collected between 2015 and 2017 within altitudinal transects of variable size, extending along the slope, from the tree located at higher elevation to the nearest closed forest border. All sampled area extension ranges from 0.07 to 1 ha (Table 1).



Figure 1a. Example of *Pinus heldreichii* (a) and *Pinus peuce* (b) encroachment in Balkans study sites (June 2016) and example of *Pinus sylvestris* (c) and *Pinus uncinata* (d) encroachment in Spanish study sites (June 2017).

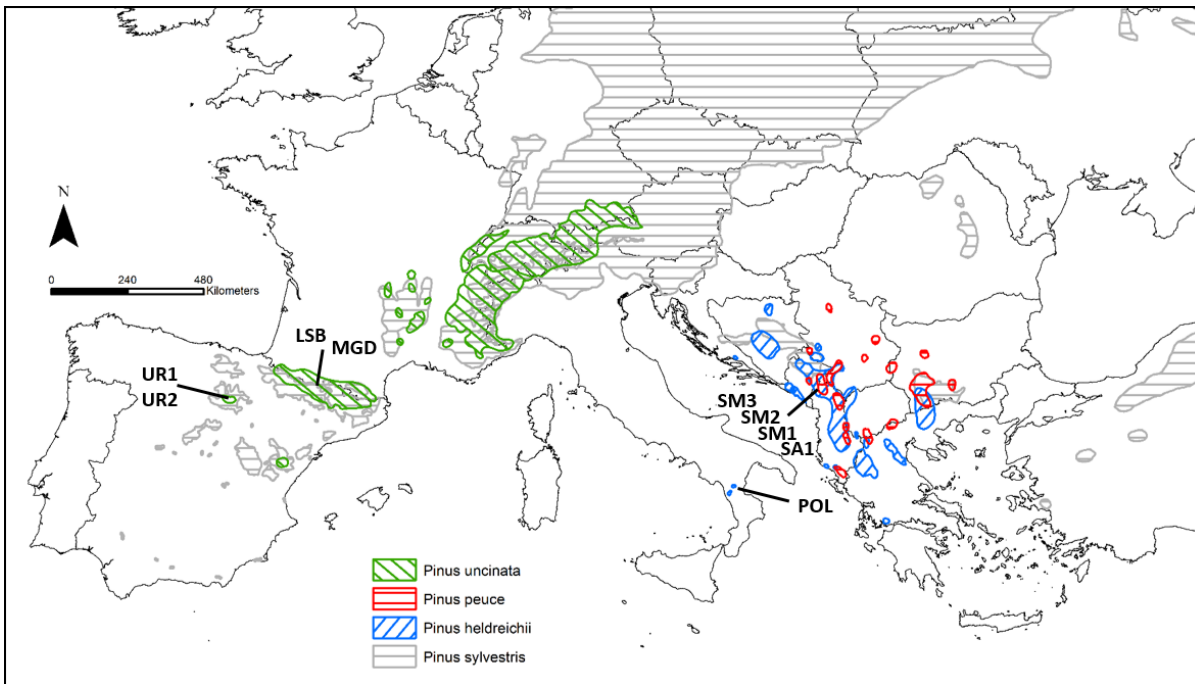


Figure 1b. Distribution map of *Pinus uncinata* (green), *Pinus heldreichii* (blue), *Pinus peuce* (red) and *Pinus sylvestris* (grey) in the Mediterranean region and the location of nine treeline study sites are overlaid. Elaboration from Chorological maps (Caudullo et al., 2017) and IUCN Red List of Threatened Species 2017.

Pinus heldreichii

Bosnian pine (*Pinus heldreichii* H. Christ. (1863) syn. *Pinus leucodermis* Ant. (1864)) is monoecious; inconspicuous female and male flowers are borne in cones on the same tree. Woody female cones mature in two years. Seed production begins at 15–20 years of age. The tree is very frost-hardy. Bosnian pine has demonstrated low susceptibility to insect attacks. The systematic and phylogenetic relationships between the Italian and Balkan populations are unclear. Some authors, based on morphological traits (height, characteristics of the bark, twig and foliage color), suggest that the populations represent two different species, *P. leucodermis* and *P. heldreichii* (Vendramin et al., 2008). Other authors consider all populations to belong to the same species or that *P. leucodermis* is a variety of *P. heldreichii*. *Pinus heldreichii* is found only in the western Balkan peninsula (Albania and Greece) at 1000–2500 m elevation, reaching the Alpine timberline (Vendramin et al., 2008). *Pinus leucodermis* (Figure 1b) occurs in the central western part of the Balkan peninsula (including Bosnia, Serbia, Montenegro and Bulgaria) and in the southern Italian Apennines (Monte Pollino), where it occupies dry, sunny sites at 900–2300 m elevation, forming mixed stands with silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) or pure stands on steep and dry rocky southern slopes (Vendramin et al., 2008).

Pinus peuce

Macedonian pine is a Tertiary relict and Balkan endemic, discovered in 1839 (Pelister, Macedonia FYR) and described in 1844 as *Pinus peuce* Griseb. It belongs to the subsection *Strobus*, but its taxonomic position is still undefined. The varieties, intermediate forms and interspecific hybrids also contribute to the confusion (Nikolic et al., 2014). It is a tree reaching up to 30-35 m in height and up to 50-60 cm in diameter. The tree height of this species diminishes strongly near the upper forest limit and may even obtain shrub sizes. The brachyblasts contain five grayish-green needles each. The cones have a two-year cycle of development. They mature in September - October of the second year and the seeds are ovate, grey-brown, from 4.7-8.9 mm long and from 3.4-6.4 mm wide (Alexandrov and Andonovski, 2011).

In the beginning, a *Pinus peuce* tree develops a well-formed central root but its lateral root system gradually develops intensively thus penetrating deep into the soil and providing a high stability. The cold mountain climate and high air humidity are the most suitable conditions for *Pinus peuce*. Though it occurs naturally from 800-900 m up to 2300-2400 m altitude, its optimum is most often from 1600-1900 m altitude, growing mainly on silicate rock types (Alexandrov and Andonovski, 2011). In Albania and Serbia, it is also found on serpentine, and in the Greek region of Macedonia, it forms pure stands on gentle mountain slopes, interspersed with grassy glades and meadows. In most areas where it occurs, it is mixed with *Picea abies* and/or *Abies alba* / *A. borisii-regis*, with which it can compete due to relatively high shade tolerance (Farjon 2017). It makes monodominant or mixed coenoses mainly near the timberline in the high mountains of Bulgaria. The Macedonian pine is rather tolerant to the abiotic factors of its environment. *Pinus peuce* is adapted to grow on areas covered by large rock pieces it can develop on soils with different depth and humidity. It is possible that the species used to be more widely distributed in the past, even dominating the coenoses, but as a result of anthropogenic activities they have been destroyed (Roussakova 2015). The natural range of this species consists of two parts separated by the valley of the Vardar River (Figure 1b). The eastern part is in southwestern Bulgaria and the western part is in Macedonia FYR, southwestern Serbia, southeastern Montenegro, eastern Albania and northwestern Greece (Alexandrov and Andonovski, 2011). Extensive exploitation in the past has undoubtedly had an impact on its abundance but no details of a possible reduction are known for much of its range, although Roussakova (2015) notes that declines from fire and exploitation continues in Bulgaria. Insect attack and fungal disease seem to be minor threats with the tree more resistant than some other pines (Alexandrov and Andonovski, 2011).

Pinus sylvestris

Scots pine (*Pinus sylvestris* L.) is widespread across Eurasia (Figure 1b), ranging in latitude from 37°N to 70°20' N; in southern Europe and Asia Minor, isolated occurrences are confined to the montane zone (up to 2200 m in altitude in the Balkans and Spain, and 2700 m in the Caucasus). Across its enormous

range, it grows naturally in a variety of habitats, the common denominator of which is deficiency of nutrients in the soil (Gardner 2013). Scots pine is a pioneer species that readily regenerates after major natural or human disturbances, if weed competition and grazing pressure are low (Mátyás et al., 2004). Natural stands are often pure and even-aged. The species grows predominantly on poorer, sandy soils, rocky outcrops, peat bogs or close to the forest limit. The species is wind-pollinated and has both male and female flowers on the same tree. Flowering is frequent; female flowering starts at the age of 15 years on solitary trees (on grafts, as early as 6–8 years) or 25–30 years in closed stands. Abundant male flowering appears some years later. Mast years are relatively frequent but at the boreal forest limit seed maturation is impeded by the short growing season; mast years may occur as seldom as once or twice in 100 years (Mátyás et al., 2004).

Pinus uncinata

Mountain pine (*Pinus uncinata*) is a small conifer closely related to the mugo pine (*Pinus mugo*). The tree naturally appears in scattered populations (Figure 1b) across the mountains of Western Europe: Pyrenees (northeastern Spain, Andorra, and southwestern France), France (Auvergne Mts. (possibly introduced), Alps, Jura, Vosges), Germany (Böhmerwald and Erzgebirge), Switzerland, Austria, and northern Italy (Farjon and Filer 2013). In the Iberian Peninsula, its main distribution area comprises subalpine forests in the Central and Eastern Pyrenees (Camarero et al., 2005). The tree now naturally grows outside its native range, because of reforestation programs in northern Europe and the Mediterranean. The extent of occurrence is in excess of the thresholds for any threatened category however, the area of occupancy is unknown (Farjon 2017). *Pinus uncinata* occurs naturally at altitudes of between 600 and 1,600 m asl. In the Alps and Pyrenees, it grows on moist slopes up to the tree line, on moist soils in attitudes from 200–2400 m. It sometimes grows with *Picea abies* or *Pinus sylvestris*; in the Pyrenees, the spruce is naturally absent (Farjon 2017). It is tolerant to cold temperatures and is often found in frost hollows and peat bog habitats. *P. uncinata* is a shade-intolerant species that colonizes all kinds of soils (Ceballos and Ruiz de la Torre, 1979). Its reproduction is mainly sexual and its small and its small winged seeds are primarily dispersed by wind in late winter, and seedling emergence occurs in April–May. Two features make this species a good invader (Richardson & Bond, 1991): a short pre-reproductive period (15–20 years) and frequent large crops every 2–4 years (Camarero and Gutierrez, 2007). Seedlings are quite frost-resistant, even under a shallow snow layer (Frey, 1983).

Site	Species	Latitude (°N)	Longitude (-W, +E)	Country	Timberline elevation (m a.s.l.)	Slope aspect	Mean slope angle (%)	Transect width x length (m)	Transect area (ha)
POL	<i>Pinus heldreichii</i>	39.897	16.206	Italy	2045	NW	38	40 x 240	0.96
SM3	<i>Pinus heldreichii</i>	42.690	19.675	Montenegro	1960	SE	45	20 x 500	1.00
SA1	<i>Pinus peuce</i>	42.505	20.006	Albania	1990	NE	30	10 x 40	0.04
SM1	<i>Pinus peuce</i>	42.508	19.908	Montenegro	2000	NE	43	10 x 170	0.17
SM2	<i>Pinus peuce</i>	42.649	19.849	Montenegro	2050	N	10	10 x 70	0.07
UR1	<i>Pinus sylvestris</i>	42.002	-2.873	Spain	2000	SW	36	20 x 360	0.72
UR2	<i>Pinus sylvestris</i>	42.001	-2.871	Spain	2000	SW	36	20 x 325	0.65
LSB	<i>Pinus uncinata</i>	42.718	-0.570	Spain	1935	W	34	20 x 185	0.37
MGD	<i>Pinus uncinata</i>	42.730	-0.571	Spain	1975	SW	50	20 x 300	0.60

Table 1. Main features of the study sites. Timberline is the upper limit of a closed canopy forest.

Field sampling

We mapped 964 pine trees growing above the timberline with a Trimble Pro 6H GPS antenna (Trimble Inc., Sunnyvale, USA). A post-processing differential correction through Pathfinder Office 4.2 software was performed with a 0.5-m estimated accuracy. We classified trees as seedlings (total height < 0.5 m) and saplings (height \geq 0.5 m), respectively and we measured basal stem diameter, total height and counted the number of cones for each pine. To classify the regeneration niche of seedlings and saplings, we estimated the microhabitat cover share (bare rock, rocky debris, grass and shrub) within circular plots of 1 m diameter around each pine stem. We compared these ground-cover proportions for each species, to detect significant differences, considering that saplings can have a higher influence on the ground vegetation than seedlings, during their growing process.

The age of all trees was determined after the extraction of one basal increment core (whenever possible) or counting the number of annual internodes (terminal bud scars) along the main stem (Camarero and Gutiérrez 1999).

Laboratory analyses

All the collected material and data were processed to determine structural features of each species (diameter, tree height and estimated age). We computed linear regressions for all pine species for

modelling tree height as a function of basal diameter and tree age as a function of basal diameter and tree height. We used χ^2 tests to compare seedlings and saplings microsites at each site. We used Generalized Linear Models (GLM) to predict the probability of cone production as a function of several relevant variables (stem diameter, tree height and age). The goodness of fit of the GLM models was assessed using McFadden's pseudo- R^2 values (Venables and Ripley 2002). The 190 collected basal cores were mounted and glued on wooden supports, thoroughly polished with progressively finer sandpaper until the tree rings were clearly visible. We used the semi-automatic LINTAB system and WinTSAP (Rinntech, Heidelberg, Germany) to measure tree-ring width at 0.01 mm precision. Most of the ring-width series were < 30 year long, and could not be subjected to the standard dendroecological statistical analysis so they were only visually crossdated. Tree-ring widths were converted into basal area increments (BAI) since this variable reflects growth changes more accurately (Biondi and Qeadan, 2008).

We divided each transects (excluding SM2) along the main altitudinal gradient: 0-33%, 34-66% and 67-100% of the entire length, obtaining three subplots with relative mean elevation assigned (low, medium, and high). We conducted a Principal Component Analysis (PCA), using the statistical package PcOrd v5 (McCune and Mefford, 1999), on the 24 subplots (3 subplots x 2 transects x 4 species) to explore the correlation structure of their mean variables: mean diameter (D), mean tree height (H), abundance (N/ha), land-cover (GRASS-DEBRIS-ROCKS-SHRUB), mean AGE and proportion of individual with cones (REPr). The statistical significance of the ordination analysis was tested using a Monte Carlo permutation method based on 10000 runs with randomized data. Mean SLOPE and RELATIVE ELEVATION were overlaid on the graph to show the location of the subplots based on these features.

Spatial analyses

Univariate and bivariate point pattern analysis (PPA) techniques were applied using trees mapped data (Moer, 1993) to characterize both the tree spatial patterns within the altitudinal transects and the association of the patterns for the two tree types (seedlings vs. saplings) and for the reproductive potential (young regeneration vs. physiologically mature individuals bearing seed cones) at different spatial scales. For the first bivariate analysis, the tree height threshold was 0.5 m. For the second bivariate analysis, reproductive trees had to bear at least one cone, and the regeneration trees had an estimated age \leq the minimum age of trees with cones. We used pair-correlation functions (g) (Stoyan and Stoyan, 1994), a second order statistic closely related to Ripley's K function (Ripley, 1977) that provides information at multiple scales, comparing the distribution of distances of all pairs of points, in our case the tree-to-tree distances, of the patterns. The pair-correlation function is non-cumulative and uses only points separated by a certain distance r . In this way, it may allow specific scales to be identified where significant point-point interactions occur (Wiegand et al., 2004).

The univariate patterns were contrasted with the Complete Spatial Randomness (CSR), i.e. the simplest and most widely used null model in this kind of analysis: it considers that any point of the pattern has an equal probability of occurring at any location within the plot (Wiegand and Moloney, 2004). For the bivariate patterns within seedlings and saplings, we adopted the same null model. For the bivariate patterns within young trees and mature trees we applied the prior conditions: since the mature (and adult) tree were already present and did not change their position during the establishment of young regeneration this null model relies on finding potential regeneration throughout the whole plot while keeping the locations of the mature/adult trees fixed (Wiegand and Moloney, 2004). The 95% confidence intervals for both univariate and bivariate analyses were computed from 999 Monte Carlo simulations (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004). The univariate spatial pattern was defined as clumped, random or regular (hyperdispersed) if the $g(r)$ values were greater than, equal to or lower than the confidence envelopes, respectively. In the bivariate analyses, values of $g_{12}(r)$ greater than, equal to or lower than the confidence envelopes reveal positive association (attraction), spatial independence and significant negative association (repulsion), respectively, between the two analyzed classes. Attraction and repulsion are defined as a tendency for trees of the two groups to be respectively closer or farther apart than would occur if they were independently distributed (Peterson and Squiers, 1995).

RESULTS

Size and age of treeline trees

Timberline elevation ranged between 1935-1975 m of Spanish *Pinus uncinata* and 2000-2050 m a.s.l. by *Pinus heldreichii* and *Pinus peuce* in Albania-Montenegro, respectively (Table 1). Pine colonization across the treeline ecotones was scattered since tree density showed vary variable values, from 87 (*Pinus heldreichii*) to 372 (*Pinus peuce*) trees ha⁻¹ (Table 2).

On average, the recruited pines correspond to 57% and 43% of seedlings and saplings, respectively. *Pinus peuce* and *Pinus sylvestris* have the maximum share of seedlings (70%), whereas *Pinus heldreichii* that of saplings (66%), while *Pinus uncinata* has a balanced proportion (Table 2). The average tree size was small, with lower mean basal diameters for *P. peuce* (2 cm) and higher mean values for *P. heldreichii* (7 cm). The mean height runs from 54 cm (*P. peuce*) to 106 cm (*P. heldreichii*) and the mean age is from 9 years (*P. peuce*) to 20 years of *Pinus heldreichii* (Table 2).

Species	No. transects	No. trees	Trees density (N° ha ⁻¹)	No. sampled cores	Trees with cones (%)	Seedlings/ saplings (%)	Mean basal diameter ± SD (cm)	Mean height ± SD (cm)	Mean age ± SD (years)
<i>Pinus heldreichii</i>	2	170	87	73	6	34/66	7 ± 5	106 ± 81	20 ± 10
<i>Pinus peuce</i>	3	450	372	29	2	71/29	2 ± 2	54 ± 80	9 ± 7
<i>Pinus sylvestris</i>	2	207	151	52	7	70/30	4 ± 5	67 ± 86	10 ± 6
<i>Pinus uncinata</i>	2	137	141	36	15	55/45	5 ± 7	95 ± 132	10 ± 8

Table 2. Main structural variables of the sampled trees that had encroached the nine study sites. Seedlings are trees with height < 0.5 m; saplings are trees with height ≥ 0.5 m.

Regeneration niche

There are relevant differences between species on microsite-cover: there is a low proportion of grass cover in PS sites, with more than 50% of trees found in shrubs and 10% of stems on rocky microsites. PH and PP sites are dominated by grassland, with 10-20% of trees on debris. PU sites have 85% of trees occurring on grass and debris microsites (Figure 2a).

Dividing the dataset by tree height, we detected significant differences in ground cover types of seedlings (height < 0.5 m) and saplings (height ≥ 0.5 m) for all species ($\chi^2 = 11.05-66.96$, $p < 0.05$ in all cases). Both *P. heldreichii* seedlings and saplings prefer grass cover (> 80%), with minor differences for shrub (8% saplings, 4% seedlings), rocks (4% saplings, 2% seedlings) and more relevant on debris cover (3% saplings, 16% seedlings). Even *P. peuce* individuals grow preferably on grass (70-80%), whereas no

seedlings are found on shrub-cover (Figure 2b). The most significant difference is the double presence of seedlings on debris microsites (28% vs. 12% of saplings). Both seedlings (50%) and saplings (54%) of *P. sylvestris* regeneration occur mainly on microsites with shrubs. The others are on grass cover (44% saplings), debris and rocky microsites (31 and 15% seedlings). Most seedlings of *P. uncinata* are on grass (62%) and debris (36%) cover. More than half of PU saplings are on grass (54%) whereas the other ones on shrub (16%), debris (15%) and rocks (13%).

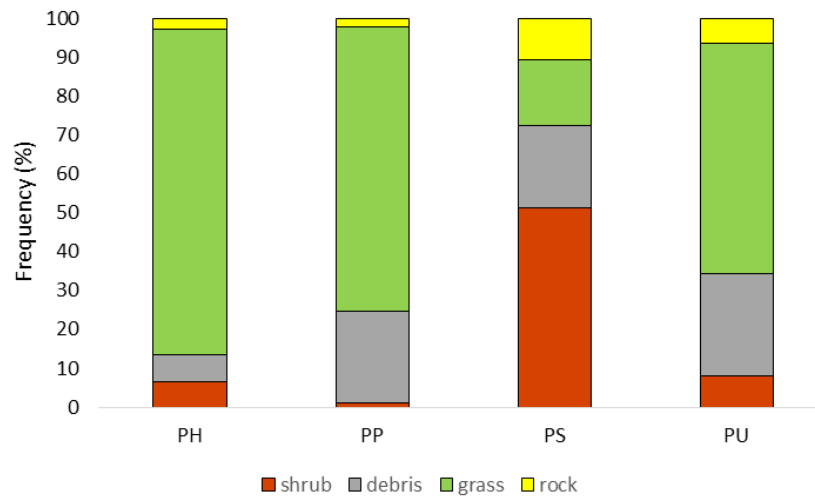


Figure 2a. Frequency of pine recruits sampled for each species and classified as a function of microsite cover types (shrub, debris, grass and rock).

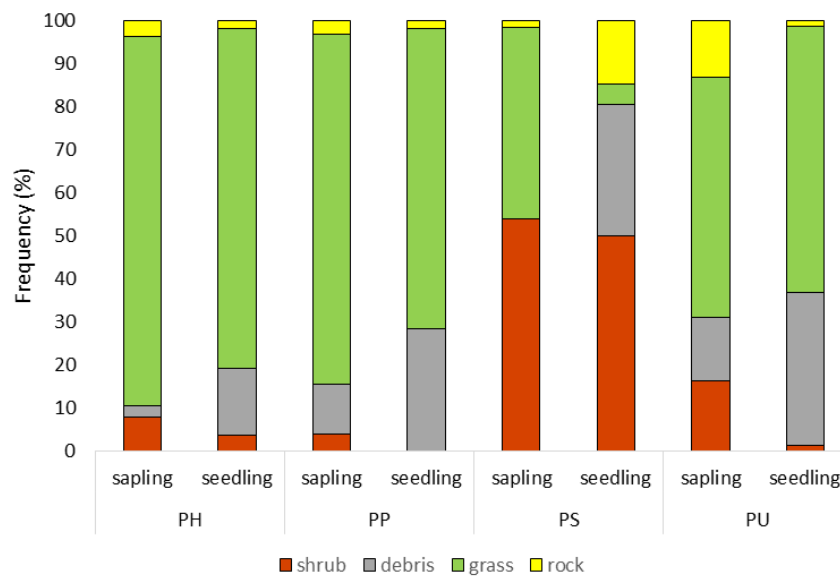


Figure 2b. Frequency of seedling and sapling of each pine species classified as a function of their microsite cover types (shrub, debris, grass and rock).

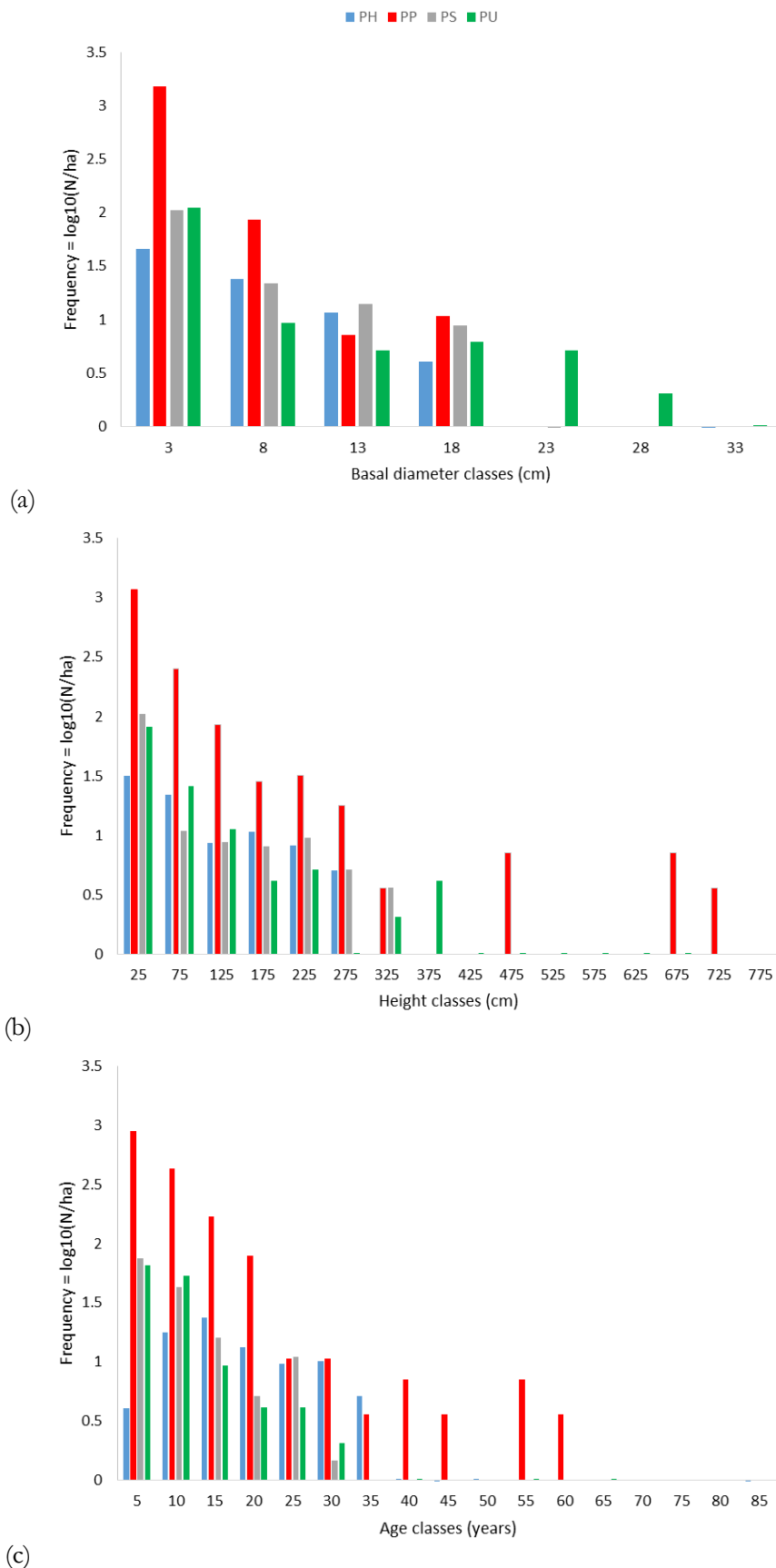


Figure 3. Frequency distribution, expressed as $\log_{10}(N/ha)$, of basal diameter (a), tree height (b) and estimated age (c) of the treeline pines sampled at each of the nine study sites: *Pinus heldreichii* (PH-blue), *Pinus peuce* (PP-orange), *Pinus sylvestris* (PS-grey) and *Pinus uncinata* (PU-green). On the x-axis are shown the central values of each classes. The bar plots of the first PP classes are cut, the corresponding values are reported above the bars.

The frequency distributions of trees prevail on first diameter classes of all species, especially for PP with more than 1500 stems ha⁻¹ in the first class (Figure 3a). Tree height and age distributions show similar patterns, with high frequency of small and young individuals (Figure 3b and 3c). PU features the maximum diameter and age of, while PP the maximum height. The tree height-basal diameter linear regressions have high values of Adjusted R², ranging from 0.70 (PP) to 0.91 (PU) (Figure S1). Lower significant values are expressed for tree age with diameter and tree height as predictors (Figure S2).

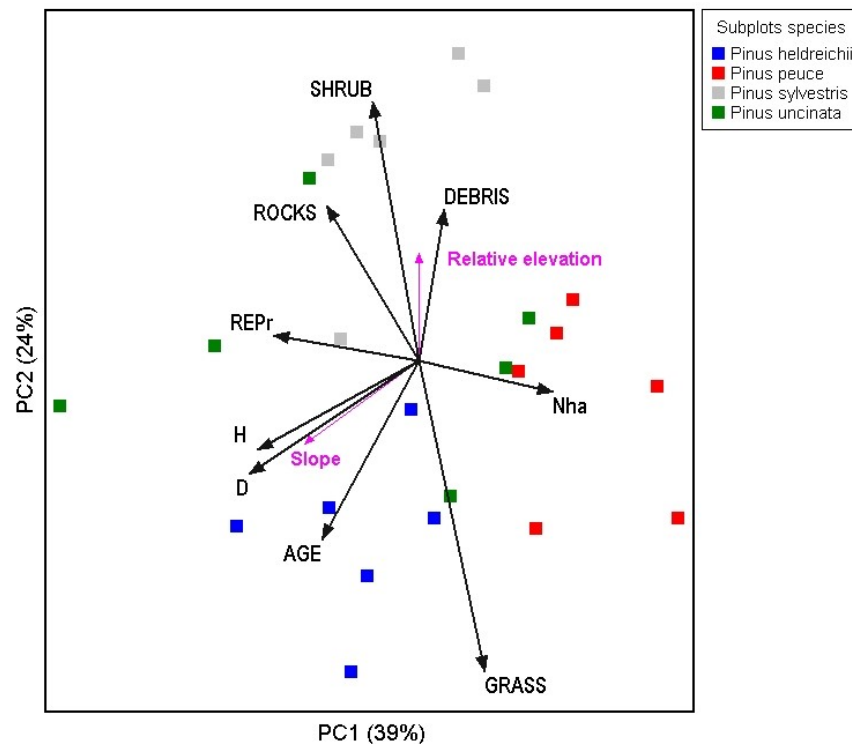


Figure 4. Biplot from Principal Components Analysis of 27 sub-plots sampled within all transects. Black linear vectors are correlations ($p < 0.01$) of ten variables with PCA axes: D: mean basal diameter; H: mean tree height; AGE: mean estimated age; N/ha: number of trees per hectare; GRASS: mean percent value of grass cover; DEBRIS: mean percent value of debris cover; SHRUB: mean percent value of shrub cover; ROCKS: mean percent value of rocky cover; REPr: proportion of individual with cones. Pink linear vectors are relative elevation and mean slope of the subplots.

The PCA results on subplots division (Figure 4) showed the general characteristics of transects and their differentiation along the relative elevation per each species subplots. *Pinus heldreichii*, *P. peuce* and *P. sylvestris* seem to be clustered by age, density and shrub cover; while *Pinus uncinata* plots were scattered mainly by density and reproductive features.

Treeline ecotone structure and spatial analysis

In general, tree diameter does not decrease with altitude (Supporting Materials, Figure S3) and neither does tree height (Figure S4) and age (Figure S5). Positive significant correlations between elevation, diameter and tree height were observed only at SA1 ($r = 0.30$, $p \leq 0.01$), while negative significant ones

were recorded for diameter-elevation ($r = -0.30$, $p \leq 0.05$) and for height-elevation ($r = -0.35$, $p \leq 0.01$) relationships only at MGD. No age and elevation significant correlations were observed for all sites.

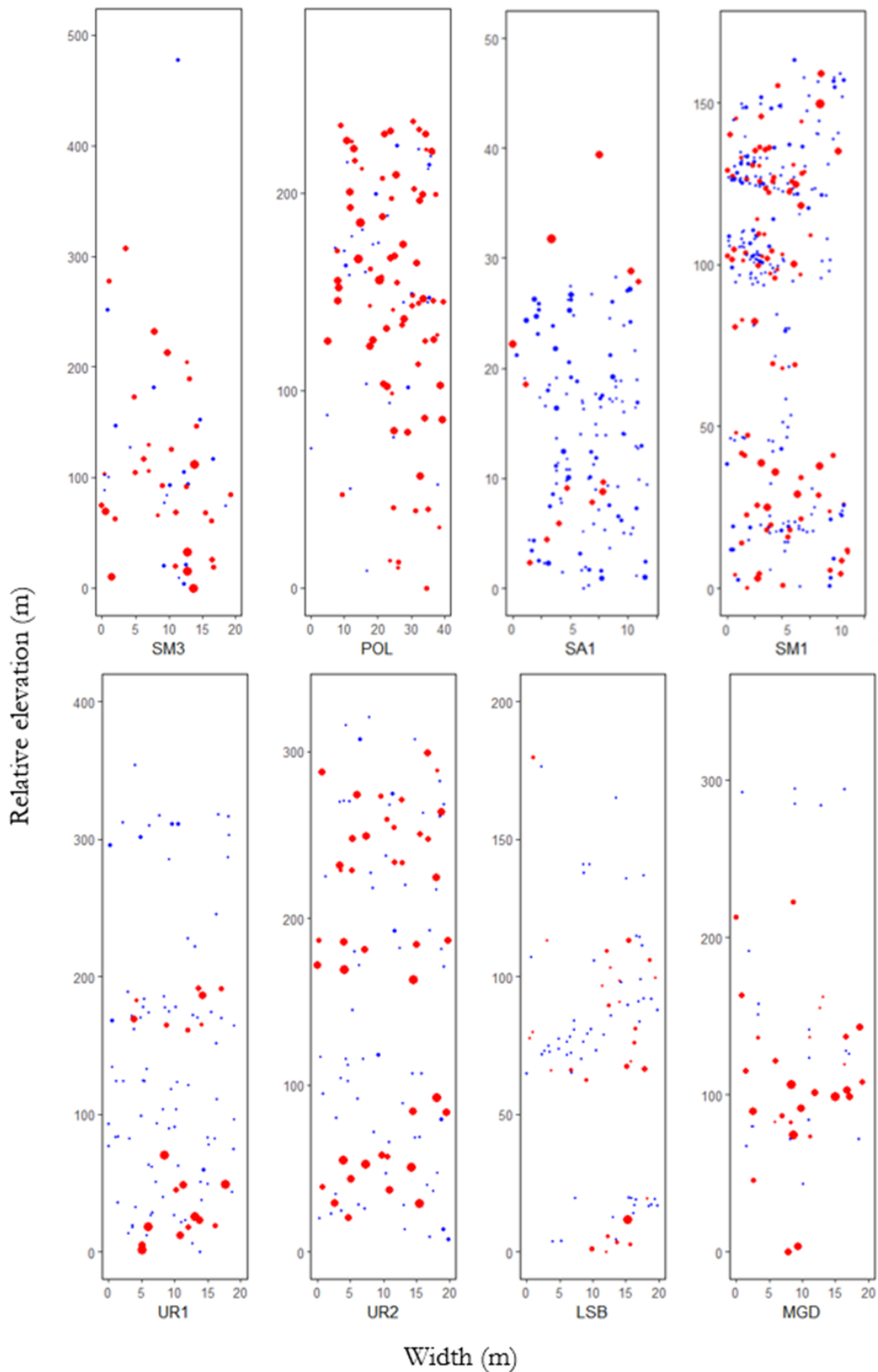


Figure 5. Mapped point patterns of all pine individuals at eight treeline ecotones (see Tables 1 and 2 for site characteristics). Blue dots are seedlings (tree height < 0.5 m) and red dots are saplings (height ≥ 0.5 m). The dot scale size is proportional to the tree height. The tree positions are reported as relative coordinates (meters).

Generally, the encroachment pattern of pines across the treeline transects was not spatially structured in cohorts (Figure 5). There are spots with higher tree density (e.g. SM1, UR1, UR2, and LSB). Seedlings (blue dots) and saplings (red dots) do not exhibit spatial segregation patterns for tree height. In some cases, many saplings are located downslope (e.g. UR1, SM3, MGD), whereas in others they are upslope (e.g. POL), but generally all the sizes are differently widespread in the study areas.

The spatial pattern of *Pinus* spp. recruitments (univariate PPA under CSR null model) showed a high significant (GoF: $p \leq 0.01$) tendency towards clustered distribution between 1 and 15 m for POL and LSB sites. The univariate analysis displayed a significant (GoF: $p \leq 0.05$) clustered distribution for SM3 (3-5 and 7-20 m), SA1 (1-10 m) and UR1 (2-15 m). SA1 shown also a repulsion pattern between 19 and 20 m. None of the other univariate tests is statistically significant (Table 3). Considering the bivariate analyses (seedlings vs. saplings and mature vs. young trees) under CSR null model, there are no significant values of clusterization/segregation.

Species	Site	Scale																				GoF	
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	p-value
PH	POL	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+					0.001
	SM3		+		+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	0.026
PP	SA1	+	+	+	+	+	+	+	+	+	+										-	-	0.015
	SM1	+	+	+	+	+	+	+	+	+		-	-	-	-	-							0.865
	SM2																						0.296
PS	UR1			+	+	+	+	+	+	+	+	+	+	+	+	+							0.023
	UR2																						0.548
PU	LSB	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+							0.001
	MGD						+	+	+	+	+	+	+	+						+	+	+	+

Table 3. Results of the univariate Point Pattern Analysis applied with Complete Spatial Randomness as Null Model and tested with GoF technique. Bold p-values are significant with $\alpha=0.05$.

Growth trends

Mean basal-area increments (BAI) for the period 1990-2015 showed different recent growth rates: 1.94 (PH), 2.26 (PS), 5.44 (PP) and 2.26 $\text{cm}^2 \text{yr}^{-1}$ (Figure S6). In the last 20 years, narrow rings were formed at all sites in 2007 in response to the warm and dry summer. *Pinus heldreichii* and *P. uncinata* formed narrow rings also in 2012, while *P. sylvestris* and *P. uncinata* in 2013.

The comparison between mean values about the all tree ring series, shown as Tree Ring Width (mm/year) and longitudinal growth rate (dm/year) had the same pattern of growth (Table 5), with *P. uncinata* with the best growth rate and *P. heldreichii* with lowest values. Looking at the Basal Area Increment (cm^2/year), the variability of species responses increases, with *Pinus peuce* and *P. uncinata* that had the highest distribution values. *Pinus sylvestris* seems to have the highest mean value of BAI.

Production of cones

The percentages of cones bearing trees are variable, ranging from 2% of *Pinus peuce* to 15% of *Pinus uncinata* (Table 2). The GLMs of cone production (Table S1 and Figure S7) showed higher McFadden's pseudo- R^2 values with height ($R^2 = 0.27-0.59$) or basal diameter ($R^2 = 0.19-0.62$) as predictors rather than using age ($R^2 = 0.04-0.58$). All the species showed common tree size and different age characteristics when they reached a 50% probability of producing cones: ca. 2-3 m of tree height, ca. 10-20 cm of basal diameter and ca. 15-80 years in age (Table 4).

Species	Sites	Height with 0.5 probability of cones production (cm)	Mean longitudinal growth rate \pm SD (cm/year)	Mean tree ring width \pm SD (mm/year)	Mean BAI \pm SD (cm ² /year)
PH	POL-SM3	300	7.1 \pm 3.8	1.5 \pm 0.7	1.8 \pm 1.7
PP	SA1-SM1-SM2	300	9.0 \pm 6.9	1.9 \pm 1.2	4.4 \pm 5.6
PS	UR1-UR2	250	11.4 \pm 5.6	2.3 \pm 1.0	2.6 \pm 2.0
PU	LSB-MGD	200	15.3 \pm 7.6	2.5 \pm 1.4	4.6 \pm 5.7

Table 5. Tree height for starting cones production, mean longitudinal growth rate and mean tree ring width of pines species sampled.

CONCLUSION

This research was presented as preliminary draft. Our challenge is to define conceptual models to forecast treelines expansion based on their spatio-temporal patterns and processes (e.g. type of regeneration niches, size-age structures, spatial distribution, individual tree growth and cone production); and to assess the occurrence of similar dynamic processes in Mediterranean human-shaped treelines hosting native pine species.

SUPPORTING MATERIALS

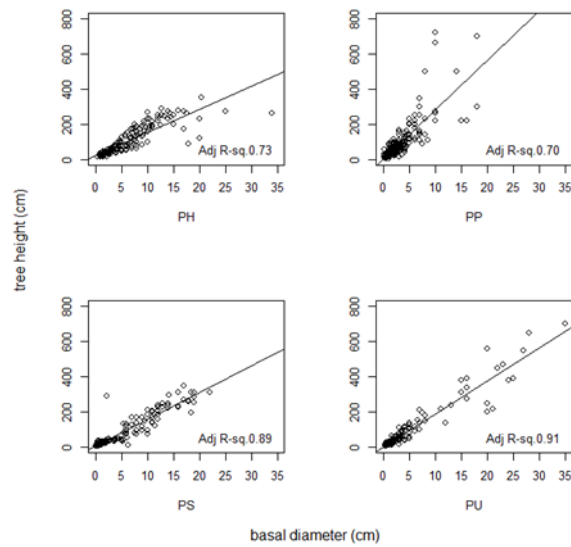


Figure S1. Adjusted R^2 values and linear regressions calculated for models of tree height as a function of basal diameter in the four pine species.

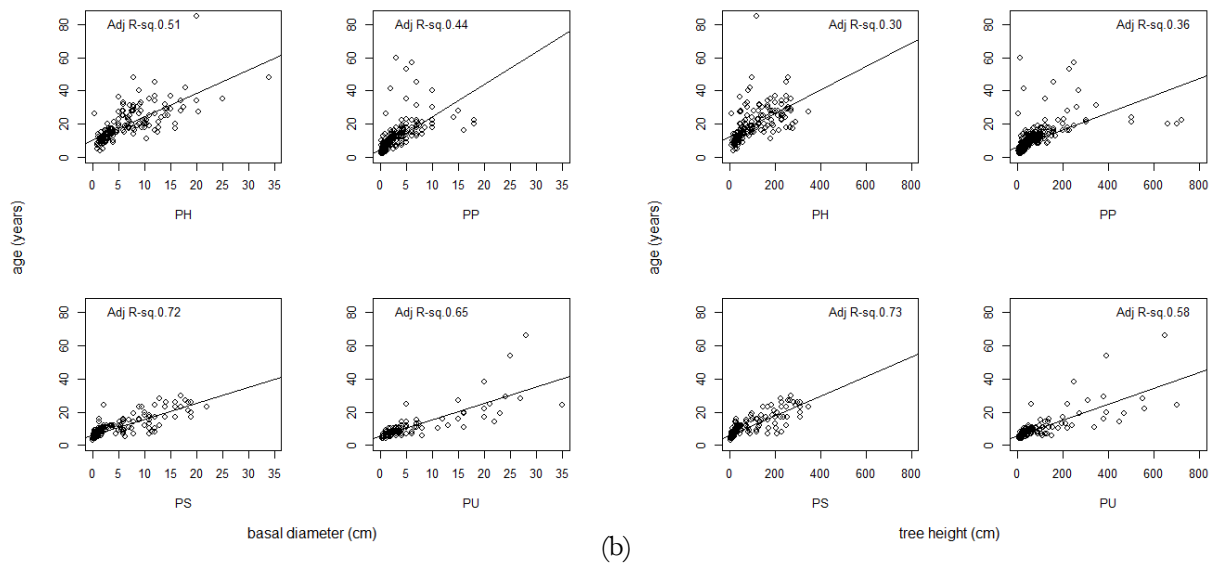


Figure S2. Adjusted R^2 values and linear regressions calculated for models of tree age as a function of basal diameter (a) and tree height (b) in the four pine species.

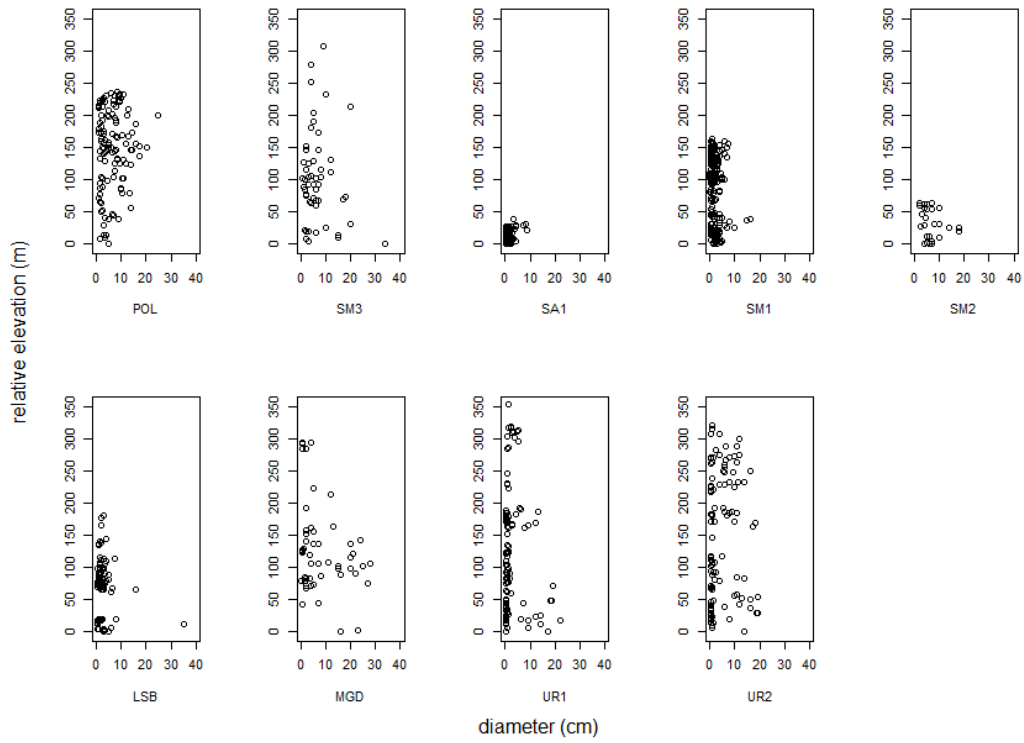


Figure S3. Relationship between diameter (cm) and relative elevation (m) for each study sites.

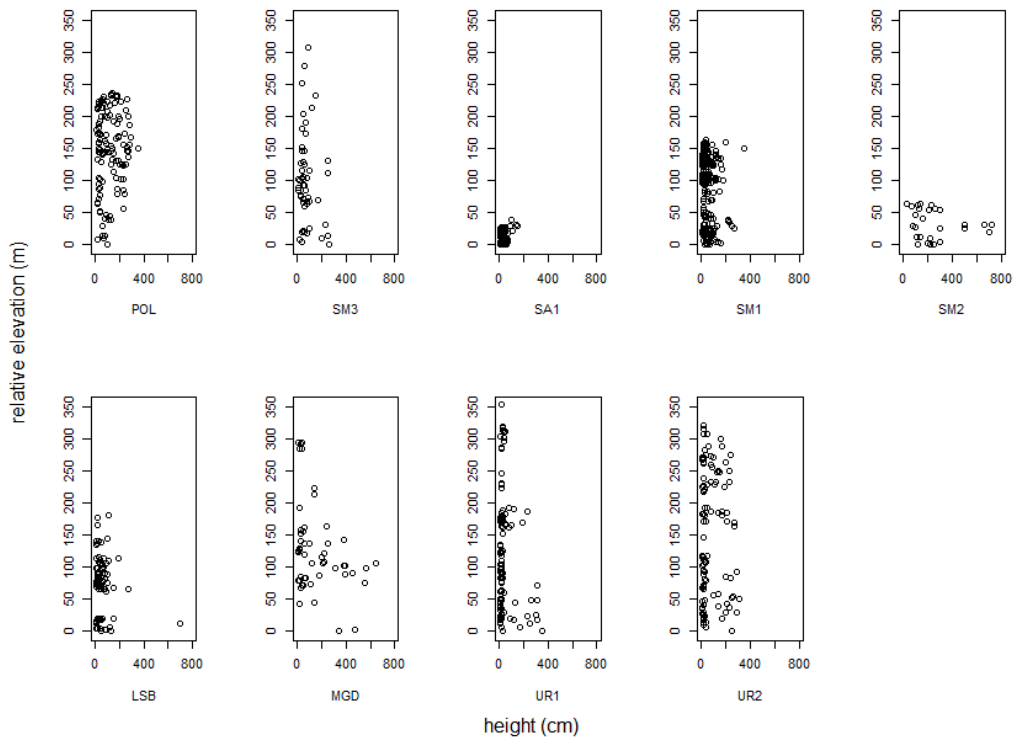


Figure S4. Relationship between tree height (cm) and relative elevation (m) for each study sites.

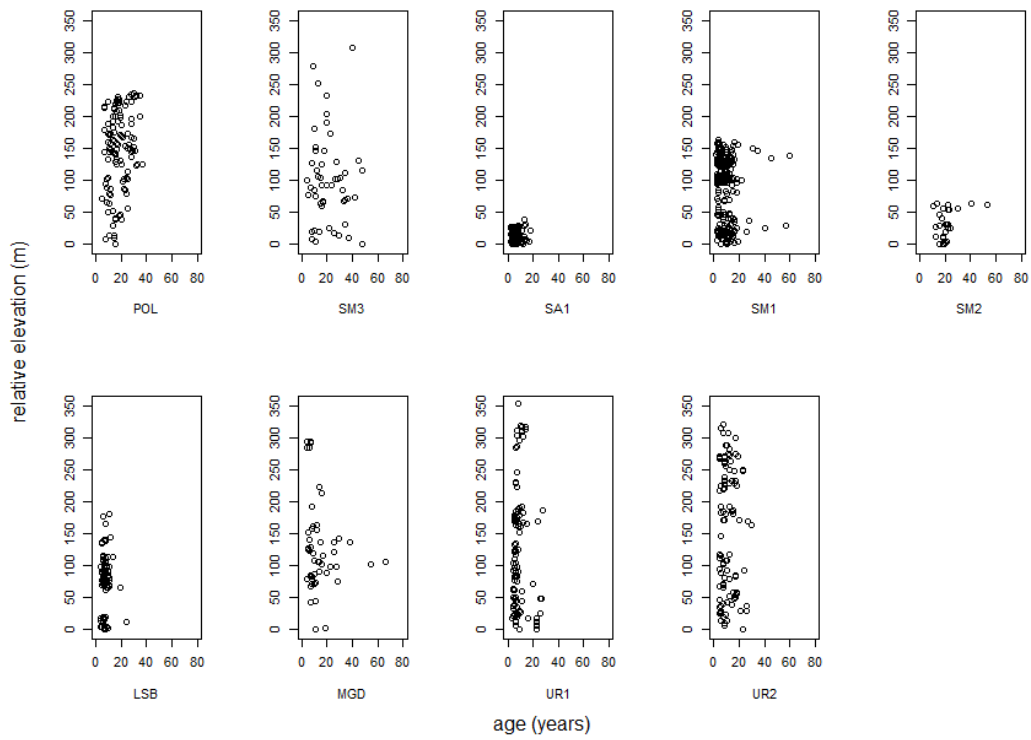


Figure S5. Relationship between estimated age (years) and relative elevation (m) for each study sites.

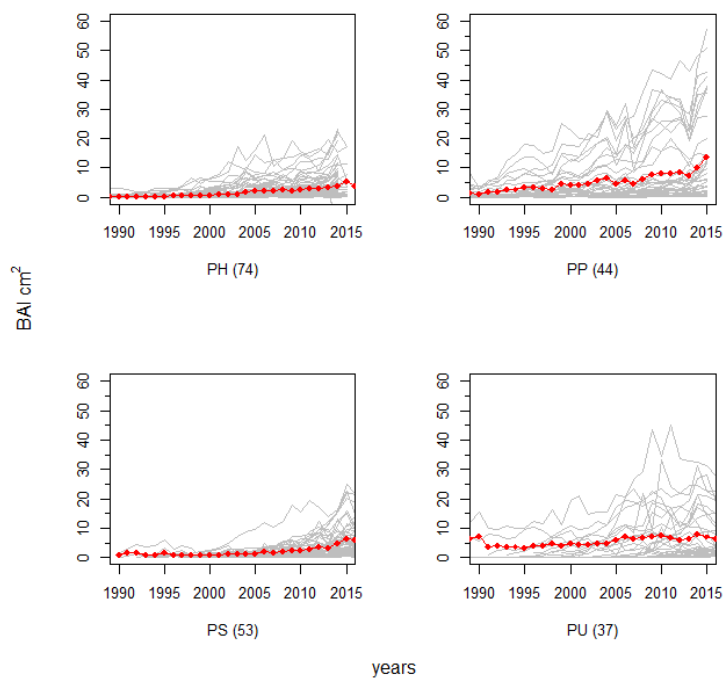


Figure S6. Radial-growth trends of all *Pinus* species at the treeline sites expressed as basal area increment (BAI). Only the portion of the recent common period (1990-2015) is plotted. Grey lines are individual series and red lines are the means of each. The numbers in brackets on the x-axis label are the number of analyzed cores for each species.

Species	Degrees of freedom	McFadden's pseudo-R ²		
		Basal diameter	Height	Age
<i>Pinus heldreichii</i>	168	0.19	0.27	0.04
<i>Pinus peuce</i>	448	0.49	0.59	0.16
<i>Pinus sylvestris</i>	205	0.43	0.51	0.29
<i>Pinus uncinata</i>	134	0.62	0.56	0.58

Table S1. Results of the Generalized Linear Models (GLMs) applied for the prediction of cone production by all pine species as a function of tree basal diameter, height and age. McFadden's pseudo-R² are reported for comparison between models.

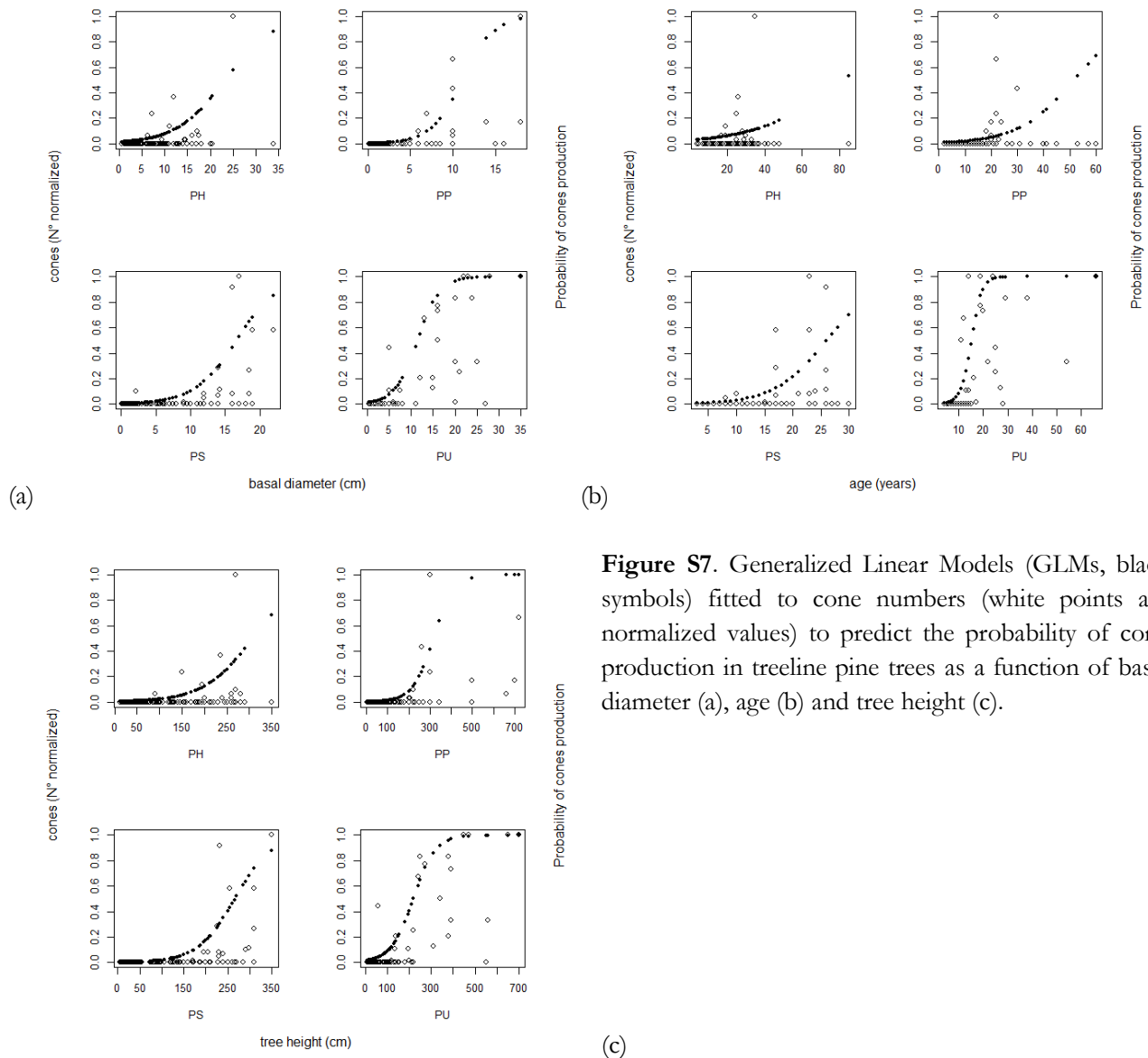


Figure S7. Generalized Linear Models (GLMs, black symbols) fitted to cone numbers (white points are normalized values) to predict the probability of cone production in treeline pine trees as a function of basal diameter (a), age (b) and tree height (c).

CHAPTER 5

Direct measurement of tree height provides different results on the assessment of LiDAR accuracy

A printable version of this chapter has been revised and published:

Sibona E.¹, **Vitali A.**², Meloni F.¹, Caffo L.³, Dotta A.³, Lingua E.⁴, Motta R.¹, Garbarino M.^{1,2} 2017. Direct measurement of tree height provides different results on the assessment of LiDAR accuracy. *Forests* 8(1), 7; [doi:10.3390/f8010007](https://doi.org/10.3390/f8010007)

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ABSTRACT

In this study, airborne laser scanning-based and traditional field-based survey methods for tree heights estimation are assessed by using one hundred felled trees as reference dataset. The comparison between remote sensing and field-based methods were applied to four circular permanent plots located in the western Italian Alps and established within the Alpine Space project NewFor. Remote sensing (ALS), traditional field-based (IND) and direct measurement of felled trees (DIR) methods were compared by using summary statistics, linear regression models and variation partitioning. Our results show that tree height estimates by aerial laser scanner (ALS) approximated to real heights (DIR) of felled trees. Considering the species separately, *Larix decidua* was the species that showed the smaller mean absolute difference (0.95 m) between remote sensing (ALS) and direct field (DIR) data followed by *Picea abies* and *Pinus sylvestris* (1.13 m and 1.04 m respectively). Our results cannot be generalized to ALS surveys with low pulses density ($< 5/\text{m}^2$) and with view angles far from zero (nadir). We observed that traditional field-based survey can be less accurate than laser scanner in estimating tree heights and this was particularly valid for tall trees with conical shape crowns.

INTRODUCTION

Sustainable forest management needs a huge amount of tree parameters such as species distribution, timber volume and average tree height as the basis of broad scale forest inventories (Koch et al., 2006). Among these, tree height is one of the most important variables in forest inventory, often used in the estimation of forest growth, biomass, carbon stock and site productivity (Andersen et al., 2006). Traditional forest inventory field methods for forest height estimation are expensive, time consuming and almost impossible to perform over large areas (Fieber et al., 2015). When dealing with large areas, a sampling plot approach is commonly arranged in order to reduce costs, and then diameter-height relations are constructed to predict individual tree heights for those areas that were not surveyed. Using remote sensing (RS) techniques allows reducing those constraints, obtaining spatially continuous data over large study areas cost efficiently (Næsset 2002). Tree heights estimation from the ground is difficult due to treetops placement, often hidden by branches of other trees. While with RS survey from above, the problem of hidden treetops is reduced, at least for canopy trees. Among RS techniques, the potential of aerial laser scanner (ALS) in tree heights estimation has been widely demonstrated (Nilsson 1996; Magnussen et al., 1998) as well as for the estimation of other forest stand attributes such as stand volume (Næsset 1997) and basal area (Lefsky et al., 1999). The impact of errors in tree height measurements has shown to have a stronger effect on individual tree volume estimates than errors in species composition (Tompalski et al. 2014), but this depends on the surveyed species and the obtained height errors. For this reason, the accuracy assessment of tree height measurement derived from ALS is a very important issue in the forestry field. The accuracy of forest attributes derived from RS data is usually assessed using traditional field surveys that can be area-based (Næsset 2002) or tree-based (Persson et al., 2002). Field-based surveys always take advantage of trigonometric approaches using rangefinder devices. These field-based data are commonly assumed as being the ground truth for RS data, but actually they are measured with errors. In spite of the huge amount of recent papers that use field-based tree height estimations as ground truth for RS data assessment (Andersen et al., 2006; Næsset 2002), the accuracy of this indirect measurement used as reference is often not declared. In this paper, we considered as ground truth (Ground Control Points, GCPs) one hundred felled trees to test tree heights measured with two estimation approaches: aerial laser scanner (ALS) and classical field surveys. Specific goals of the paper are: 1) to evaluate the use of ALS data for tree height estimation in a comparison with traditional field-based survey method; 2) to use tree height of felled trees to assess the accuracy, bias and precision of field-based survey method and its influence on ALS testing; 3) to study the relative influence of tree size and species on the divergence between ALS remote sensing and direct field-based estimations.

METHODS

Study area

The Cotelivier forest is about 4000 ha and is located on the right bank of the Upper Susa Valley (Piedmont, Italy), between Oulx and Bardonecchia (45°2'N 6°46'E). It is a North facing slope ranging from the montane belt (about 1000 m a.s.l.) up to the treeline (about 2200 m a.s.l.). The mean annual temperature is 6.7 °C and the total precipitation is about 614.9 mm (Bardonecchia Pian del Sole, 1585 m a.s.l., 2004-2015 period). The topography of the area is complex with steep slopes and high roughness. Both productive and protective forests are present, with intense forest exploitation on more accessible sites, but topography limits the use of a massive mechanization. *Pinus sylvestris* L. stands dominate at lower elevation, instead *Picea abies* (L.) H.Karst. and *Larix decidua* Mill. at higher elevations. This mixed conifers forest is characterized by a high structural diversity: *Larix* stands range from wood pasture with sparse big trees on more accessible sites (Garbarino et al., 2013) to dense and young stands, while *Pinus* and *Picea* stands show less structural diversity.

Sampling design & data collection

Four permanent circular plots having 20 m radius were established during a field campaign in 2013 within the “NewFor” Alpine Space project (Berger et al., 2014). Within these plots, we estimated the total height of 100 trees (28% of the surveyed trees within the plots) by using three different survey methods: a) traditional field-based survey here defined as “indirect” measurement (IND); b) remote sensing measurement through aerial laser scanner (ALS); c) direct measurement on felled trees, referred as “direct” measurement (DIR).

Indirect field-based survey (IND)

*Field-Map*TM integrated system (<http://www.fieldmap.cz>) was used to accomplish the traditional field-based survey that was done during June – July 2012. It includes a GPS receiver (*Trimble*TM *GeoXM 2005*) to obtain georeferenced data of the plot center (differential correction in laboratory with post-processing method), and a laser rangefinder (*TruPulse*TM *360b*) to measure tree heights and relative positions (distances and angles) to the plot center. A field computer (*DRStech*TM *ARMOR*) equipped with mobile GIS software was used for real time data mapping and 3-D visualization of trees. Diameter (DBH), crown projections measure and species have been collected for all 100 trees (DBH > 4cm).

LiDAR survey (ALS)

ALS data were acquired in June 2012 by a helicopter flight, which covered the whole study area. The LiDAR sensor used was an *Optech*TM *ALTM 3100EA*, that allowed a planimetric position accuracy of

less than 0.30 m and an elevation accuracy (Z) of less than 0.15 m. Four echoes of each laser pulse were recorded flying at an average altitude of 400 m a.s.l., resulting in an average point sampling density of 10 points/m² (on the last return). The ALS point cloud was used to generate the DTM (Digital Terrain Model) and DSM (Digital Surface Model) of the area. These layers were subtracted to produce the CHM (Canopy Height Model) that was employed as a base raster for trees positions and heights detection (Koch et al., 2006; Hyypä and Hyypä 2001; Sambugaro et al., 2013; St-Onge 1999). The CHM raster (0.5 m spatial resolution) has undergone a surface smoothing using a Gaussian kernel filter (Hyypä and Hyypä 2001). Then focal statistics with a local maximum detection algorithm (“Pouring” algorithm implemented in HALCON, similar to an inverted, classical watershed-algorithm (Koch et al., 2006) were used to extract potential treetops from the smoothed CHM. The detected trees were then analyzed through a conditional script that considers a minimum distance and height difference from the nearest trees in order to identify and delete potential false positives (St-Onge 1999). The method is fully automated and has been implemented as a workflow of geoprocessing tools (Model Builder) within the software *ESRI ArcGIS*TM. The output is a shapefile containing tree position and height (Sambugaro et al., 2013). We manually co-registered the remote sensing data to the field dataset by using a very high spatial resolution (20 cm) aerial image acquired a month before the ALS data in order to correctly match the trees detected remotely to each GPS-positioned tree (St-Onge 1999; Eysn et al., 2015). False negative have been consequently detected by experienced human interpreter (Eysn et al., 2015). Only correctly assigned tree (true positive) were used in this work.

Direct field-based survey (DIR)

The 100 felled trees were the result of two different harvesting methods: a clearcut on an almost pure *L. decidua* stand (plot 1) and thinning in multilayered mixed conifer stands (plots 2, 3, 4) (Table 1). Tree length plus the stump height was measured for each felled tree to get “direct” data, which have been considered in the analysis process as ground truth.

Data analysis

We obtained three datasets that were used to compare remote sensing (ALS) and field-based estimation methods (IND) by using direct measurements on felled trees (DIR) as ground control measure. We tested the statistical difference between the three measurements by using a Kruskal-Wallis chi-squared non-parametric test. We calculated standard summary statistics of tree height measures for both the whole sample and the three main species (*Larix*, *Picea*, *Pinus*) separately. We subtracted tree heights measured by ALS from the two field measurements, obtaining real (positive/negative) delta values (Δ) that were made absolute and then averaged. We performed a regression analysis between ALS and IND data against our ground truth (DIR), again both for the entire sample and for each species separately to further

investigate the observed differences. Then we regressed heights from the two field datasets (IND and DIR) against each other. We calculated the root mean square error (RMSE) for all the linear regression models that were previously performed. We applied the hierarchical partitioning approach (Chevan et al., 1991) through the statistical package hier.part (Walsh et al., 2013) to calculate the independent contribution of tree attributes (real height, Dbh, crown surface area and species) in determining the difference in absolute value between DIR and ALS estimates. Because of a non-uniform distribution of species along the range of tree heights the hierarchical partitioning was applied to the whole dataset and to the species separately. Summary statistics, regression analyses and hierarchical partitioning were performed in R software (R Core Team 2016).

Whole plot	Plot 1	Plot 2	Plot 3	Plot 4
Slope (°)	11	21	28	28
Elevation (m a.s.l.)	1588	1365	1364	1407
Tree Density (tph)	477	772	716	883
BA (m ² /ha)	40.40	37.77	42.79	37.58
Vertical Structure	single layered	multilayered	multilayered	multilayered
Larix decidua (BA %)	99	20	11	44
Picea abies (BA %)	1	65	42	26
Pinus sylvestris (BA %)	0	9	9	30
Other Species (BA %)	0	6	38	0
Felled trees				
N	47	18	16	19
Tree Height Mean (m)	28.61	19.64	18.69	17.17
Tree Height Min (m)	19.80	14.00	13.70	12.00
Tree Height Max (m)	34.90	25.50	25.50	23.00
Tree Height SD (m)	3.18	2.93	3.39	3.10
DBH (cm)	34.04	28.56	30.71	28.68
BA (m ² /ha)	4.84	1.23	1.40	1.30
Crown H (m)	18.40	9.01	11.32	6.94
Crown A (m ²)	8.87	11.84	13.06	10.13

Table 1. Site characteristics, stand structure descriptors and species composition of the four permanent plots as a whole and considering only the felled trees. Tree heights are obtained from DIR measurement, instead DBH, basal area (BA), bole height (Crown H) and crown area (Crown A) are obtained from IND survey method.

RESULTS

L. decidua was the tallest species in our dataset followed by *P. abies* and *P. sylvestris* (Figure 1), and some differences between estimation methods existed. However, the three estimation methods were not statistically different from each other (Kruskal-Wallis test, $p = 0.991$). From a comparison between ALS and IND measurements (Table 2), emerged that ALS slightly overestimated tree heights (23.40 m vs 23.33 m) and this trend was more pronounced for *Larix* (28.84 m vs 28.45 m). The biggest average difference in absolute value between ALS and IND measurements was observed for *Larix* (1.39 m) and the smallest for *Picea* (0.80 m). Every model obtained through regression analysis showed an overestimation of small trees and an underestimation of the taller ones. The differences between the models lie in the magnitude of these over/underestimates. All the regressions were significant ($p < 0.001$) and every model gave very good fit if we consider the population as a whole ($R^2 > 0.9$). In the ALS vs IND models (Figure 2) *P. sylvestris* achieved a poorer fit ($R^2 = 0.67$), while *L. decidua* achieved a better fit ($R^2 = 0.73$) and *P. abies* emerged as being the best fitting species ($R^2 = 0.95$). All *P. abies* trees were underestimated by ALS as well as *L. decidua* taller trees (Figure 2). A similar pattern was observed in the ALS vs DIR model, but with less underestimation (Figure 3a).

From a comparison between ALS and real tree heights (DIR) was revealed that the mean value was identical (23.40 m), but some differences emerged averaging the absolute values of deltas (Table 3). The biggest average difference in absolute value between ALS and DIR measurements was observed for *Picea* (1.13 m) and the smaller one for *Larix* (0.95 m), but considering all the species together the mean difference was close to 1 m. Delta values increased to 1.25 m in the comparison between DIR and IND measurements where *P. sylvestris* showed the smaller difference (0.88 m). In the ALS vs DIR model (Figure 3a) among the studied species *P. sylvestris* achieved a poorer fit ($R^2 = 0.69$), while *P. abies* and *L. decidua* performed better ($R^2 = 0.79$ and 0.81 respectively). In the regression between DIR and IND measurements (Figure 3b) *P. sylvestris* and *P. abies* were the best fitting species ($R^2 = 0.80$) followed by *L. decidua* ($R^2 = 0.71$). In this model *L. decidua* was underestimated by IND, instead *P. sylvestris* and *P. abies* showed a high correspondence between the two measurements (Figure 3b). The error in the individual tree height estimation was higher ($RMSE = 1$ m) when ALS was tested against IND than in the case of DIR ($RMSE = 0.76$ m).

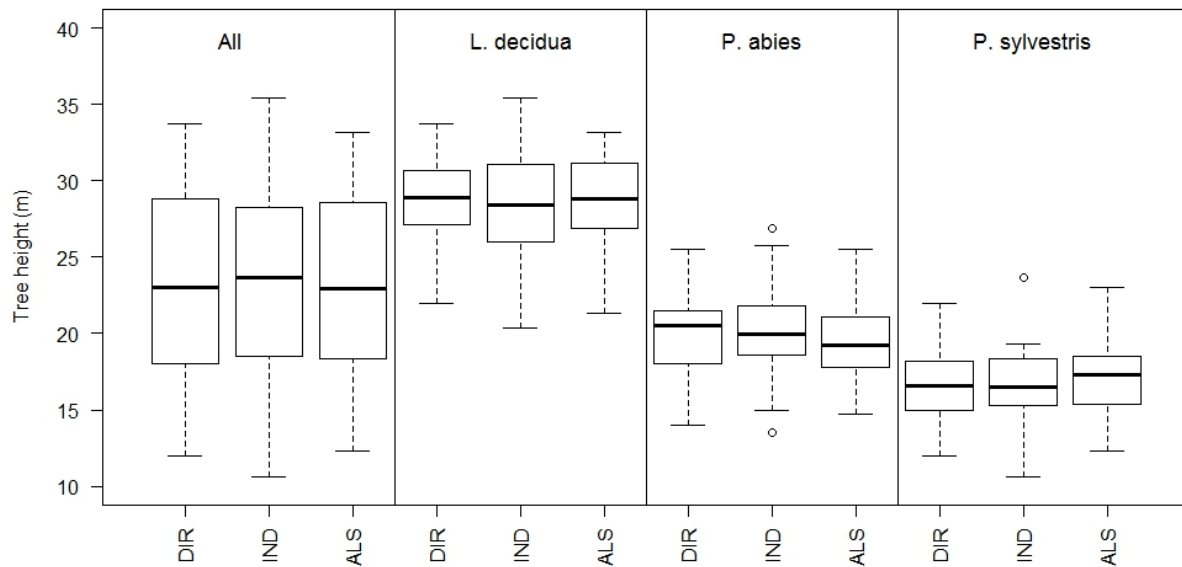


Figure 1. Box plots of tree heights distribution as measured by three survey methods (DIR = field direct measurement of felled trees; IND = traditional field-based; ALS = aerial laser scanner) of the whole dataset and considering the species.

Species	Felled trees	IND (m) <i>mean (sd)</i>	ALS (m) <i>mean (sd)</i>	IND vs ALS Δ <i>mean (sd)</i>	IND vs ALS <i>RMSE</i>	IND vs ALS <i>r</i>
All	100	23.33 (5.92)	23.40 (5.90)	1.12 (1.01)	1.00	0.97
<i>L. decidua</i>	48	28.45 (3.39)	28.84 (2.73)	1.39 (1.19)	1.42	0.85
<i>P. abies</i>	31	20.15 (3.03)	19.53 (2.67)	0.80 (0.58)	0.62	0.97
<i>P. sylvestris</i>	21	16.74 (2.61)	17.07 (2.59)	0.98 (0.93)	1.28	0.87

Table 2. Average and standard deviation (in brackets) values of tree heights measured by two estimation methods: field INDirect and aerial laser scanner (ALS). Absolute values of the differences (Δ) between IND and ALS are reported as averages and standard deviations (in brackets). Root Mean Square Error (*RMSE*) and Pearson correlation coefficients (*r*) between IND and ALS for the whole dataset (All) and divided by species is also presented in the last two columns.

Species	DIR (m) <i>mean (sd)</i>	DIR vs IND			DIR vs ALS		
		<i>mean abs. Δ</i>	<i>RMSE</i>	<i>r</i>	<i>mean abs. Δ</i>	<i>RMSE</i>	<i>r</i>
All	23.40 (6.02)	1.25	1.08	0.96	1.02	0.76	0.98
<i>L. decidua</i>	28.86 (2.71)	1.49	1.84	0.83	0.95	1.21	0.89
<i>P. abies</i>	19.91 (3.00)	1.16	1.34	0.90	1.13	1.21	0.89
<i>P. sylvestris</i>	16.47 (2.49)	0.88	0.94	0.92	1.04	1.25	0.87

Table 3. Average and standard deviation (in brackets) values of tree heights as measured by DIRect field survey (felled trees). Absolute values of the differences (Δ) DIR-IND and DIR-ALS are reported as averages. Root Mean Square Error (*RMSE*) and Pearson correlation coefficients (*r*) between DIR vs IND and DIR vs ALS for the whole dataset (All) and divided by species are also presented in the last columns.

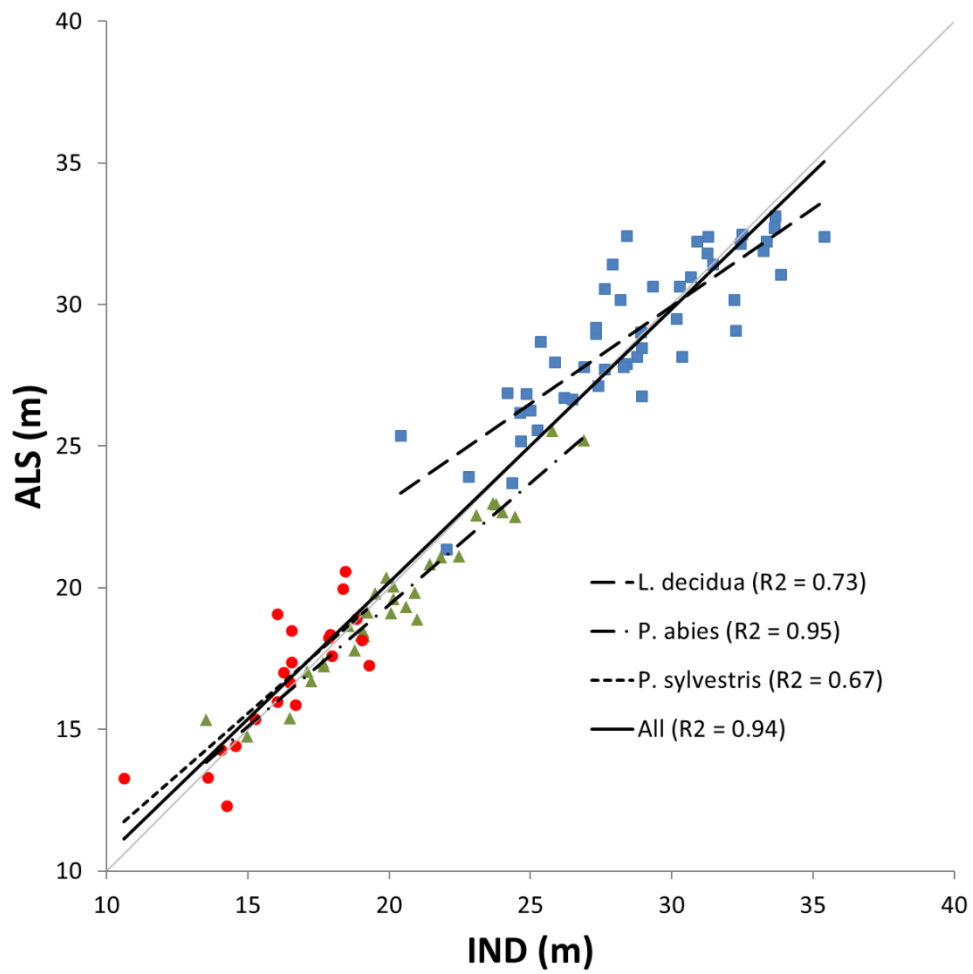


Figure 2 - Regression analysis between tree height derived by airborne laser scanner data (ALS) and tree height derived from indirect field-based measurement (IND), considering the whole dataset (All) and the three species separately. Each dot corresponds to a single tree (blue square = *Larix*; green triangle = *Picea*; red circle = *Pinus*).

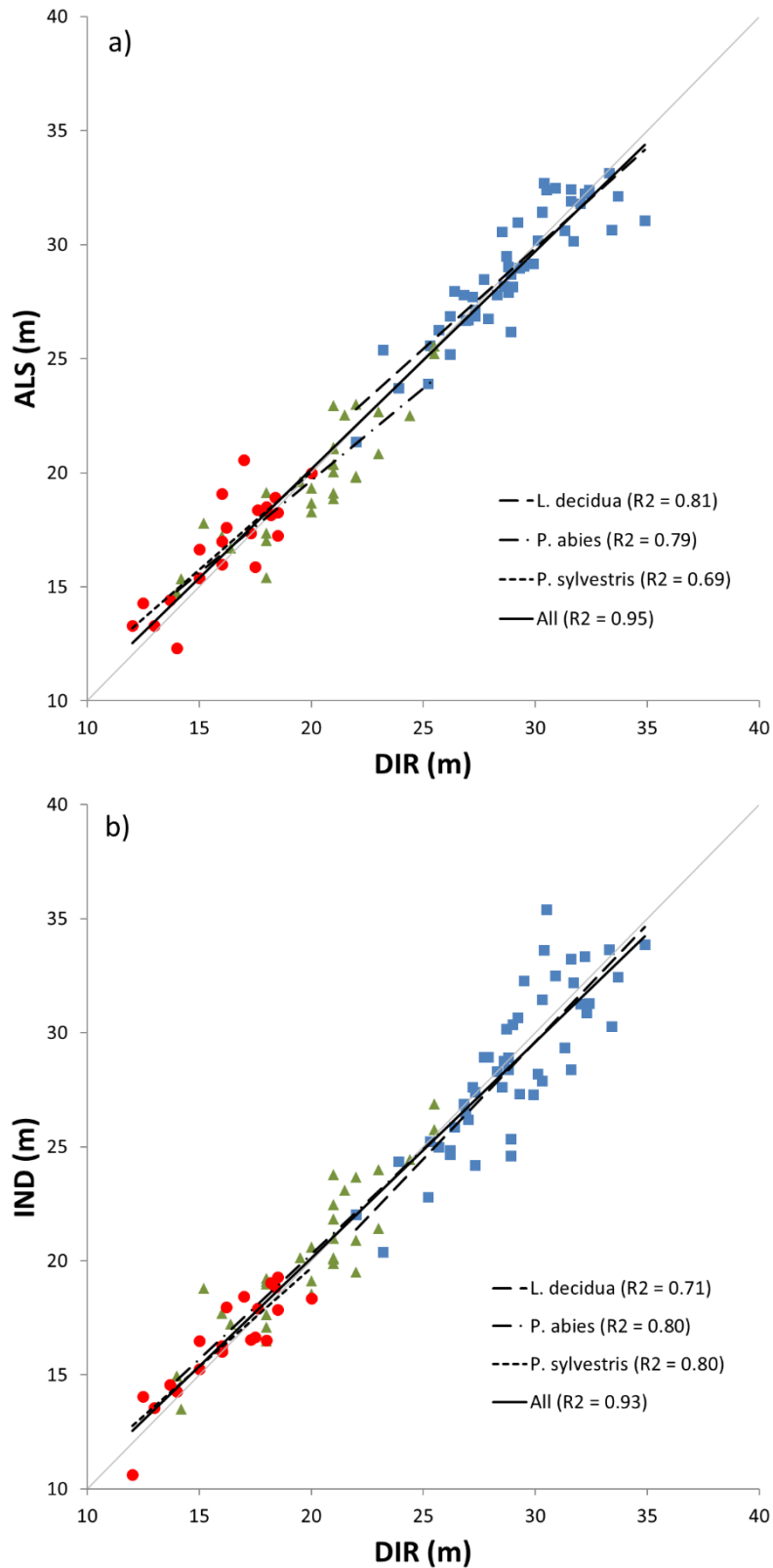


Figure 3 - Regression analysis between (a) tree heights derived by airborne laser scanner data (ALS) and tree heights derived from direct field-based measurement (DIR), (b) tree heights derived from indirect field-based measurement (IND) and DIR, considering the whole dataset (All) and the three species separately. Each dot corresponds to a single tree (blue square = *Larix*; green triangle = *Picea*; red circle = *Pinus*).

From the variation partitioning approach on the whole dataset, was revealed that species had the highest independent effect (54.8 %) on the absolute value of the difference between DIR and ALS followed by real tree height (DIR, 41.4 %), Dbh (2.8 %) and crown surface area (1%). Applying the variation partitioning to the species separately we observed that the independent effect of crown surface area was much higher for *P. sylvestris* (22.4%) than for the other species (*L. decidua* 2.2%; *P. abies* 8%). Real tree height (DIR) showed a stronger independent effect on delta estimations in *L. decidua* (95.6%) than in other species (*P. abies* 73.3%; *P. sylvestris* 57.5%).

DISCUSSION

We used one hundred felled trees as ground truth to investigate the impact of species composition on the accuracy of individual tree height estimates. Our results show that tree height measurements performed with aerial laser scanner (ALS) approximated to real heights (DIR) of felled trees. Interestingly, ALS estimates were closer to DIR ones than those obtained through traditional field-based surveys (IND). This was also highlighted by the lower error (*RMSE*) observed when the DIR measurement was used as ground truth. Considering the species separately, *L. decidua* showed the smaller mean difference in absolute values (0.95 m) between remote sensing (ALS) and direct field (DIR) data followed by *P. abies* and *P. sylvestris* (1.13 and 1.04 respectively). *P. abies* was the only species showing a smaller difference in tree height between ALS and IND (0.80 m) than between ALS and DIR (1.13 m). This was probably because *P. abies* has a simple and dense canopy that is easier to collimate from the ground.

Tree height obtained through direct measurements on felled trees (DIR) emerged as being an important factor influencing the accuracy of remote and field surveys. Our regression linear models showed that ALS-derived height estimations of tall trees were underestimated while small ones were overestimated by ALS technique. The underestimation of tall trees by ALS has been commonly found in several studies and relates to the missing of points corresponding to the highest point of the crown (Wing et al., 2010). Underestimation of tree height using small-footprint laser scanner systems (ALS) was documented early in the 1980's (Nelson et al., 1988). Main factors affecting underestimation of tree heights are: density and coverage of laser pulses; algorithm used to obtain DTM and CHM; pulses penetration into the canopy; amount and height of understory vegetation; tree shape and species (Hyypä et al., 2008). The overestimation by ALS of small trees is an artefact of receiving pulses from nearby taller tree (Farid et al., 2006), but other causes can be related to DTM errors related to filtering and interpolation methods. The architecture of the crown can also determine an overestimation, especially for those species without a strong monopodial shape such as broadleaves and some pine species (e.g. *P. sylvestris*). This fact had an important influence on the observed differences between species. *Pinus* trees were smaller than the other two species and this is likely an explanation for the height overestimation by ALS.

From a variation partitioning analysis was revealed that species attribute was more important than tree height and Dbh for influencing the difference between ALS and DIR measurements, this was probably because our dataset was composed by small *Pinus*, intermediate *Picea* and tall *Larix* trees. However, from the variation partitioning analysis applied to each species we observed that for *Pinus* crown surface area was an important variable for influencing the difference between ALS and DIR measurements, this was probably due to the complex crown shape of this species. Instead, *Larix* and *Picea* have a simpler pyramid-shape crown architecture (Korpela et al., 20120), this can explain why real height (DIR) become the most important factor for influencing the difference between ALS and DIR measurements. Similar differences between crown architecture of pines and fir-spruce species were find by other authors (Andersen et al., 2006; Persson et al. 2002; Yu et al., 2004) and recently the importance of tree crown architecture for wood volume estimation has been outlined (Hess et al., 2015).

In spite of the small size of the sample, we observed that traditional field-based survey can be less accurate than laser scanner in estimating tree heights. This was particularly valid for tall trees having regular crowns and has important implications for the use of ALS techniques in forest inventories Tompalski et al., 2014; Chave et al., 2005). Anyway we are aware that our results cannot be generalized to ALS surveys with low pulses density ($< 5/m^2$) and with view angles far from zero (nadir). Pulse density is a limit for singletree height estimation (Hyypä et al., 2008), but is not a constraint at the plot scale until pulse densities drops below 1 pulse/ m^2 (Jakubowski et al., 2013). The source of error on tree height field measurement can be related to the instrument used, to the skills and experience of surveyor and to the tree and stand characteristics (Gaudin and Richard 2014). There are only few papers that compare tree height measurements obtained by handled instruments with actual height obtained by direct measurement (Larjavaara et al., 2013), but as far as we know none comparing LiDAR derived height with direct measurements. Field-based surveying method can influence the accuracy of tree height estimation and usually are affected by lack of precision (Nelson et al., 2003; West 2009). The model of handheld laser rangefinder (e.g. Impulse or Truepulse) affects the quality of compass measurements (Brach et al., 2013; Tomaštik and Tunák 2015). Moreover, field crew judgement and precision is another important factor affecting the accuracy of field-based surveys with handheld laser rangefinders (Ferrarese 2013). The use of tacheometer, total station and accurate GPS receiver can significantly improve field measurements and thus the accuracy assessment of ALS data (Maltamo et al., 2004; Salas et al., 2012; Holmgren et al., 2003). Other authors found that field methods were more accurate than LiDAR data (Andersen et al., 2006; Larjavaara et al., 2013), but point density was almost half of the present study. In any case, the authors agreed in considering that the discrepancy in height accuracy was greatly compensated by the higher cost efficiencies and wider coverage guaranteed by LiDAR. Further case study, species, instruments, and field crew should be tested in order to have a clearer idea of the issue. However, we suggest always providing an accuracy assessment of field indirect measurements through the use of felled trees. This operation is

required when tree height obtained through field indirect measurement is used as reference ground truth to validate remote sensing derived data.

CONCLUSIONS

Our study demonstrates that direct field measurements on felled trees improve the assessment of small-footprint airborne laser scanner (ALS) estimation of tree heights. Adopting direct measurements as ground truth for remote sensing tree height estimation we obtained a reduction in the magnitude of errors (RMSE). The proposed method of using felled trees as ground control points is time consuming and expensive, but highlights the fact that traditional field-based surveys methods are estimations in turn. With this paper, we propose to select a small sample of felled trees to validate the traditional field-based survey methods.

CHAPTER 6

General conclusions

The research carried on during the three-year doctorate contributed to shed some light on anthropogenic treelines in relevant mountain ranges of southern Europe. Human-shaped treelines are the most widespread on earth and where human impacts have been (or still are) the major drivers of their current structure and their responses to changing environmental conditions. The multiple spatio-temporal scales approach and the use of altitudinal transects as permanent plots, should guarantee further investigations and monitoring in the near future.

As for most European mountain area, rural population decrease and forest cover increase are ongoing processes also in the Apennines. Our results suggest that human direct or indirect activities are by far the strongest limiting factor in Apennine treelines, lowering their elevation and reducing species composition (only *Fagus sylvatica* as dominant tree species). The south-western sites, the most severely impacted by previous human activities, have also experienced the greatest recent land cover changes. At this regard in the Apennines, we would expect that the widespread beech treelines would slowly shift upslope in the future. In contrast, the less common, but faster successional processes in *Pinus* spp. treelines are expected to be remarkably faster. As anthropogenic treelines will respond differently than climatic treelines to drivers of global environmental dynamics, models of treeline responses to global change need to account for land-use history. More treeline studies are needed integrating the synergic effects of both natural and anthropogenic drivers on treeline position and structure, fostering interpretation of potential climate change responses in the context of historical and ongoing land-use change.

We investigated the patterns and processes of the recent encroachment of black pine (*Pinus nigra*) cohorts taking place at various anthropogenic treelines in the Central Apennines due to the abandonment of traditional land-uses. Treeline encroachment was mainly driven by microsite topography and the presence of nearby seed sources (pine plantations). Overall, the high growth rates found at high elevation and the rapid and often clustered encroachment patterns indicate that these human-shaped treelines can also respond quickly to the future global change.

The presence of non-native *Pinus nigra* plantations promoted recent recolonization processes above the current timberline that appear as the only short-term trajectory for rebuilding the former broadleaf-coniferous transition in the Apennine mountain range, as expected from global theory.

Comparing similar high elevation encroachment processes of four native *Pinus* species (*Pinus heldreichii*, *Pinus peuce*, *Pinus sylvestris* and *Pinus uncinata*) at nine sites of the Mediterranean basin (Balkans and Spain), we detected more similarities than differences with *P. nigra* in the Apennines.

In addition, this research demonstrates that direct field measurements on felled trees improve the assessment of small-footprint airborne laser scanner (ALS) estimation of tree heights. Adopting direct measurements as ground truth for remote sensing tree height estimation we obtained a reduction in the magnitude of errors. We tested that the remote sensing technologies can improve the detection of treelines and individual tree stems, monitoring the position and potential movement of these ecotones and allowing collecting data on large study areas and where rugged terrain can prevent access to sampling areas.

Finally, I hope that the results of my research could contribute to a better understanding of spatio-temporal dynamics of European treeline ecotones, where the human-footprint is still a noise over the climatic signals. The collaborations developed during the last two years with Spanish and Balkan colleagues are a significant benefit to this PhD experience and hopefully would be the fundamentals for building broader research networks to develop these enticing investigations at the upper margins of our forests at the top of our domesticated but gorgeous mountains.

CHAPTER 7

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