



UNIVERSITÀ POLITECNICA DELLE MARCHE  
Repository ISTITUZIONALE

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

This is the peer reviewed version of the following article:

*Original*

Effects of natural and anthropogenic drivers on land-cover change and treeline dynamics in the Apennines (Italy) / Vitali, Alessandro; Urbinati, Carlo; Weisberg, Peter J.; Urza, Alexandra K.; Garbarino, Matteo. - In: JOURNAL OF VEGETATION SCIENCE. - ISSN 1100-9233. - ELETTRONICO. - (2018). [10.1111/jvs.12598]

*Availability:*

This version is available at: 11566/254869 since: 2022-06-01T12:08:25Z

*Publisher:*

*Published*

DOI:10.1111/jvs.12598

*Terms of use:*

The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. The use of copyrighted works requires the consent of the rights' holder (author or publisher). Works made available under a Creative Commons license or a Publisher's custom-made license can be used according to the terms and conditions contained therein. See editor's website for further information and terms and conditions.

This item was downloaded from IRIS Università Politecnica delle Marche (<https://iris.univpm.it>). When citing, please refer to the published version.

(Article begins on next page)

1 **TITLE**

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

4

5

6 **AUTHOR LIST**

7 Vitali Alessandro, Urbinati Carlo, Weisberg Peter J., Urza Alexandra K. & Garbarino Matteo

8

9 Vitali, Alessandro<sup>1</sup> (Corresponding author, a.vitali@pm.univpm.it)

10 Urbinati, Carlo<sup>1</sup> (c.urbinati@univpm.it)

11 Weisberg, Peter J.<sup>2</sup> (pweisberg@cabnr.unr.edu)

12 Urza, Alexandra<sup>2</sup> (alexandra.urza@gmail.com)

13 Garbarino Matteo<sup>3</sup> (matteo.garbarino@unito.it)

14

15 <sup>1</sup>Marche Polytechnic University, Department of Agricultural, Food and Environmental Sciences, Ancona, AN,  
16 IT

17 <sup>2</sup>University of Nevada, Department of Natural Resources and Environmental Science, Reno, NV, USA

18 <sup>3</sup>University of Turin, Department of Agricultural, Forest and Food Sciences, Turin, TO, IT

**19 ABSTRACT****20 Questions**

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

**23 Location**

24 Apennine Mountains, Italy.

**25 Methods**

26 At the regional scale (n=776 municipalities covering 43 000 km<sup>2</sup>), we assessed the relationship between  
27 human demographic processes and forest cover dynamics for the 1990-2012 period using Corine Land  
28 Cover maps and a national census dataset. At the landscape scale (n=18 landscape units of 16 km<sup>2</sup> each),  
29 we tested the effects of site topography on forest cover changes between 1954 and 2012. At the local scale  
30 (n=5484 sampling points), we extracted the location and species composition of the current treeline (year  
31 2012) using semi-automatic segmentation methods. We quantified the association of climatic, topographic  
32 and anthropogenic variables with the position of upper treelines in the Apennines.

**33 Results**

34 Regional scale: human population in the Apennines decreased by 3% between 1991 and 2011. During the  
35 same time period, there was an increase in the extent of shrublands (+7%) and forests (mixed +4%, conifers  
36 +2%, broadleaf +1%) and a decrease in the extent of pastures (-9%). Landscape scale: forests expanded  
37 more on southwest (+109%) than on northeast slopes (+19%). Local scale: the mean treeline altitude was  
38 1755 m a.s.l. *Fagus sylvatica* L. was the most widespread species (94%), but we also found *Pinus nigra* Arn.  
39 plantations and *Pinus mugo* Turra shrublands in the central Apennines and *Pinus heldreichii* H.Christ in the  
40 southern Apennines. Overall, the elevations of the current treelines are negatively related to population  
41 density, road proximity and southwest exposures, especially among *Pinus nigra* stands.

**42 Conclusions**

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

53

## 54 INTRODUCTION

55

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

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

75 Numerous studies on European treelines have concluded that recent tree establishment above  
76 upper treeline results primarily from reduced human pressure (Gehrig-Fasel et al., 2007; Motta et al. 2006;  
77 Treml et al., 2016) because of a progressive decline in the profitability of mountain agriculture (Gotsch et  
78 al. 2004, Leuch 2005). In the Apennines, land abandonment occurred later and was related to property  
79 shifts and urbanization processes in the lowland, favoring the natural secondary succession (Torta 2004;  
80 Caballero et al. 2009; Pelorosso et al. 2009, Bracchetti et al. 2012; Vacchiano et al. 2017). Shifting  
81 agricultural economies have caused an increasing exodus from mountain and rural areas in general  
82 (Chauchard et al., 2007; Didier 2001; Motta and Garbarino 2003), causing widespread spontaneous  
83 reforestation (MacDonald et al., 2000; Conti and Fagarazzi, 2005; Gellrich et al., 2007). Nonetheless,  
84 recruitment of tree cohorts above the current treelines is likely to occur only if climatic and edaphic  
85 conditions are favorable and if land uses are suitable for their establishment and range expansion (Ott et al.  
86 1997; Weisberg et al. 2013). Within this context, understanding the interacting influences of climate,  
87 topography and human pressure is essential for predicting trajectories of change for alpine treelines.  
88 Importantly, human shaped treelines respond differently to climate warming than undisturbed treelines,  
89 providing useful information for climate sensitivity modelling (Batllori et al. 2010).

90 Factors controlling treeline structure and dynamics are strongly scale dependent (Malanson et al.,  
91 2007), and treeline elevation varies at a range of scales in response to multiple biotic and abiotic factors  
92 (Jobbágy & Jackson 2000; Case & Duncan 2014). In this study, we adopted a multiscale approach to study  
93 the spatial-temporal dynamics of the anthropogenic treelines of the Apennines. We hypothesized that: (1)  
94 forest cover dynamics at the regional scale correlate with human demographic processes; (2) the dominant  
95 exposure of the Apennines (northeast vs. southwest) is a major driver of high-elevation forest cover change  
96 at landscape scales; (3) climate, topography and human pressure influence current treeline position and  
97 species composition at local scales.

98

## 99 **METHODS**

### 100 **Study Area**

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

110 The Apennine climate is a mountain variant of the Mediterranean type, with mean temperature  
111 ranging from 0 to 11 °C in January and from 24 to 28 °C in July; the total annual precipitation varies  
112 between 600 and 4500 mm, with frequent snowfall events above 1000 m a.s.l. (Vacchiano et al., 2017). The  
113 montane zone (800-2000 m a.s.l.) is largely dominated by *Fagus sylvatica*, locally mixed with *Abies alba*.  
114 *Fagus sylvatica* (European beech) is one of the most important and widespread broadleaf tree species in  
115 Europe, maintaining high growth rates until late maturity. It is a hardy, shade tolerant species and not  
116 particularly soil-sensitive, but its optimal growth is in humid soils situated on calcareous or volcanic parent  
117 material (Houston Durrant et al. 2016). In Italy, *Fagus sylvatica* forests are more widespread on northern  
118 slopes and under conditions of high relative humidity (Nocentini 2009).

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

126 transhumance, but still providing species-rich ecosystems especially on fertile limestone soils (Catorci et al.  
127 2012).

128

## 129 **DATA COLLECTION AND ANALYSIS**

130 Upper treeline structure and dynamics were assessed at three spatial scales: i) at a regional scale  
131 across the entire Apennine chain; ii) at a landscape scale with 18 sites of 16 km<sup>2</sup> each; and iii) at a local  
132 scale with 5484 sampling points at 500-m distance along the current treeline (Figure 1).

133

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

135 At the regional scale, the study area was composed of 776 “mountain municipalities” (*sensu* ISTAT,  
136 Italian Statistic head office classification), excluding those geographically separated from the main  
137 mountain range (Figure 1A). Within this 43 000-km<sup>2</sup> area, we assessed population density and land cover  
138 changes. We extracted human population data for the 1991-2011 period from national censuses (ISTAT  
139 1999, 2011) and geo-referenced them using mountain municipalities’ administrative boundaries as basic  
140 units. We produced a map of demographic change by calculating the change in population density for each  
141 municipality between 1991 and 2011. For the land cover change analysis, we produced matrices of Land  
142 Cover Change (LCC) obtained by comparing CORINE Land Cover (CLC Level 3) maps from 1990 (CLC1990)  
143 and 2012 (CLC2012) with 100 m of resolution. We obtained land cover changes at the regional scale by  
144 merging the 44 classes of the original CORINE maps to generate a reduced set of land cover classes,  
145 excluding water and non-vegetated classes for the following analysis. We developed a transition matrix for  
146 the whole region by calculating changes in areal extent for selected land cover classes: broadleaf forests,  
147 conifer forests, mixed forests, shrublands and transitional woodlands, pastures, agriculture lands, orchards  
148 and artificial areas. We focused mainly on the transitions between forested and non-forested cover classes.  
149 We calculated the proportional change for each cover class to describe individual class dynamics. We  
150 computed the relative weight of each category as the percentage of the total changed area. We performed  
151 a correlation analysis between population and forest changes at the municipality level and we compared  
152 human density change classes (threshold =  $\pm 20\%$  of population) to forest cover gain and loss.

153

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

155 For landscape-scale analyses, we selected nine major mountain peaks with a minimum elevation of  
156 2000 m a.s.l. (see Table S1 in Supplementary Materials). For each peak, we selected two landscapes  
157 stratified according to predominant slope exposure, northeastern (NE) vs. southwestern (SW), for a total of  
158 18 landscapes analyzed throughout the study area (Figure 1A). To assess land cover changes (LCC) at high  
159 elevation, we used aerial images from 1954 (IGMI - GAI database: Italian Military Geographic Institute –  
160 Aerial Italian Group flight) and 2012 (orthoimages from AGEA database: Agency of Supplies in Agriculture).  
161 Historical aerial photographs were scanned and orthorectified at 1-m resolution using PCI Geomatica

162 (version 10.2, PCI Geomatics Enterprises Inc., Richmond Hill, ON). The aerial photographs were processed  
163 with the software eCognition Developer 64 (version 8.9, Trimble Navigation) through automatic  
164 segmentation (scale parameter = 100, color parameter = 0.5) and a manual classification (Definiens 2004).  
165 We classified each landscape into two land cover classes: forest (>50% crown cover) and non-forest cover  
166 (Figure 1B). The 36 resulting maps (i.e. 18 landscapes x 2 years) with a cell size of 1 meter were then  
167 enhanced in a GIS environment in order to reduce the effect of differing input image quality, and to achieve  
168 a minimum mapping unit of 100 m<sup>2</sup> (Garbarino et al. 2011). We also used a 3x3-majority filter to reduce the  
169 “salt and pepper” effect.

170 The landscape pattern analysis was limited to broadleaf forests to focus on natural dynamics and  
171 ecological succession, excluding the recently established coniferous plantations (mainly *Pinus nigra* stands).  
172 We excluded other sites with some peculiarities (e.g. presence of *Pinus mugo* or *Pinus heldreichii*) in order  
173 to standardize the dataset and to compare all landscapes together. Therefore all sites of landscape analysis  
174 are located in central Apennines plus one in northern Apennines. An accuracy assessment was performed  
175 on each map resulting in the K statistic ranging from 0.68 (77% overall accuracy) for 1954 to 0.74 (84%  
176 overall accuracy) for 2012. As control data, we randomized 100 points in a GIS environment for each  
177 landscape and classified them visually using the same land cover classes adopted in the automatic  
178 segmentation (Garbarino et al. 2013). We analyzed the percentage change in relative cover for broadleaf  
179 forests at higher elevations (>1500 m a.s.l.) between 1954 and 2012. We obtained forest class metrics  
180 (cover, mean patch area, patch density, mean shape index) from raster images using the FRAGSTATS 4  
181 statistical package (McGarigal et al., 2012). We categorized the 18 landscapes based on their prevailing  
182 exposure (9 northeast vs. 9 southwest) and we analyzed each exposure separately. We applied a Mann-  
183 Whitney test to compare the medians of these two prevailing exposures.

184

#### 185 **Local scale: current treeline position and natural and anthropogenic constraints**

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

195 We established 5484 sampling points (1 per 500 m) along the resulting treelines in a GIS  
196 environment (Case & Duncan 2014) (Figure 1C). In order to quantify the risk of overestimation for  
197 misclassification associated with shadows, or underestimation due to variable tree crown spectra, we

198 adopted an accuracy/validation assessment method. We based the validation procedure on a random  
199 extraction of 55 sampling points (1%) and we visually assessed the percentage of well-classified points  
200 using the aerial imagery. We correctly identified 76% of the points as occurring at treeline, with 16%  
201 overestimation and 8% underestimation error. The average horizontal distance between inaccurate points  
202 and the correct treeline position was <5 m. We considered this a sufficient precision threshold because the  
203 geographic data sources used are raster files with a spatial resolution of  $\geq 30$  m.

204 For all sampling points, we used the “value to points” GIS tool to derive nine predictor variables  
205 describing the potential influences of topography, climate, soil, vegetation and human proxy variables  
206 (Table 1). Topographic features were obtained from the digital elevation model (ELEV) of ASTER GDEM2,  
207 having a geometric resolution of 30 m (Tachikawa et al. 2011). We derived northeastness index (NE) and  
208 slope (SLO) maps from digital elevation models. We derived sand proportion in the soil texture (SAND) from  
209 the ISRIC SoilGrid map (Hengl et al. 2014). We extracted spatially distributed climate variables (PREC and  
210 TEMP) from the WorldClim database (1 km resolution), representing the 1950-2000 climate conditions  
211 (Hijmans et al. 2005). Given the difficulty of obtaining high-quality data on past land use, we used the  
212 proximity to the closest road (ROAD) as a proxy for past anthropogenic impact (Garbarino et al. 2009;  
213 Dainese et al. 2017). Population density (POP) at the municipality level (year of census: 2011) was selected  
214 as an indirect measure of current anthropogenic impact (Weisberg et al. 2013). We derived the dominant  
215 treeline species by photo-interpretation of aerial images, using local vegetation maps as reference (Table  
216 S1). In order to identify broad geographic and climatic trends, we plotted the mean elevations of treelines,  
217 annual precipitation and annual mean temperature as functions of latitude. We applied simple linear  
218 regression models to quantify effect sizes of each predictor ( $\beta$ -value of linear models). We derived mean  
219 treeline elevations directly from sample points and extracted climatic variables for an elevation range of  
220 1700-1800 m a.s.l., to reduce any confounding influences from adiabatic and orographic effects. Data were  
221 summarized for each selected mountain peak along the Apennines.

222 We conducted a Principal Component Analysis (PCA), using the statistical package PcOrd v6  
223 (McCune and Mefford, 1999), to explore the correlation structure of the eight predictor variables (Table 1,  
224 excluding VEG) and to identify key factors underlying position, landscape pattern, and forest tree species  
225 composition of the Apennine treelines. We overlaid treeline species composition (VEG variable) as  
226 centroids and convex hull polygons on the ordination biplot of 5484 sampling points to illustrate the mean  
227 environmental characteristic of the species groups. The statistical significance of the ordination analysis  
228 was tested using a Monte Carlo permutation method based on 10 000 runs with randomized data.

229

## 230 **RESULTS**

### 231 **Regional scale**

232 Human population decreased by 3.4% during the 1991-2011 period in the 776 “mountain  
233 municipalities”, with a stronger reduction in the southeastern and northern regions of the Apennines

234 (Figure S1 in Supplementary Materials). On average across municipalities, there was a reduction of 2.8  
235 inhabitants/km<sup>2</sup> (SD ± 11.2). However, there was no correlation between population change and forest  
236 cover change at the municipality level (Pearson's  $r = 0.009$ ), from which we infer that the gain and loss of  
237 forest cover within municipalities was not associated with a corresponding trend in recent human  
238 population change. The analysis of land cover change at the regional scale showed that forests covered  
239 approximately 50% of the Apennine land area in both 1990 and 2012. We observed an increase of 4% (4141  
240 ha) for mixed forests, 2% (1191 ha) for coniferous forests and 1% (11 119 ha) for broadleaf forests. In the  
241 same period, there was a 9% decrease of pastures (45 613 ha) and a 7% increase of shrublands (18 626 ha).  
242 Expressing the changes within each category relative to the total area subjected to land-cover change  
243 (100% = 104 804 ha), pastures experienced the greatest relative variation (44%), followed by shrublands  
244 (18%), broadleaf forests (11%), mixed forests (4%) and coniferous forests (1%). The residual change (23%)  
245 can be attributed to other merged classes. Transitions that most closely describe the succession to forest  
246 vegetation types include those from pastures to shrublands (9.05%) and from shrublands to broadleaf  
247 forests (13.75%). Other minor reforestation processes (Table S2 in Supplementary Materials) were from  
248 artificial lands (0.46%), agriculture (1.21%), orchards (0.40%), and pastures (1.68%) to broadleaf forests.  
249 Transitions to coniferous and mixed stands also originated from shrublands (0.54% and 0.62% respectively)  
250 and pastures (0.12% and 0.10% respectively).

251

### 252 **Landscape scale**

253 At the landscape scale, high elevation broadleaf forest dynamics were related to exposure. There  
254 was a significant difference (Mann-Whitney  $U = 8$ ,  $p$ -value < 0.005) between forest cover change on the  
255 northeast (NE) and southwest (SW) aspects of the mountain range: on average, forests expanded more on  
256 SW (+109%) than on NE (+19%) slopes (Figure S2 in Supplementary Materials). The other class metrics were  
257 not statistically significant at a critical alpha value of 0.05: mean patch area ( $U = 33$ ;  $p=0.55$ ) increased more  
258 on SW slopes (+96%) than NE (+61%); patch density ( $U = 0.34$ ;  $p=0.61$ ) increased on SW slopes (+42%) but  
259 decreased on NE slopes (-20%); and mean Shape Index ( $U = 37$ ;  $p=0.80$ ) increased more on SW slopes  
260 (+19%) than on NE slopes (+15%).

261

### 262 **Local scale**

263 The mean elevation of the upper treelines observed in our study area was 1755 m a.s.l. (SD ± 133  
264 m). Treeline elevations exceed 2000 m a.s.l. in many sites, especially at Mt. Pollino (mean 1942 m a.s.l., SD  
265 ± 91) and in the Majella Mts. (mean 1854 m a.s.l., SD ± 220). The lowest mean treeline location is in the  
266 Sibillini Mts. (1600 m a.s.l., SD ± 73). From north to south, the mean annual temperature of treeline  
267 increases ( $\beta = 9.2$ ,  $p < 0.05$ ), the mean elevation increases ( $\beta = 2.2$ ,  $p < 0.05$ ) and precipitation decreases ( $\beta$   
268 = -3.1,  $p < 0.05$ ; Figure 2). Across the study area, the mean annual temperature is 5.7 °C (SD ± 1). The  
269 cumulative annual mean precipitation ranges from 879 mm (Sibillini Mts.) to 753 mm (Matese Mts.).

270 *Fagus sylvatica* (Fs) is the dominant tree species in 94% of all treeline samples and at some sites is  
271 the only tree species present. The central position of the species' centroid in ordination space and the size  
272 of its convex hull confirms its wide distribution unrelated to a specific variable (Figure 3). Plantations of  
273 *Pinus nigra* ssp. *nigra* Arn. comprise 2.3% of forest limits, with a maximum relative abundance (13%) of this  
274 species recorded in the central Apennines (Gran Sasso Mts.). *Pinus mugo* Turra (3.2%) dwarf shrublands are  
275 the dominant communities only at the highest elevations (up to > 2500 m a.s.l.) of the Majella and Meta-  
276 Petroso Mts. In the southern Apennines, *Pinus heldreichii* H.Christ var. *leucodermis* comprises a small  
277 proportion of the uppermost forests (0.1% of sampled points), forming 3% of treelines in the Mt. Pollino  
278 mountain group. Human population density was negatively associated with the NE index and elevation of  
279 the treeline site (Figure 3). Moreover, the highest treelines are at greater distances from roads. *Pinus nigra*  
280 (Pn) stands were associated with lower elevation sites (1659 m a.s.l. SD  $\pm$  89 m), closer proximity to roads  
281 and on SW slopes. *Pinus mugo* (Pm) reached the highest elevations (2084 m a.s.l. SD  $\pm$  185 m), where the  
282 lowest mean annual temperatures occur. The *Pinus heldreichii* (Ph) centroid and convex hull polygon  
283 represent the very clustered and limited presence of this species at Mt. Pollino, related to high  
284 precipitation and low temperatures (2037 m a.s.l. SD  $\pm$  38 m). . Treelines formed by plantations of *Picea*  
285 *abies* (L.) Karst occurred only at Mt. Cimone (0.3%), in the northern Apennines.

286

## 287 **DISCUSSION**

### 288 **Forest cover expansion and human population decrease**

289 Agro-pastoral practices over past millennia have greatly modified Mediterranean mountain-forest  
290 landscapes (Chauchard et al. 2007). Forest clearing has given way to forest expansion processes since the  
291 19<sup>th</sup> century, following the progressive abandonment of pastures and croplands. This occurred first in  
292 marginal areas and mountain regions (Navarro & Pereira 2012), followed by a more widespread post-World  
293 War II rural depopulation process (MacDonald et al. 2000). In our regional study area of 776 Apennine  
294 municipalities, population decreased by 3.4% between 1991 and 2011, with the most rapid declines in the  
295 southeastern and northern sectors. In Europe, the rural population decreased by 17% from 1961 to 2010  
296 (FAOSTAT 2010). In Italy, the overall population increased on average by 3.3% from 1960 to 1990; but the  
297 median change within municipalities was a population loss of 5.7% and most of the administrative units  
298 featuring a population decrease are located in the Apennines, in the Alps and in the mountainous regions  
299 of Sicily and Sardinia (Falcucci et al. 2007). Demographic changes often trigger forest cover expansion in  
300 inhabited regions, but this process is not straightforward. In our study area, recent changes in forest cover  
301 were not statistically correlated to recent population dynamics within the same municipalities. Possible  
302 reasons are: i) down-valley migrations within the same municipality, ii) shifts of workers between job  
303 sectors (e.g. gain and loss of agricultural workers); iii) a lag in vegetation responses to demographic  
304 changes.

305 Spontaneous reforestation is a widespread process in Europe. Previous studies in the Apennines  
306 have found an increase in forest cover, excluding coniferous plantations, of 131%, (Assini et al. 2015), 45%  
307 (Bracchetti et al. 2012) and 48% (Rocchini et al. 2006), and a decrease of grassland cover of 67%, 57% and  
308 71% respectively. However, these studies differed in categorical definitions, time period length, type of  
309 landscape and study area extent and thus are challenging to compare directly. In our study, the increase in  
310 forest cover accounted for 1% of broadleaf forest area and 4% of mixed woodland area, for a total increase  
311 of 15 260 ha. Our finding of limited land-cover change is due to the shorter time period analyzed (22 years)  
312 and, more importantly, to the much larger size of the study area (4.3 million hectares), that included a  
313 larger variety of land-cover classes and a more diversified human presence. Importantly, the time span for  
314 our study did not include the effects of the most relevant socio-economic migrations that occurred in the  
315 1960's, after the fall of "mezzadria", a medieval agricultural management system that was used in central  
316 Italy. Natural reforestation is a complex, transient process dependent on previous land cover, and tree  
317 encroachment is usually faster in former pastures (Chauchard et al. 2007). In our study, 45 613 ha of  
318 pastures (9%) became shrublands. Many of these shrublands are likely to transition into forests in the near  
319 future, as shrub species commonly facilitate tree establishment near and above treeline (Weisberg et al.  
320 2013). This process is already occurring, given that 14% of shrublands have converted to forests over the  
321 22-year period studied. Other recent studies confirm this highly dynamic character of shrubland  
322 communities in Mediterranean mountains (Gartzia et al. 2014).

323

#### 324 **Forest cover changes and topography**

325 The influence of land-use changes on new forest dynamics is evident in most southern European  
326 mountain ranges that historically experienced long-term anthropogenic pressure, followed by a subsequent  
327 reduction or total cessation of intensive land use (Albert et al., 2008; Ameztegui et al., 2015). In the  
328 Apennines, anthropogenic pressure has historically taken the form of intensive grazing on high-elevation  
329 pastures and short-rotation coppicing in forests. The relatively recent decline of such traditional practices  
330 has progressively changed the mosaic structure of mountain landscapes. The observed increase of high-  
331 elevation forest cover (> 1500 m a.s.l.), due to gap-filling and upward tree expansion, was significantly  
332 greater on SW slopes that have experienced more intensive land uses in the past. The more rapid forest  
333 cover change on SW slopes is also consistent with climatic influences. On these warmer slopes, the upper  
334 forest limit is at lower elevations providing a more extended gradient for natural recolonization. In  
335 addition, the NE slopes, particularly on the Adriatic side, are steeper and cooler, possibly reducing the  
336 expansion rate of forest woody species (Gellrich et al. 2007; Gartzia et al. 2014). Our findings from the  
337 Apennines are consistent with recent Alpine studies (Garbarino et al., 2013; Tasser et al., 2007). In general,  
338 SW exposures in the northern hemisphere are warmer and expected to host forests at higher elevation  
339 than northern slopes (Danby and Hik 2007). Downslope expansion of alpine pastures, treeline elevation  
340 depression and forest clear-cuts are all common human-induced features on southern aspects of mountain

341 regions in the Tropics (Miehe and Miehe, 2000). In the Himalayan region, south-facing slopes are more  
342 severely disturbed, particularly due to cattle grazing (Miehe et al. 1998; Schickhoff 2005; Schickhoff et al.,  
343 2015). In the central Pyrenees, rates of woody plant encroachment and forest productivity correlate  
344 positively with westerly aspects, due to the harsher climate conditions on north-facing slopes (Poyatos et  
345 al., 2003; Gartzia et al., 2014).

346

#### 347 **Effects of climate, topography and human pressure on treeline position**

348 In the northern hemisphere, when comparing lower latitude sites with higher latitude sites at the  
349 same elevation, the former receive on average more radiant energy per unit area and tend to be warmer  
350 than the latter, , causing a negative relationship between treeline elevation and latitude (Case & Duncan  
351 2014). According to an empirical climatic relationship between treeline elevation and latitude (Hermes,  
352 1955; Körner, 1998), we expect a decrease of 130 m in treeline elevation for each latitudinal degree along  
353 the entire temperate-subtropical transition zone (30°-50°N). Along the 4.4° of latitudinal range in the  
354 Apennines, we would expect a difference of 572 m in treeline elevation between the extreme northern and  
355 southern limits. However, we found a difference of only 243 m between the mean value at Mt. Cusna-  
356 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  
357 uppermost forest limit in the Apennines is 1755 m a.s.l. (SD ± 133 m), 900 m lower than what would be  
358 expected based on global climatic relationships between temperature and treeline position (Körner 2007).  
359 Most Apennine mountain peaks do not overpass 2000 m a.s.l., indeed in the absence of edaphic limiting  
360 factors, they could be completely covered by forests. This suggests a widespread anthropogenic impact  
361 along the entire range, which caused lower treelines and substantial changes in their structure and  
362 composition. Multivariate statistics showed that topographic variables and human pressure were important  
363 drivers of treeline positioning. The highest treelines are located far from roads, particularly on NE  
364 exposures, and in municipalities with lower population density. On NE exposures, the presence of  
365 unfavorable soils for cattle grazing and steeper, colder conditions likely protected the treeline forests from  
366 past over-exploitation and left the treeline ecotone in a semi-natural condition. Monitoring tree  
367 regeneration dynamics above the current treelines could confirm what we have observed at the landscape  
368 scale: a more rapid expansion where the severity of human disturbance was historically higher. In  
369 mountains with prevalent agro-pastoral abandonment, forest migration associated with climate warming  
370 may lead to increased contrast in the forest-alpine ecotone between areas with and without intensive land  
371 use (Weisberg et al. 2013). Variables representing slope steepness and climate explained a relatively small  
372 portion of the variation of treeline position, considering that the ordination explained 39% of the total  
373 variation in the data.

374

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

376 Globally, human pressure has acted as a selective process, modifying the density and distribution of  
377 woody species according to their life history traits and commercial value. For example, in the Swiss Alps,  
378 some species were disadvantaged by intense burning and browsing; some were purposely cultivated for  
379 increased demand of food supply (e.g. *Castanea sativa*) and for other uses like charcoal and litter (e.g.  
380 *Fagus sylvatica* and deciduous *Quercus* spp.; Conedera et al. 2017). In the Apennines, human impact,  
381 geomorphology and environmental conditions likely acted concurrently to define tree species distributions  
382 in high elevation forests. *Fagus sylvatica* is by far the dominant species of the Apennine treelines (94%),  
383 forming the typical abrupt transition from forest to grasslands at the upper treeline ecotone. Today the  
384 main ecosystem services of these forests are slope protection and biodiversity conservation, but until the  
385 1960's they provided wood, charcoal production and wood pastures. Although all treeline forms may be  
386 affected by land use, abrupt treelines are most frequently associated with past human impact (Harsch &  
387 Bader 2011). Similar spatial patterns occur in beech forests of the Carpathians (Weisberg et al. 2013),  
388 *Polylepis* communities in South America (Kessler 2002), and *Nothofagus* forests of New Zealand (Cullen et  
389 al. 2001).

390 Apennine treelines with *Fagus sylvatica*, together with temperate southern hemisphere  
391 *Nothofagus* treelines and Pacific Island treelines with *Metrosideros* species, all represent taxa-specific  
392 rather than tree life-form boundaries (Körner & Paulsen 2004). Prostrate *Pinus mugo* treelines (3% of all  
393 sampled data) located at high elevations (> 2500 m a.s.l.) at Mt. Majella and Mt. Meta-Petroso in central  
394 Italy were associated with the lowest mean annual temperature and the highest mean value of the  
395 northeastness index. Some of the treelines found at the lowest elevations (mean 1659 m a.s.l.) are *Pinus*  
396 *nigra* plantations (2% of all sampled data). They occur mainly in the central Apennines and exclusively on  
397 limestone slopes. These forests were planted for slope erosion control after deforestation and intensive  
398 grazing (Barbero et al. 1998). Natural *Pinus nigra* stands are usually located within the optimal altitudinal  
399 range of 800-1500 m. However, *Pinus nigra* can grow on extremely dry sites and recent studies in the  
400 central Apennines showed that microsite topography and distance to seed source control *Pinus nigra*  
401 colonization of treeless areas (Piermattei et al. 2016; Vitali et al. 2017). Although its past distribution in  
402 Europe is difficult to reconstruct, more localized studies suggest that large populations of *Pinus nigra*  
403 (together with *Juniperus* spp.) were already present during the late Pleistocene and the Holocene in areas  
404 of the northwestern Mediterranean basin (Barbero et al. 1998; Roiron et al. 2013) and in the central  
405 Apennines during the post-Würmian period (Coltorti et al., 1998), supporting the hypothesis of an upper  
406 treeline ecotone above the closed *Fagus sylvatica* forest made of open pine woodlands and dwarf junipers  
407 (Marchetti 1936; Stanisci 1997).

408

## 409 CONCLUSION

410 Land cover changes due to demographic variations of local populations have occurred during recent  
411 decades across Europe, especially in mountainous areas (Navarro & Pereira 2012). Spontaneous

412 reforestation is a widespread process in mountain landscapes that were subjected to long-term  
413 anthropogenic pressure (Ameztegui et al., 2015; Gehrig-Fasel et al., 2007). In the Apennines, rural  
414 population decrease and forest cover increase are ongoing processes. Our results suggest that human  
415 impact is the major control on Apennine treelines, by lowering treeline elevation and constraining species  
416 composition (one dominant tree species). Moreover, the sites most severely impacted by historical human  
417 activities, on southwest aspects, have also experienced the greatest recent land cover changes.

418         Within the context of continuous land-use changes in the Apennines, we would expect that the  
419 widespread *Fagus* treelines would slowly shift upslope in the future, if future conditions will provide higher  
420 rainfall rates associated with increased growing season length and atmospheric CO<sub>2</sub> concentration.  
421 Otherwise, the negative influence of increasing temperatures may cause a retreat of *Fagus sylvatica*  
422 distribution in southern Europe (Jump et al. 2006; Sabaté et al. 2002). In general, deciduous species  
423 marking the upper tree limit in the Apennines appear to have ample opportunity to expand to climatically  
424 favorable sites at higher elevations, and more research on the constraints to *Fagus sylvatica* regeneration  
425 at high elevation is needed (Harsch et al. 2012). In contrast, the faster successional processes of *Pinus* spp.  
426 are expected to result in more rapid responses within these ecotones.

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

432

#### 433 **ACKNOWLEDGEMENTS**

434 This study was funded by Marche Polytechnic University through the "Ricerca Scientifica di Ateneo 2016"  
435 project (award number 123). We wish to thank Francesco Malandra for providing laboratory assistance.

## 436 REFERENCES

437

438 Albert, C.H., Thuiller, W., Lavorel, S., Davies, I.D., & Garbolino, E. 2008. Land-use change and subalpine tree  
439 dynamics: colonization of *Larix decidua* in French subalpine grasslands. *Journal of Applied Ecology* 45:  
440 659–669.

441 Ameztegui, A., Coll, L., Brotons, L., & Ninot, J.M. 2015. Land-use legacies rather than climate change are  
442 driving the recent upward shift of the mountain tree line in the Pyrenees. *Global Ecology and*  
443 *Biogeography* 25: 263–273.

444 Assini, S., Filipponi, F., & Zucca, F. 2015. Land cover changes in an abandoned agricultural land in the  
445 Northern Apennine (Italy) between 1954 and 2008: Spatio-temporal dynamics. *Plant Biosystems* 149 (5):  
446 807-817.

447 Barbero, M., Loisel, R., Quezel, P., Richardson, D.M., & Romane, F. 1998. Pines of the Mediterranean Basin.  
448 In *Ecology and biogeography of Pinus*/edited by David M. Richardson. Cambridge University Press.

449 Batllori, E., Gutiérrez, E. 2008. Regional treeline dynamics in response to global change in the Pyrenees.  
450 *Journal of Ecology*, 96: 1275-1288.

451 Batllori, E., Camarero, J.J., Gutiérrez, E., 2010. Current regeneration patterns at the tree line in the Pyrenees  
452 indicate similar recruitment processes irrespective of the past disturbance regime. *Journal of*  
453 *Biogeography* 37:1938–1950

454 Bracchetti, L., Carotenuto, L., & Catorci, A. 2012. Land-cover changes in a remote area of central Apennines  
455 (Italy) and management directions. *Landscape and Urban Planning* 104: 157–170.

456 Caballero, R., Fernandez-Gonzalez, F., Badia, R.P., Molle, G., Roggero, P.P., Bagella, S., D’Ottavio, P.,  
457 Papanastasis, V.P., Fotiadis, G., Sidiropoulou, A., Ispikoudis, I. 2009. Grazing systems and biodiversity in  
458 Mediterranean areas: Spain, Italy and Greece. *Pastos* 39: 9–154.

459 Camarero, J.J., Gutiérrez, E. 2004. Pace and pattern of recent treeline dynamics: response of ecotones to  
460 climatic variability in the Spanish Pyrenees. *Climatic Change*, 63, 181–200.

461 Catorci, A., Gatti, R., Cesaretti, S. 2012. Effect of sheep and horse grazing on species and functional  
462 composition of sub-Mediterranean grasslands. *Applied Vegetation Science* 15: 459–469.

463 Case, B.S., & Duncan, R.P. 2014. A novel framework for disentangling the scale-dependent influences of  
464 abiotic factors on alpine treeline position. *Ecography* 838–851.

465 Chauchard, S., Carcaillet, C., & Guibal, F. 2007. Patterns of land-use abandonment control tree-recruitment  
466 and forest dynamics in Mediterranean mountains. *Ecosystems* 10: 936–948.

467 Coltorti, M., Albanelli, A., Bertini, A., Ficarelli, G., Laurenzi, M.A., Napoleone, G., Torre, D. 1998. The colle  
468 Curtimammal site in the Colfiorito area (Umbria-Marche Apennine, Italy): geomorphology, stratigraphy,  
469 paleomagnetism and palynology. *Quaternary International* 47-48: 107–116

- 470 Conedera, M., Colombaroli, D., Tinner, W., Krebs, P., & Whitlock, C. 2017. Insights about past forest  
471 dynamics as a tool for present and future forest management in Switzerland. *Forest Ecology and*  
472 *Management* 388: 100–112.
- 473 Conti, G., & Fagarazzi, L. 2005. Forest expansion in mountain eco- systems: “environmentalist’s dream” or  
474 societal nightmare? *Planum* 11: 1–20.
- 475 Cullen, L., Stewart, G., Duncan, R., & Palmer, J. 2001. Disturbance and climate warming influences on New  
476 Zealand *Nothofagus* tree-line population dynamics. *Journal of Ecology* 89: 1061–1071.
- 477 Dainese, M., Aikio, S., Hulme, P.E., Bertolli, A., Prosser, F., Marini, L. 2017. Human disturbance and upward  
478 expansion of plants in a warming climate. *Nature Climate Change*.
- 479 Danby, R.K., & Hik, D.S. 2007. Variability, contingency and rapid change in recent subarctic alpine tree line  
480 dynamics. *Journal of Ecology* 95: 352–363.
- 481 Daniels, L.D., Veblen, T.T. 2004. Spatio-temporal influences of climate on altitudinal treeline in northern  
482 Patagonia. *Ecology*, 85, 1284–1296.
- 483 Definiens Imaging. 2004. eCognition professional. Munich.
- 484 Dibari, C., Argenti, G., Catolfi, F., Moriondo, M., Staglianò, N., & Bindi, M. 2015. Pastoral suitability driven by  
485 future climate change along the Apennines. *Italian Journal of Agronomy* 10: 109.
- 486 Didier, L. 2001. Invasion patterns of European larch and Swiss stone pine in subalpine pastures in the  
487 French Alps. *Forest Ecology and Management* 145: 67–77.
- 488 Dirnböck, T., Dullinger, S., & Grabherr, G. 2003. A regional impact assessment of climate and land-use  
489 change on alpine vegetation. *Journal of Biogeography* 30: 401–417.
- 490 Falcucci, A., Maiorano, L., & Boitani, L. 2007. Changes in land-use/land-cover patterns in Italy and their  
491 implications for biodiversity conservation. *Landscape Ecology* 22: 617–631.
- 492 FAOSTAT. 2010. <http://faostat.fao.org>. Accessed 10 Dec 2015.
- 493 Garbarino, M., Weisberg, P.J., & Motta, R. 2009. Interacting effects of physical environment and  
494 anthropogenic disturbances on the structure of European larch (*Larix decidua* Mill.) forests. *Forest*  
495 *Ecology and Management* 257: 1794–1802.
- 496 Garbarino, M., Lingua, E., Subirà, M.M., & Motta, R. 2011. The larch wood pasture: Structure and dynamics  
497 of a cultural landscape. *European Journal of Forest Research* 130: 491–502.
- 498 Garbarino, M., Lingua, E., Weisberg, P.J., Bottero, A., Meloni, F., & Motta, R. 2013. Land-use history and  
499 topographic gradients as driving factors of subalpine *Larix decidua* forests. *Landscape Ecology* 28: 805–  
500 817.
- 501 Gartzia, M., Alados, C.L., & Perez-Cabello, F. 2014. Assessment of the effects of biophysical and  
502 anthropogenic factors on woody plant encroachment in dense and sparse mountain grasslands based on  
503 remote sensing data. *Progress in Physical Geography* 38: 201–217.
- 504 Gehrig-Fasel, J., Guisan, A., & Zimmermann, N.E. 2007. Tree line shifts in the Swiss Alps: Climate change or  
505 land abandonment? *Journal of Vegetation Science* 18: 571–582.

- 506 Gellrich, M., Baur, P., Koch, B., & Zimmermann, N.E. 2007. Agricultural land abandonment and natural  
507 forest re-growth in the Swiss mountains: A spatially explicit economic analysis. *Agriculture, Ecosystems  
508 and Environment* 118: 93–108.
- 509 Gotsch, N., Flury, C., Kreuzer, M., Rieder, P., Heinemann, H.R., Mayer, A.C. & Wettstein, H.-R. 2004. Land-  
510 und Forstwirtschaft im Alpenraum - Zukunft im Wandel. Synthesebericht des Polyprojektes «PRIMALP  
511 ETH Zürich». Wissenschaftsverlag Vauk Kiel KG, Kiel, Germany.
- 512 Harsch, M.A., & Bader, M.Y. 2011. Treeline form - a potential key to understanding treeline dynamics.  
513 *Global Ecology and Biogeography* 20: 582–596.
- 514 Harsch, M. a., Buxton, R., Duncan, R.P., Hulme, P.E., Wardle, P., & Wilmshurst, J. 2012. Causes of tree line  
515 stability: Stem growth, recruitment and mortality rates over 15 years at New Zealand *Nothofagus* tree  
516 lines. *Journal of Biogeography* 39: 2061-2071.
- 517 Hengl, T., de Jesus, J.M., MacMillan, R.A., Batjes, N.H., Heuvelink, G.B.M., Ribeiro, E., Samuel-Rosa, A.,  
518 Kempen, B., Leenaars, J.G.B., Walsh, M.G., & Gonzalez, M.R. 2014. SoilGrids1km - Global Soil  
519 Information Based on Automated Mapping. *PLoS ONE* 9(8): e105992.
- 520 Hermes, K. 1955. Die Lage der oberen Waldgrenze in den Gebirgen der Erde und ihr Abstand zur  
521 Schneegrenze. Kolner Geographische Arbeiten, Heft 5, Geographisches Institut, Universität Koln.
- 522 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, G., & Jarvis, A. 2005. Very high resolution interpolated  
523 climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
- 524 Hofgaard, A. 1997. Inter-Relationships between treeline position, species diversity, land use and climate  
525 change in the Central Scandes Mountains of Norway. *Global Ecology and Biogeography Letters* 6: 419–  
526 429.
- 527 Holtmeier, F.-K., & Broll, G. 2005. Sensitivity and response of northern hemisphere altitudinal and polar  
528 treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography* 14:  
529 395-410.
- 530 Houston Durrant, T., de Rigo, D., Caudullo, G., 2016. *Fagus sylvatica* and other beeches in Europe:  
531 distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston  
532 Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg.
- 533 ISTAT. 1999. 13° Censimento generale della popolazione e delle abitazioni 1991. <http://www.istat.it/>.  
534 Accessed 10 Dec 2015.
- 535 ISTAT. 2011. 15° Censimento della popolazione e delle abitazioni 2011. <http://www.istat.it/>. Accessed 10  
536 Dec 2015.
- 537 Jobbágy, E.G., & Jackson, R.B. 2000. Global controls of forest line elevation in the northern and southern  
538 hemispheres. *Global Ecology & Biogeography* 9: 253–268.
- 539 Jump, A.S., Hunt, J.M., Penuelas, J., 2006. Rapid climate change-related growth decline at the southern  
540 range edge of *Fagus sylvatica*. *Global Change Biology*: 12, 2163–2174.
- 541 Kessler, M.M. 2002. The “Polylepis problem”: Where do we stand? *Ecotropica* 8: 97–116.

- 542 Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115:  
543 445–459.
- 544 Körner, C. 2007. Climatic treelines: conventions, global patterns, causes. *Erdkunde* 61: 316-324.
- 545 Körner, C. 2012. Alpine Treelines. *Springer*, Berlin.
- 546 Körner, C., & Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures. *Journal of*  
547 *Biogeography* 31: 713–732.
- 548 Leonelli, G., Pelfini, M., Morra di Cella, U., & Garavaglia, V. 2011. Climate Warming and the Recent Treeline  
549 Shift in the European Alps: The Role of Geomorphological Factors in High-Altitude Sites. *Ambio* 40: 264–  
550 273.
- 551 Leuch, M. 2005. Die Alpwirtschaft heute und morgen. LID Dossier 409: 2–15.
- 552 MacDonald, D., Crabtree, J., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J., & Gibon, A.  
553 2000. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy  
554 response. *Journal of Environmental Management* 59: 47–69.
- 555 Malanson, G.P., Butler, D.R., Fagre, D.B., Walsh, S.J., Tomback, D.F., Daniels, L.D., Resler, L.M., Smith, W.K.,  
556 Weiss, D.J. (...) & Millar, C.I. 2007. Alpine Treeline of Western North America: Linking Organism-To-  
557 Landscape Dynamics. *Physical Geography* 28: 378–396.
- 558 Malanson, G.P., Resler, L.M., Bader, M.Y., Holtmeier, F.K., Butler, D.R., Weiss, D.J., Daniels, L.D., & Fagre,  
559 D.B. 2011. Mountain treelines: a roadmap for research orientation. *Arctic, Antarctic, and Alpine*  
560 *Research* 43: 167–177.
- 561 Marchetti, M. 1936. Ricerche sulla vegetazione dell'Etruria marittima VI—Analisi pollinica della torbiera di  
562 Campotosto (Appennino abruzzese). *Nuovo Giornale Botanico Italiano* 43: 831-871.
- 563 McCune, B., Mefford, M.J. 1999. PC-ORD. MjM Software Design, Gleneden Beach.
- 564 McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: spatial pattern analysis program for categorical  
565 and continuous maps. University of Massachusetts, Amherst.
- 566 Miehe, G., Miehe, S., Huang, J., Otsu, T. 1998. Forschungsdefizite und -perspektiven zur Frage der  
567 potentiellen natürlichen Bewaldung in Tibet. *Petermanns Geographische Mitteilungen* 142: 155-164
- 568 Miehe, G., Miehe, S. 2000. Comparative high mountain research on the treeline ecotone under human  
569 impact. *Erdkunde* 54: 34–50.
- 570 Motta, R. & Garbarino, F. 2003. Stand history and its consequences for the present and future dynamic in  
571 two silver fir (*Abies alba* Mill.) stands in the high Pesio Valley (Piedmont, Italy). *Annals of Forest Science*  
572 60: 361-370.
- 573 Motta, R., Morales, M. & Nola, P. 2006. Human land-use, forest dynamics and tree growth at the treeline in  
574 the Western Italian Alps. *Annals of Forest Science* 63: 739–747.
- 575 Navarro L.M., & Pereira, H.M., 2012. Rewilding abandoned landscapes in Europe. In: Rewilding European  
576 Landscapes (Eds: H.M. Pereira, L.M. Navarro). Springer International Publishing, pp. 3-23.

- 577 Nocentini, S., 2009. Structure and management of beech (*Fagus sylvatica* L.) forests in Italy. *iForest*: 2 (3),  
578 105–113.
- 579 Ott, E., Frehner, M., Frey, H.U. & Lüscher, P. 1997. Gebirgsnadelwälder, ein praxisorientierter Leitfa- den für  
580 eine standortgerechte Waldbehandlung. Verlag Paul Haupt, Bern, Switzerland.
- 581 Palombo, C., Chirici, G., Marchetti, M., & Tognetti, R. 2013. Is land abandonment affecting forest dynamics  
582 at high elevation in Mediterranean mountains more than climate change? *Plant Biosystems* 147: 1–11.
- 583 Pelorosso, R., Leone, A., Boccia, L. 2009. Land cover and land use change in the Italian central Apennines: a  
584 comparison of assessment methods. *Applied Geography* 29: 35–48.
- 585 Piermattei, A., Garbarino, M., Renzaglia, F., & Urbinati, C. 2013. Climate influence on the expansion and  
586 tree-ring growth of *Pinus nigra* L. at High Altitude in the Central Apennines. *The Open Forest Science*  
587 *Journal* 6: 54–56.
- 588 Piermattei, A., Garbarino, M., & Urbinati, C. 2014. Structural attributes tree-ring growth and climate  
589 sensitivity of *Pinus nigra* Arn. at high altitude: common patterns of a possible treeline shift in the central  
590 Apennines (Italy). *Dendrochronologia* 32: 210–219.
- 591 Piermattei, A., Lingua, E., Urbinati, C., & Garbarino, M. 2016. *Pinus nigra* anthropogenic treelines in the  
592 central Apennines show common pattern of tree recruitment. *European Journal of Forest Research* 135:  
593 1119–1130.
- 594 Poyatos, R., Latron, J. & Llorens, P. 2003. Land use and land cover change after farmland abandonment. The  
595 case of a mediterranean mountain area (Catalan Pre-Pyrenees). *Mountain Research and Development*  
596 23: 362-368.
- 597 Rocchini, D., Perry, G.L.W., Salerno, M., Maccherini, S., & Chiarucci, A. 2006. Landscape change and the  
598 dynamics of open formations in a natural reserve. *Landscape and Urban Planning* 77: 167–177.
- 599 Roiron, P., Chabal, L., Figueiral, I., Terral, J.F., & Ali, A.A. 2013. Palaeobiogeography of *Pinus nigra* Arn.  
600 subsp. *salzmannii* (Dunal) Franco in the north-western Mediterranean Basin: A review based on  
601 macroremains. *Palaeobotany and Palynology* 194: 1–11.
- 602 Sabaté, S., Gracia, C.A., Sánchez, A., 2002. Likely effects of climate change on growth of *Quercus ilex*, *Pinus*  
603 *halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region.  
604 *Forest Ecology and Management* 162, 23–37.
- 605 Schickhoff, U. 2005. The upper timberline in the Himalayas, Hindu Kush and Karakorum: A review of  
606 geographical and ecological aspects. *Mountain Ecosystems. Studies in Treeline Ecology*. Springer. pp.  
607 275-354.
- 608 Schickhoff, U., Bobrowski, M., Bohner, J., Burzle, B., Chaudhary, R.P., Gerlitz, P., Heyken, H., Lange, J.,  
609 Muller, M., (...) & Wedegartner, R. 2015. Do Himalayan treelines respond to recent climate change? An  
610 evaluation of sensitivity indicators. *Earth System Dynamics* 6: 245–265.
- 611 Stanisci, A. 1997. Gli arbusteti altomontani dell'Appennino centrale e meridionale. *Fitosociologia* 34: 3-46.

- 612 Tachikawa, T., Kaku, M., Iwasaki, A., Gesch, D., Oimoen, M., Zhang, Z., Danielson, J., Krieger, T., Curtis, B.,  
613 (...) & Carabajal, C. 2011. ASTER Global Digital Elevation Model Version 2 – Summary of Validation  
614 Results. NASA Land Processes Distributed Active Archive Center.
- 615 Tasser, E., Walde, J., Tappeiner, U., Teutsch, A., & Nogglér, W. 2007. Land-use changes and natural  
616 reforestation in the Eastern Central Alps. *Agriculture, Ecosystems and Environment* 118: 115–129.
- 617 Todaro, L., Andreu, L., D’Alessandro, C.M., Gutiérrez, E., Cherubini, P., & Saracino, A. 2007. Response of  
618 *Pinus leucodermis* to climate and anthropogenic activity in the National Park of Pollino (Basilicata,  
619 Southern Italy). *Biological Conservation* 137: 507–519.
- 620 Torta, G. 2004. Consequences of rural abandonment in a Northern Apennines landscape (Tuscany, Italy). In:  
621 Mazzoleni S, Di Pasquale G, Mulligan M, Di Martino P, Rego F (eds) Recent dynamics of the  
622 mediterranean vegetation and landscape. Wiley, Chichester, pp. 157–165.
- 623 Treml, V., Senfeldr, M., Chuman, T., Ponocna, T., & Demkova, K. 2016. Twentieth century treeline ecotone  
624 advance in the Sudetes Mountains (Central Europe) was induced by agricultural land abandonment  
625 rather than climate change. *Journal of Vegetation Science* 27: 1209–1221.
- 626 Vacchiano, G., Garbarino, M., Lingua, E., & Motta, R. 2017. Forest dynamics and disturbance regimes in the  
627 Italian Apennines. *Forest Ecology and Management* 388: 57–66.
- 628 Vitali, A., Camarero, J.J., Garbarino, M., Piermattei A., Urbinati, C. 2017. Deconstructing human-shaped  
629 treelines: Microsite topography and distance to seed source control *Pinus nigra* colonization of treeless  
630 areas in the Italian Apennines. *Forest Ecology and Management* 406: 37-45.
- 631 Weisberg, P.J., Shandra, O., & Becker, M.E. 2013. Landscape influences on recent timberline shifts in the  
632 Carpathian mountains: abiotic influences modulate effects of land-use change. *Arctic, Antarctic, and  
633 Alpine Research* 45: 404–414.
- 634 Woods, K.D., 2014. Problems with edges: tree lines as indicators of climate change (or not). *Applied  
635 Vegetation Science* 17: 4-5
- 636

637 **LIST OF ALL APPENDICES**

638

639 Appendix 1. Supplementary Materials for Online Publication Only: Table S1, Table S2, Figure S1 and Figure S2.

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

Category	Code	Variable Description	Unit	Source	Scale/pixel size
Topography	ELEV	Elevation a.s.l.	m	Aster GdemV2	30 m x 30 m
	NE	Northeastness Index	-	Aster GdemV2	30 m x 30 m
	SLO	Slope angle	°	Aster GdemV2	30 m x 30 m
Climate	TEMP	Annual mean temperature	°C	Worldclim BIO <sub>1</sub>	1 km x 1 km
	PREC	Annual precipitation	mm	Worldclim BIO <sub>12</sub>	1 km x 1 km
Soil	SAND	Sand proportion in the soil texture	%	ISRIC SoilGrid	1 km x 1 km
Human infrastructure	ROAD	Proximity to the closest road	m	OpenStreetMap	vector
	POP	Current population density	inhabitants/km <sup>2</sup>	ISTAT database	vector
Vegetation	VEG	Dominant treeline species	-	Thematic maps	vector

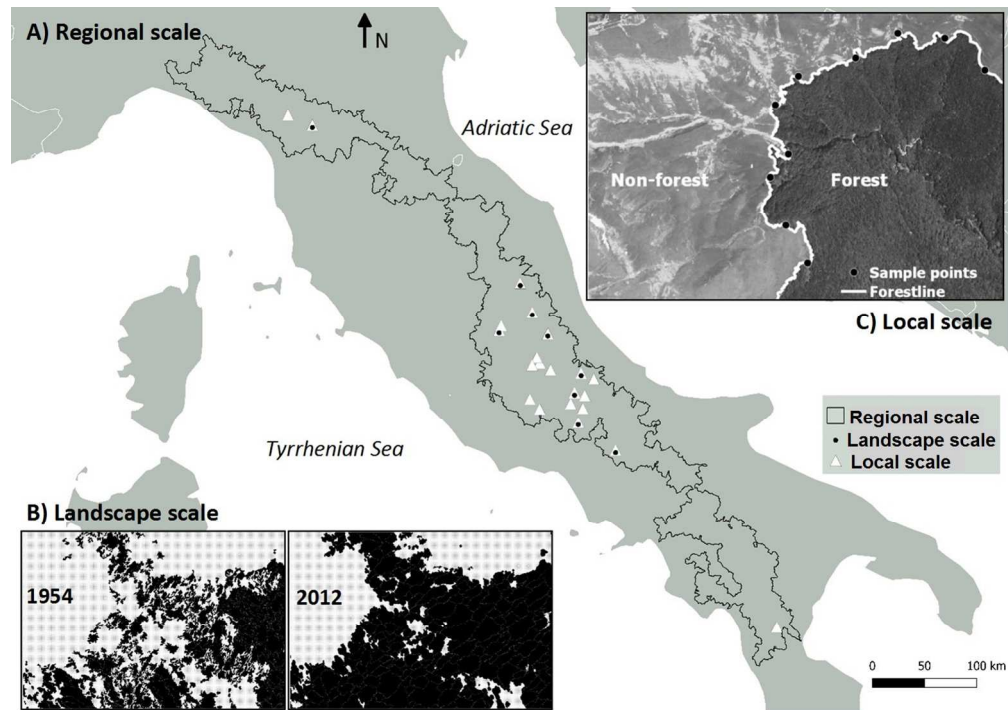


Figure 1 – A) Black contour line: the regional scale study area along the Apennines; Black dots: the nine landscape scale study sites; White triangles: the 22 local scale sampled segments; B) example of sample design procedure for the landscape scale analysis (forest cover and metrics changes); C) example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

132x95mm (300 x 300 DPI)

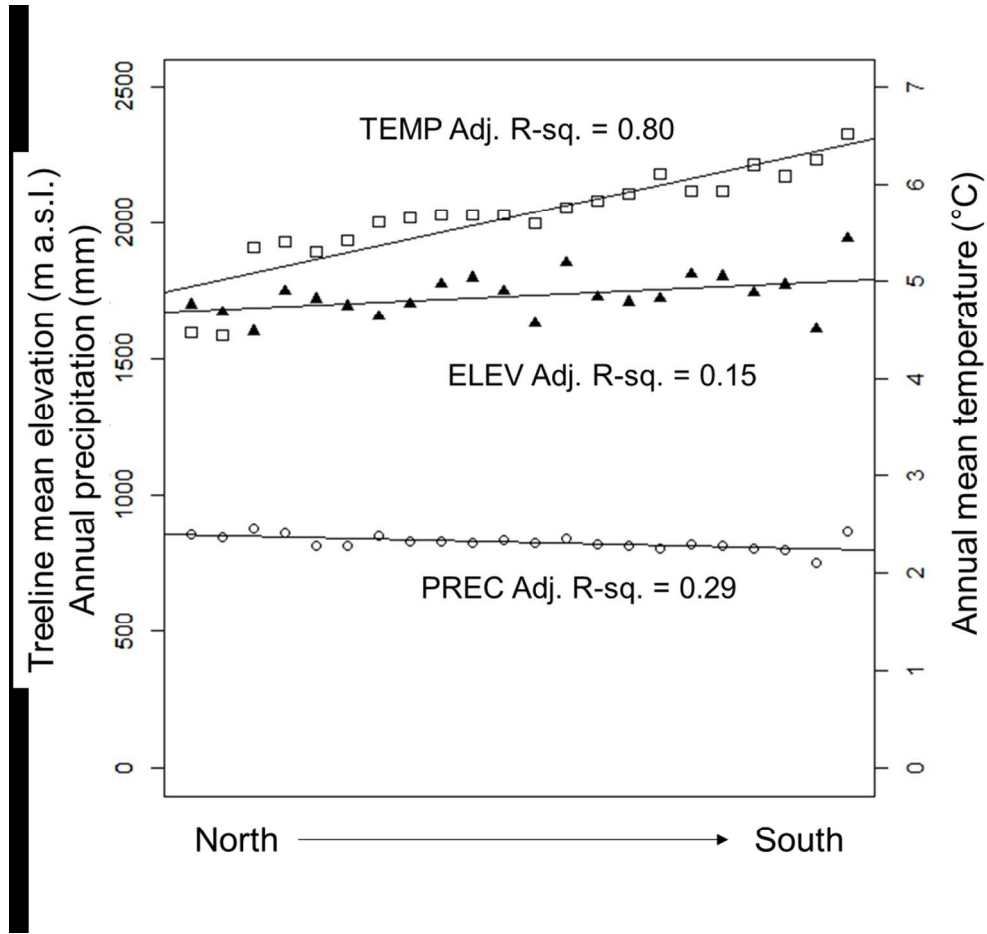


Figure 2 - Mean annual temperature (white squares), annual precipitation (white dots) and treeline elevation (black triangles) along the latitudinal range of the Apennines from North (left) to South (right).

93x86mm (300 x 300 DPI)

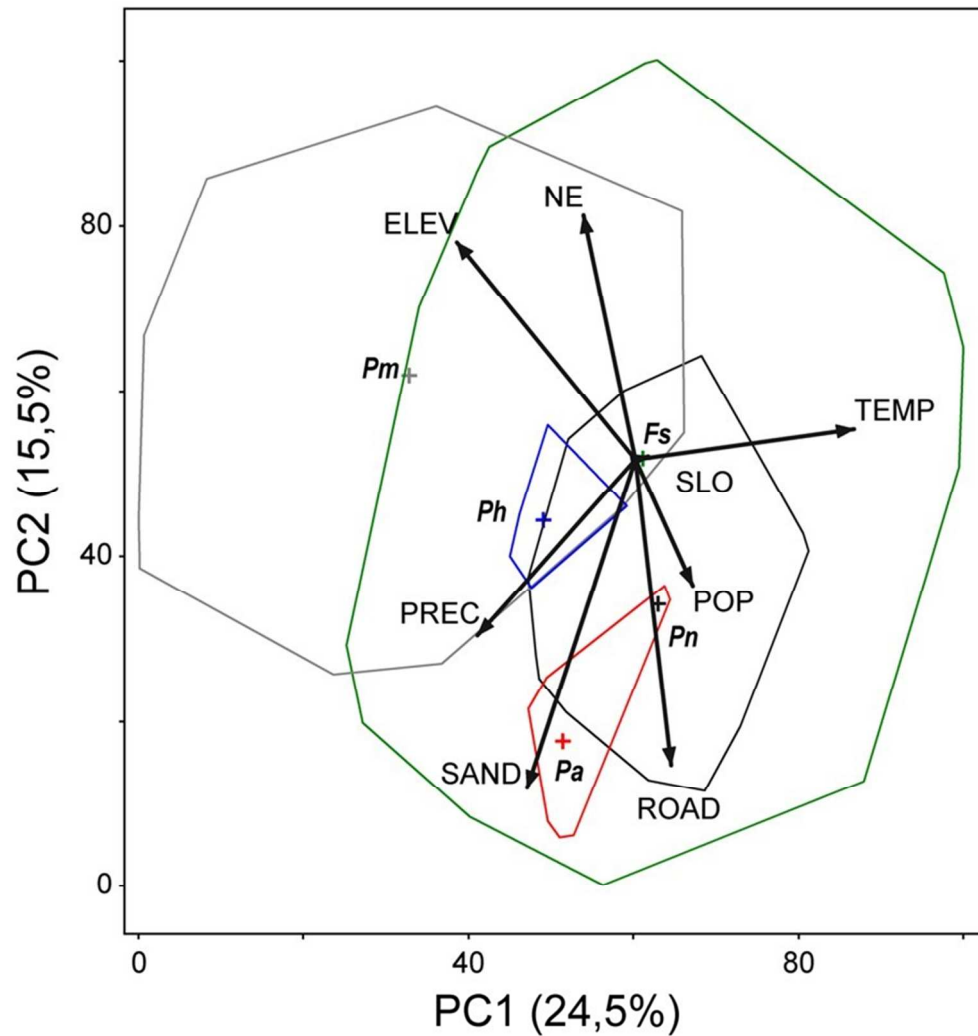


Figure 3 - Biplot from Principal Components Analysis of 5484 sampled points with tree species distribution polygons and centroids (cross): *Fs*=*Fagus sylvatica* (green), *Pn*= *Pinus nigra* (black), *Pa*=*Picea abies* (red), *Pm*=*Pinus mugo* (grey), *Ph*=*Pinus heldreichii* (blue). Linear vectors are 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.

78x85mm (300 x 300 DPI)

## SUPPLEMENTARY MATERIALS FOR ONLINE PUBLICATION ONLY

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

Local scale mountain range	Latitude WGS 84 [°]	Longitude WGS 84 [°]	Mean treeline elevation ( $\pm$ SD) [m a.s.l.]	Local scale area > 1500 m a.s.l. [km <sup>2</sup> ]	Landscape scale mountain peaks	Landscape scale area [km <sup>2</sup> ]	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
1990	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

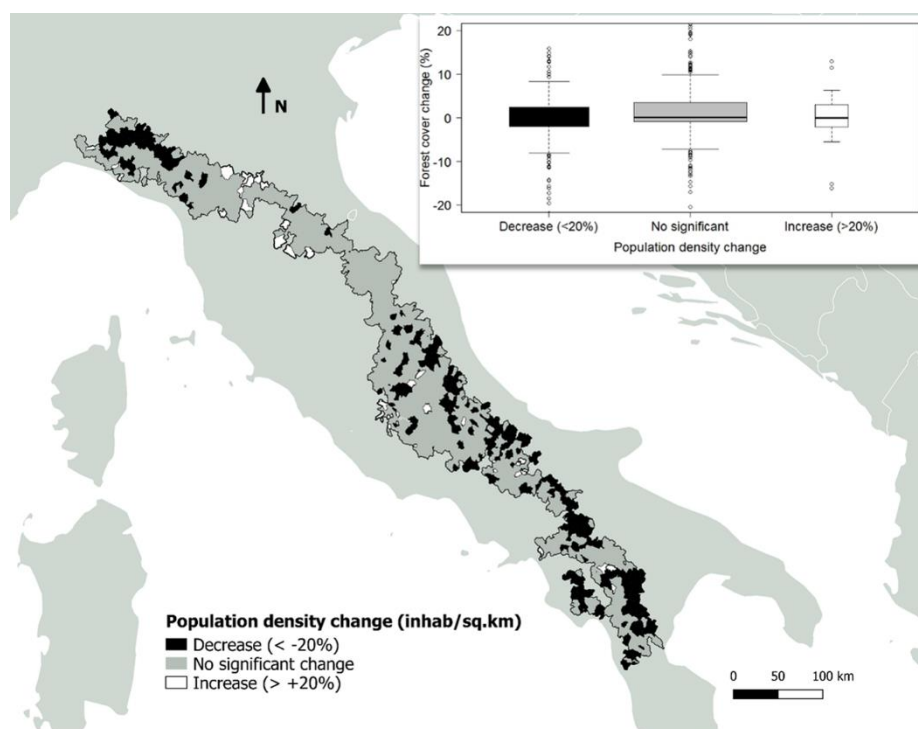


Figure S1 – Population density change (inhabitants per square kilometer) expressed in percentage for the period 1991-2011. White and black areas indicate municipalities with positive and negative relevant changes. Grey municipalities are those without significant change in population density ( $-20\%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

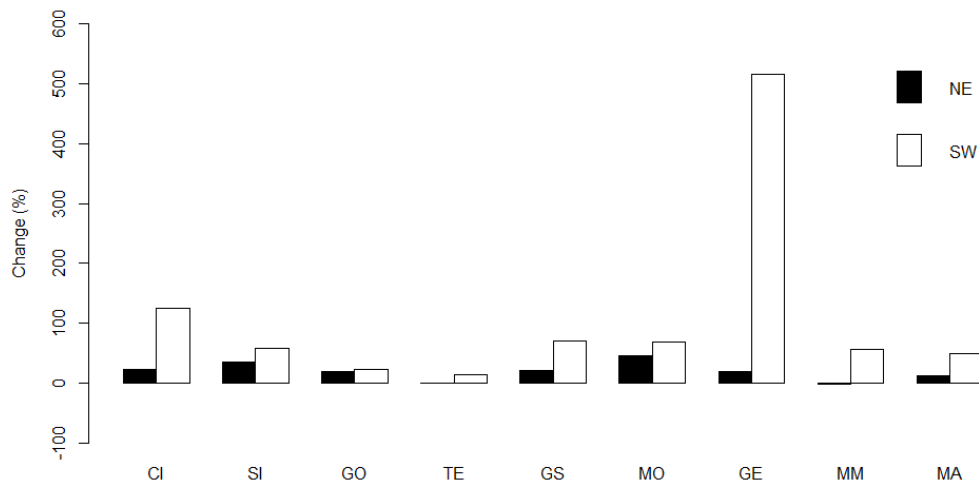


Figure S2 - Percent of relative broadleaf forest cover changes (1954-2012) above the elevation threshold of 1500 m a.s.l. by the two main exposures. Mountain peak codes on the X-axis are listed from North (left) to South (right): CI= Mt. Cimone, GE= Mt. Genzana, GO= Mt. Gorzano, GS= Mt. Gran Sasso, MA=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

Multiscale approach is an excellent tool to detect the recent dynamics of Mediterranean anthropogenic treelines. Along the Apennines man lowered treeline elevation and constrained forest species composition. Beech is the dominant species and the altitudinal transition broadleaf-conifer species does not generally occur. Apennine treelines will react differently to global environmental changes than climatic ones requiring the analysis of land-use history.



1004x1004mm (72 x 72 DPI)