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TITLE

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

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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 km^2), 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 km^2 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 km^2 each; and iii) at a local scale with 5484 sampling points at 500-m distance along the current treeline (Figure 1).

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-km^2 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 = ± 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 m^2 (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 ≥ 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 ≥ 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.

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/km^2 (SD ± 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 ± 133 m). Treeline elevations exceed 2000 m a.s.l. in many sites, especially at Mt. Pollino (mean 1942 m a.s.l., SD ± 91) and in the Majella Mts. (mean 1854 m a.s.l., SD ± 220). The lowest mean treeline location is in the Sibillini Mts. (1600 m a.s.l., SD ±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 ± 1). The cumulative annual mean precipitation ranges from 879 mm (Sibillini Mts.) to 753 mm (Matese Mts.).

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 ± 89 m), closer proximity to roads and on SW slopes. *Pinus mugo* (Pm) reached the highest elevations (2084 m a.s.l. SD ± 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 ± 38 m). . Treelines formed by plantations of *Picea abies* (L.) Karst occurred only at Mt. Cimone (0.3%), in the northern Apennines.

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 ± 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), *Polylepis* 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 CO_2 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.

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LIST OF ALL APPENDICES

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_1	1 km x 1 km
	PREC	Annual precipitation	mm	Worldclim BIO_{12}	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/km²	ISTAT database	vector
Vegetation	VEG	Dominant treeline species	-	Thematic maps	vector

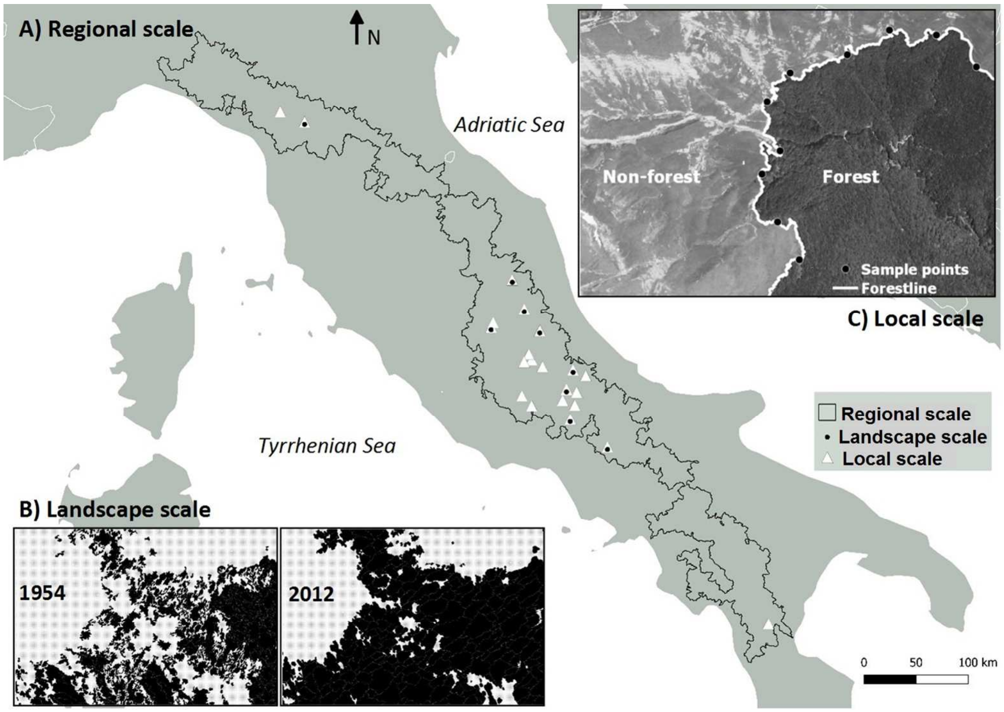

Figure 1 – A) Black contour line: the regional scale study area along the Apennines; Black dots: the nine landscape scale study sites; White triangles: the 22 local scale sampled segments; B) example of sample design procedure for the landscape scale analysis (forest cover and metrics changes); C) example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

132x95mm (300 x 300 DPI)

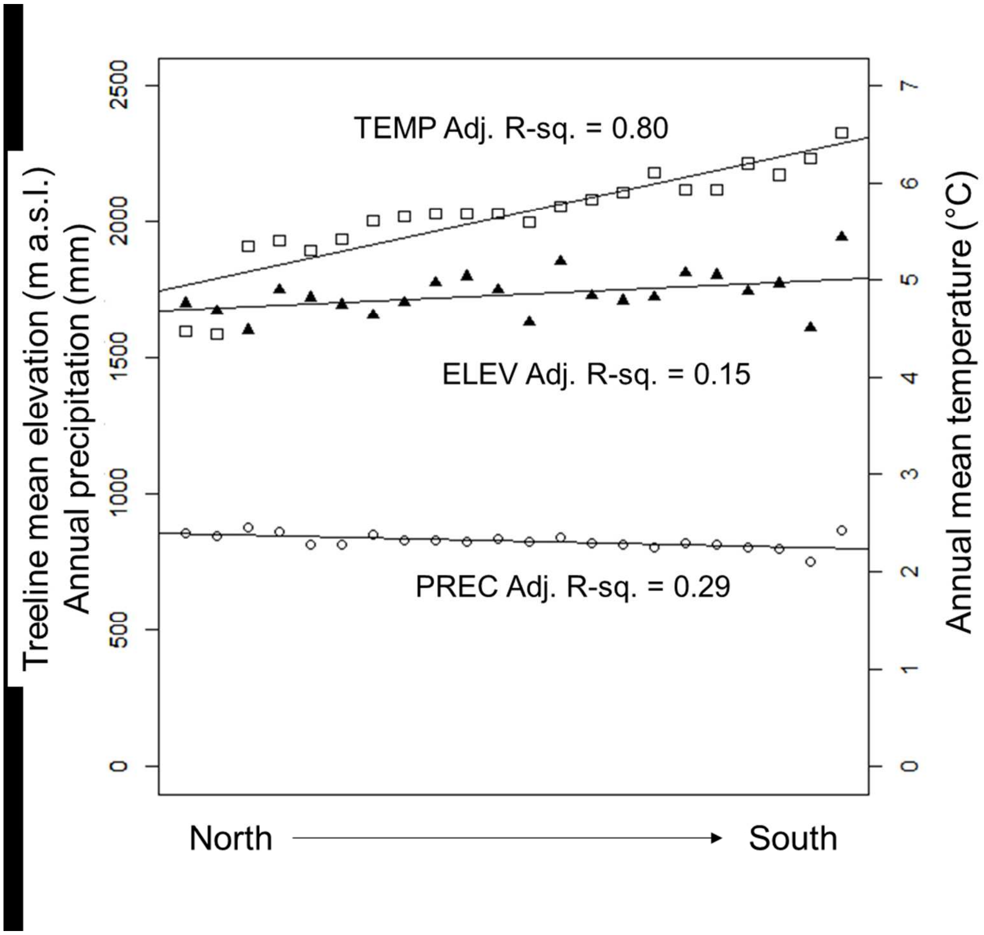

Figure 2 - Mean annual temperature (white squares), annual precipitation (white dots) and treeline elevation (black triangles) along the latitudinal range of the Apennines from North (left) to South (right).

93x86mm (300 x 300 DPI)

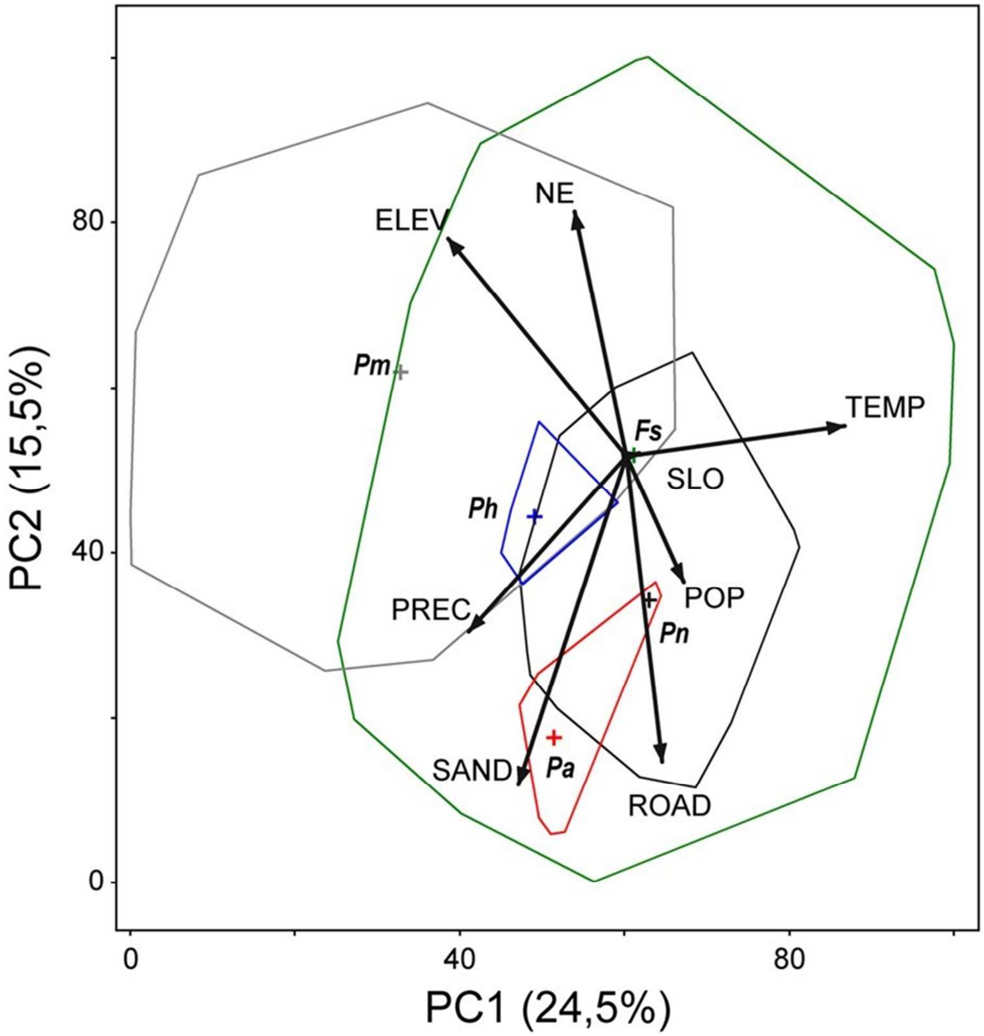

Figure 3 - Biplot from Principal Components Analysis of 5484 sampled points with tree species distribution polygons and centroids (cross): Fs=Fagus sylvatica (green), Pn= Pinus nigra (black), Pa=Picea abies (red), Pm=Pinus mugo (grey), Pl=Pinus heldreichii (blue). Linear vectors are correlations (p 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

78x85mm (300 x 300 DPI)

SUPPLEMENTARY MATERIALS FOR ONLINE PUBBLICATION 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 (± SD) [m a.s.l.]	Local scale area > 1500 m a.s.l. [km²]	Landscape scale mountain peaks	Landscape scale area [km²]	Vegetation maps source
Mt. Prado - Mt. Cusna	44.27	10.40	1699 (±47)	31			Carta aree forestali Regione Emilia-Romagna Inventario Forestale Regione Toscana
Mt. Cimone	44.19	10.70	1670 (±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 (±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 (±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 (±84)	11			Carta Forestale Regione Lazio
Reatini (Mt. Terminillo)	42.47	13.00	1693 (±83)	27	TE NE (Mt. Terminillo) - TE SW (Mt. Terminillo)	16 - 16	Carta Forestale Regione Lazio
Gran Sasso	42.45	13.57	1655 (±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 (±105)	35			Carta Forestale Regione Abruzzo
Mt. Sirente-Mt. Velino (Mt. Rotondo)	42.20	13.48	1774 (±96)	9			Carta Forestale Regione Abruzzo
Mt. Sirente-Mt. Velino (Mt. Velino)	42.18	13.39	1799 (±90)	131			Carta Forestale Regione Abruzzo
Mt. Sirente-Mt. Velino (Mt. Sirente)	42.14	13.61	1750 (±91)	41			Carta Forestale Regione Abruzzo
Mt. Morrone	42.12	13.97	1627 (±73)	11	MO NE (Mt. Morrone) - MO SW (Mt. Morrone)	16 - 16	Carta Forestale Regione Abruzzo
Majella	42.07	14.11	1854 (±220)	146			Carta Forestale Regione Abruzzo
Mt. Genzana	41.95	13.89	1728 (±98)	27	GE NE (Mt. Genzana) - GE SW (Mt. Genzana)	16 - 16	Carta Forestale Regione Abruzzo
Mt. Rotella	41.93	14.01	1710 (±88)	13			Carta Forestale Regione Abruzzo
Monti Càntari (Mt.Viglio)	41.89	13.37	1723 (±75)	15			Carta Forestale Regione Abruzzo Carta Forestale Regione Lazio
Monti Marsicani (Mt.Marsicano)	41.85	13.85	1812 (±101)	81			Carta Forestale Regione Abruzzo
Monti Marsicani (Mt.Greco)	41.81	13.99	1803 (±107)	76			Carta Forestale Regione Abruzzo
Monti Simbruini	41.80	13.49	1743 (±89)	14			Carta Forestale Regione Abruzzo Carta Forestale Regione Lazio
Monti della Meta	41.69	13.94	1772 (±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 (±53)	10	MA NE (Mt. Miletto) - MA SW (Mt. Miletto)	16 - 16	Carta Forestale Regione Molise
Pollino	39.91	16.19	1942 (±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

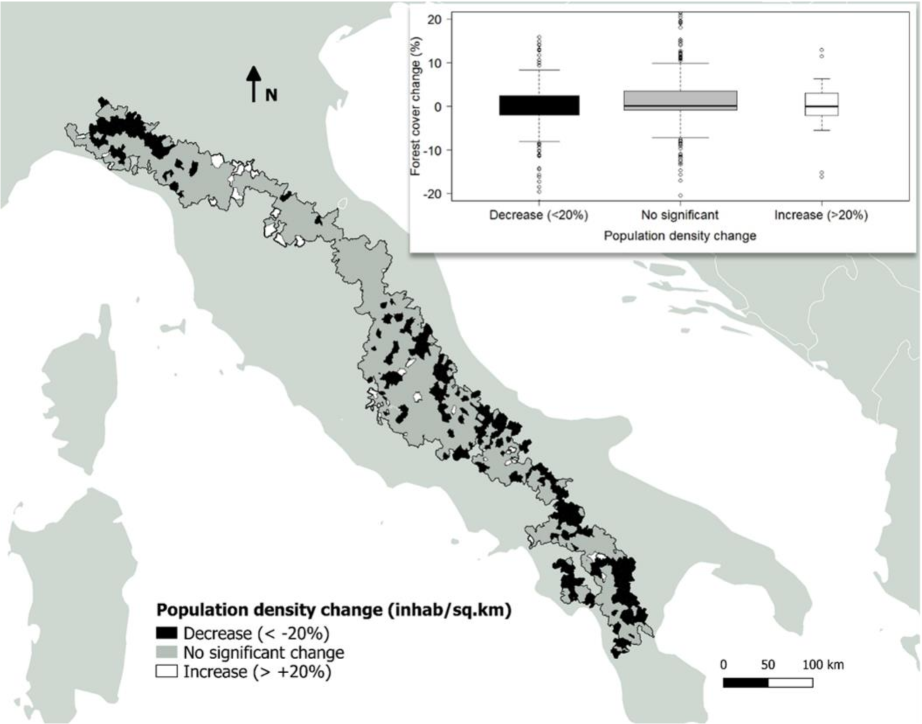

Figure S1 – Population density change (inhabitants per square kilometer) expressed in percentage for the period 1991-2011. White and black areas indicate municipalities with positive and negative relevant changes. Grey municipalities are those without significant change in population density (-20% <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

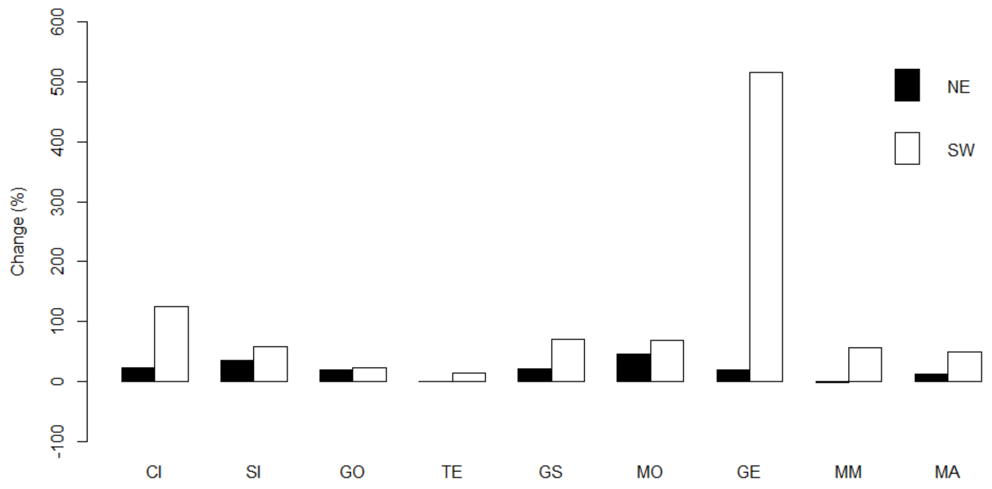

Figure S2 - Percent of relative broadleaf forest cover changes (1954-2012) above the elevation threshold of 1500 m a.s.l. by the two main exposures. Mountain peak codes on the X-axis are listed from North (left) to South (right): CI= Mt. Cimone, GE= Mt. Genzana, GO= Mt. Gorzano, GS= Mt. Gran Sasso, MA=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

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