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

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Original

Deconstructing human-shaped treelines: Microsite topography and distance to seed source control Pinus nigra colonization of treeless areas in the Italian Apennines / Vitali, Alessandro; Camarero, J. Julio; Garbarino, Matteo; Piermattei, Alma; Urbinati, Carlo. - In: FOREST ECOLOGY AND MANAGEMENT. - ISSN 0378-1127. - ELETTRONICO. - 406:(2017), pp. 37-45. [10.1016/j.foreco.2017.10.004]

Availability:

This version is available at: 11566/252130 since: 2022-07-07T07:57:40Z

Publisher:

Published DOI:10.1016/j.foreco.2017.10.004

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| 3          | areas in the Italian Apennines   |
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| 21         |  |
| 22         | Keywords   |
| 23         |  |
| 24         | Anthropogenic treeline, black pine, pasture abandonment, pine recruitment. Mediterranean   |
| 25         | mountains  |
| 26         |  |
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#### 27 Highlights

Land-use changes can trigger tree colonization in high-elevation grasslands.
Rapid recruitment and high tree growth rates facilitate treeline upward shift.
Microsite topography and distance from pine plantations influence treeline dynamics. *Pinus nigra* treelines in Italy can respond quickly to the future global change.

# 33 Abstract

Human-shaped treelines are a common feature in mountain landscapes across Europe, and 34 particularly in secularly managed Mediterranean high-elevation areas. The abandonment of 35 traditional land use, and especially the reduction in grazing pressure at high elevations, triggered 36 secondary succession in treeless grassland areas, and favored the upward shift of anthropogenic 37 treelines in some cases. We investigated this process in four anthropogenic treeline ecotone sites in 38 39 the Central Apennines, Italy, populated by European black pine (Pinus nigra Arn.). The upward treeline shift was controlled by microsite topography and the proximity to plantations acting as seed 40 source. We found a 50% probability of producing cones in trees with basal diameters of 15–25 cm. 41 heights of 2-5 m and ages of 20-25 years. The role played by climate on growth and the recruitment 42 processes seems to be secondary, or could be masked by human-shaped processes. The presence of 43 44 reproductive age trees at the treeline, mainly growing on debris-rich and steep slope sites, could indicate that the recruitment process will increase in future, leading to patchy tree patterns at 45 46 different elevations. The high growth and encroachment rates observed at these human-shaped 47 treelines would indicate that general growth dynamics are speeding up, including the tree 48 colonization of treeless areas. These succession processes could cause a significant long-term decline in plant diversity in species-rich grasslands. Nonetheless, tree encroachment could increase 49 50 forest protection against landslides and avalanches in the context of global change.

# 52 1. Introduction

53 Alpine treeline ecotones are sensitive indicators when assessing the ecological effects of two global-change components on forests, namely climate warming and land-use modification (Harsch 54 and Bader 2011). The greater sensitivity of these high altitude tree populations to temperature 55 variability confirms that growth and tree recruitment in these marginal populations respond to 56 climate variation (Daniels and Veblen 2004, Camarero and Gutiérrez 2004). However, climate 57 58 warming is only one aspect of global change that may affect the location of treelines (Holtmeier and Broll 2005). If traditional human activities near the treeline are common (Körner 2012), the forest-59 grassland ecotones are usually affected by changes in the anthropogenic disturbance regimes (, 60 61 Batllori and Gutiérrez 2008, Woods 2014).

Anthropogenic treelines develop under severe human impact that alters site conditions, such 62 as forest clearing, fire or livestock grazing (Holtmeier and Broll 2005). Moreover, land-use shifts 63 64 can severely influence treeline physiognomy masking or reversing the response of treelines to climate warming (Harsch and Bader 2011, Woods 2014). Although land use is more frequently 65 associated with an abrupt transition from forested to treeless areas, different treeline types and 66 structures may be the result of various past human influences (Batllori and Gutiérrez 2008, Harsch 67 and Bader 2011). Land-use changes are long-term broad-scale disturbances and should be 68 69 considered as major drivers of treeline formation in human-disturbed mountain areas (Foster et al. 1998). Their effects on treeline dynamics can persist long after the abandonment of human activities 70 (Camarero et al. 2017, Gimmi et al. 2008). 71

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

The Apennines are a mountainous range extending for 1200 km NW-SE across Italy with 85 numerous peaks higher than 2000 m a.s.l. (maximum elevation Mt. Corno Grande 2912 m a.s.l.). 86 87 The vegetation zones of the Apennines have been severely shaped by climate change and millenary human activities, and now are mainly covered by deciduous forests and woodlands. European beech 88 (Fagus sylvatica L.) is the main species of the mountainous zone ranging from 800-900 m to 1700-89 90 1800 m and forming the treeline at most sites (Vitali et al. 2017. Submitted). In Paleo and Neolithic times, high-elevation Apennine forests (1900-2200 m a.s.l.) were extensively cleared for hunting of 91 92 wild herbivores and were transformed into wood pastures or grasslands (Piermattei et al. 2014). In the central Apennines, the decrease of agro pastoral exploitation and the migration of rural 93 populations toward urban areas increased during the last 60 years (Falcucci et al. 2007). These 94 95 changes, together with climate warming, enhanced tree encroachment and forest expansion at high elevations (Dibari et al. 2015). European black pine (Pinus nigra Arn.) was extensively used in 96 mountain plantations during the 20<sup>th</sup> century reforestation programs for landslide and erosion 97 control due to its pioneering character and fast land cover capacity (Isajev et al. 2004, Piermattei et 98 al. 2016). Black pine revealed a natural inclination to expand on treeless areas above the closed 99 100 forest limit exclusively on the limestone soils of central Apennines, reaching unexpectedly high elevations (> 2000 m a.s.l.) and suggesting the formation of new and higher treeline ecotones 101 (Piermattei et al. 2012, 2014, 2016). 102

Black pine was more dynamic and expanded upslope more rapidly than most of the other 103 104 woody species (Juniperus species, Rhamnus alpina, Fagus sylvatica) in the central Apennines. This process could rearrange anthropogenic treelines and timberlines (sensu Körner 2012) ecotones 105 above secularly disturbed mountain forests. This upslope spread of black pine could be regarded as 106 an "advance guard" of a conifer-dominated anthropogenic treeline (Piermattei et al. 2012). The 107 black pine upward expansion started 30-40 years ago and its spatial distribution at higher elevations 108 109 generally appeared random with no evident patterns (Piermattei et al. 2012) or even over-dispersed along the slope (Piermattei et al. 2016). The radial growth of planted black pine is particularly 110 sensitive to maximum temperatures and water availability during the growing season forming 111 112 numerous intra-annual density fluctuations (IADF) (Piermattei et al. 2014). In a recent study in the 113 central Apennines the spatial pattern of black pine encroachment revealed that its expansion pattern is independent of site location and local disturbance histories (Piermattei et al. 2016). This process 114 115 of secondary succession is considered to be complex and depends on several factors such as masting occurrence, seed availability and dispersal, suitability of regeneration niches (sensu Grubb 116 1977), growth rates and tree establishment (Piermattei et al. 2012, 2016). Some of these variables 117 are linked to tree growth rates, and could be enhanced by the observed temperature increase 118 119 (Camarero et al. 2017). Nevertheless, site micro-topography is a major factor in treeline dynamics 120 since concave and wind-sheltered lee slopes can promote the formation of thick and long-lasting snowpack, affecting tree establishment (Hagedorn et al. 2014, Kullman and Öberg 2009). 121

We investigated a recent process leading to a treeline upshift, testing the predicting role of microsite topography and the distance of individual trees from neighboring black pine plantations acting as seed sources. We tested whether trees that had encroached at the higher elevations in the late 20<sup>th</sup> century acted as a secondary source of regeneration. We also investigated how tree size and age could influence cone production which would facilitate in turn the ascent of new individuals and the treeline (Piermattei et al. 2016). We used tree height rather than tree diameter because height is the variable that defines treeline position and determines the tree uncoupling from soil microclimate conditions (Körner 2012). Finally, we compared the microhabitat type closely around
the seedlings or saplings (classes defined by tree height), assuming that saplings ground vegetation
is influenced by vegetation dynamics under the influence of established trees.

In particular with this study, we searched for answers to the following questions: (i) are 132 there differences between seedlings and saplings vegetation ground-cover?; (ii) what are the main 133 abiotic variables affecting tree growth in these treeline populations?; (iii) is there a minimum 134 reproductive age threshold for newly encroached pines?; and (iv) does microsite topography and/or 135 the presence of cone-producing trees allow tree encroachment to be successfully predicted? We 136 hypothesized that microsite topography and distance to seed sources were the main factors 137 138 influencing the black pine colonization process at high elevation, and that this expansion process could be spatially aggregated. 139

## 141 **2. Materials and Methods**

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143 *2.1 Study sites* 

We sampled four mountain treeline ecotones situated in the central Apennines (Italy). Sites were 144 located in the Marche (Mt. Bove, hereafter BOV site) and Abruzzo regions (Mt. Ocre, OCR; Mt. 145 Morrone, MOR; Mt. Genzana, GEN), where black pine encroachment is widespread (Tables 1 and 146 147 2; supporting information, Figure A1). We selected the sampling sites after examining and interpreting aerial photographs and then carried out field visits. Selected sites fulfilled three 148 requirements: i) the presence of a timberline located over 1500 m; ii) the existence of mountain 149 150 peaks with elevation higher than 2000 m a.s.l. and iii) the potentiality of the upward shift up to the mountain peak without geomorphological constrains. Field data was collected between 2013 and 151 2015 within altitudinal transects (width 50 m and variable length) running from the timberline up to 152 the uppermost black pine tree (Figure 1). All sampled area surfaces range from 2.25 to 4.50 ha 153 (Table 1). We regarded the timberline as the upper limit of a closed canopy forest (tree cover > 50154 %), either broadleaf natural forest or conifer plantation, and the treeline as the highest elevation 155 where we found trees with height > 2 m. All study sites were included in different types of 156 protected areas: BOV is located in the Sibillini Mountains National Park, OCR in the Mount Ocre-157 158 Acquazzese State Forest, MOR in the Majella National Park, and GEN in the Natural Reserve of Mts. Genzana and Alto Gizio. 159

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

- **Table 1.** Main features of the study sites. *Timberline* is the upper limit of a closed canopy forest (tree cover > 50 %). *Treeline* is the altitude of the upper sampled tree with a height  $\ge 2$  m. The growing season length was set from May to September.
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Livestock grazing, especially by sheep, cows, and more recently horses, was the most important human-induced pressure at all four sites. Grazing intensity has decreased significantly over the last 40 years in the study region (Santilocchi and D'Ottavio, 2005). Past uncontrolled intensive grazing caused widespread slope erosion that required extensive pine plantations between the 1950s and 1970s. Today, less disturbed treeline ecotones are formed by forests and woodlands of European beech (*Fagus sylvatica* L.) along the Apennines, and by species-rich dry grasslands dominated by *Sesleria*, *Bromus* and *Festuca* species (Halada et al. 2011). All study areas are mainly 177 located on calcareous bedrock. They share a temperate oceanic climate (Rivas-Martinez et al. 2004) 178 with a Mediterranean influence characterized by summer drought downwards and the main 179 precipitation peaks in spring and autumn. Summer precipitation is not a limiting factor for treeline 180 shift since it increases upwards as in other mountain chains (Körner 2012). Snowfall is more 181 common and abundant in late winter to early spring, especially from February to the end of March 182 (De Bellis et al. 2010). The mean growing season (May to September) temperatures at the four sites 183 are 11-13 °C (SD  $\pm$  3 °C), with extreme mean values ranging from 7° to 16 °C.

184

#### 185 *2.2 Field sampling*

186 We mapped 429 Pinus nigra trees that had encroached above the timberline with a Trimble Pro 6H GPS antenna (Trimble Inc., Sunnyvale, USA). A post-processing differential correction through 187 Pathfinder Office 4.2 software was performed with a 0.5-m estimated accuracy. We measured basal 188 189 stem diameter, total height and counted the number of cones for each individual pine (Table 2). To characterize the regeneration niche of seedlings and saplings, we quantified the percentage cover of 190 microhabitat types (rock, debris, grass and shrub) within a circular plot with a 0.5 m radius around 191 each pine stem. The age of all the trees with a basal stem diameter  $\geq 4$  cm was determined after the 192 extraction of one basal increment core. For trees with a basal stem diameter < 4 cm we counted the 193 194 number of annual internodes (terminal bud scars) along the main stem to estimate their age (Camarero and Gutiérrez 1999). We classified trees as seedlings (tree height < 2 m) and saplings 195 (height  $\geq 2$  m), respectively. 196

|      | No.   | Tree                              | No.           | Trees with | Seedlings /      | Mean basal diameter | Mean height     | Mean age ± |
|------|-------|-----------------------------------|---------------|------------|------------------|---------------------|-----------------|------------|
| Site | trees | density<br>(N° ha <sup>-1</sup> ) | sampled cores | cones (%)  | (%) saplings (%) | ± SD (cm)           | $\pm$ SD (m)    | SD (years) |
| BOV  | 228   | 63                                | 71            | 4          | 87 / 13          | 6 ± 7               | 1.09 ± 1.36     | 10 ± 5     |
| OCR  | 39    | 17                                | 23            | 26         | 77 / 23          | $9\pm7$             | 1.41 ± 1.23     | $16 \pm 6$ |
| MOR  | 113   | 25                                | 84            | 23         | 54 / 46          | 11 ± 6              | $1.81 \pm 1.03$ | $16 \pm 5$ |

| GEN         49         11         35         24 $67/33$ $11 \pm 9$ $2.08 \pm 2.42$ $17 \pm 12$ | GEN 49 | 49 11 35 | 24 67 / 33 | $11 \pm 9$ $2.08 \pm 2.42$ | $17 \pm 8$ |
|--|--------|----------|------------|----------------------------|------------|
|--|--------|----------|------------|----------------------------|------------|

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

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We estimated the competition index for each sampled tree by calculating a distancedependent competition index at the individual scale, taking into account the number and size of the neighboring competitors and their distance to the focal tree (Hegyi, 1974). We calculated the competition index as the sum of the diameter quotients obtained for all the neighboring trees located within a 2-m radius from the focal tree, divided by the distance between focal trees and neighborhoods. We corrected edge effects by omitting trees with distances from the plot limits of lower than 2 m from the calculation.

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### 210 2.3 Topographic, climatic and microsite ground-cover data

Topographic variables were extracted from the 10-m-resolution DEM for the Italian territory 211 (Tarquini et al. 2012) for each pixel covering the mapped altitudinal transects. Specifically, we 212 calculated: i) the slope; ii) the north-eastness index with values ranging between -1 (sunniest 213 exposure) and +1 (shadiest exposure) and iii) the plan curvature index perpendicular to the 214 215 maximum slope and ranging from -1 (concave) to +1 (convex). Mean monthly temperatures for the period 1950-2015 were obtained using the procedure reported in Carturan et al. (2016) and in 216 217 Brunetti et al. (2012). In the field, we assessed the seedling and saplings ground-cover, according to four cover types: grass, shrub, debris, and bare rock. We compared these ground-cover proportions 218 219 in each site, to detect significant differences, considering that saplings can have a higher influence on the ground vegetation than seedlings, during their growing process. 220

221

222 *2.4 Growth data* 

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

230

#### 231 2.5 Statistical analyses

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

We fitted linear mixed-effect models (LME) to radial growth data at each site considering 236 pine trees as random factors. We applied the autoregressive process (AR(1)) which describes the in-237 tree correlation structure of radial growth which was quantified as basal area increment. We 238 considered the following as fixed factors in the LMEs: basal diameter, year, elevation, ground 239 240 curvature, competition index and mean spring monthly temperatures (March April and May) that can play a crucial role at the beginning of the growing season. We ranked all the potential models 241 according to the Akaike Information Criterion (AIC) and then selected the most parsimonious 242 243 models showing the lowest AIC value (Burnham and Anderson, 2002). We also used the Akaike weights (Wi) of each model to measure the conditional probability of the candidate model assuming 244 it was the best one. We assessed the fit of the models by graphical examination of the residual and 245 fitted values (Zuur et al. 2010). 246

Finally, we fitted negative binomial GLMs to predict the number of pines (the density of pines in 100 m<sup>2</sup> subplots) as a function of four topographic variables (elevation difference from plantation, slope, north-eastness and curvature indices). These models were ranked according to their AIC values and we selected the best ones (Burnham and Anderson, 2002). Then we applied the Akaike weights (*Wi*) to each model (Zuur et al., 2010).

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

256

#### 257 **3. Results**

### 258 *3.1 Size and age of treeline trees*

Mean timberline elevation was 1650 m and ranged between 1542 m (MOR) and 1715 m a.s.l. 259 (BOV), whilst the mean treeline elevation was 1858 m and ranged between 1708 m (OCR) and 260 261 2016 m (GEN) (Table 1). Black pine colonization across the treeline ecotone was scattered since tree density showed a wide range of values, from 11 to 63 trees ha<sup>-1</sup> (Table 2). On average, these 262 recruited pines corresponded to 71% and 29% of seedlings and saplings, respectively. Overall, the 263 average tree size was small, with lower values at the BOV site and higher values at the GEN site. 264 The mean basal diameter was 9 cm, the mean height was 1.60 m, and the mean age was 15 years 265 266 (Table 2). Most sampled trees had basal diameters of lower than 15 cm and heights of lower than 2 m (Figure 2). On average, trees took 10-15 years to reach a height of 2 m (Supporting Information, 267 Figure A2). Modal age values varied between 5 and 20 years. The oldest trees suggested that 268 269 colonization started at least 30 years ago (1985–1990).

270





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

275

# 276 *3.2 Treeline structure and regeneration niche*

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

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

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

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

297

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

302

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

308



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

313

309

314 *3.3 Growth trends* 

Basal-area increment (BAI) data showed high recent growth rates (5-10 cm<sup>2</sup> yr<sup>-1</sup>), and narrow rings were formed one year later in response to the warm-dry summer conditions observed in 2003, 2007 and 2011 (Supporting Information, Figure A3). LMEs fitted to BAI data showed that tree age and basal diameter were the most important predictors of growth, whereas elevation and mean spring temperatures played a minor role (Table 4). Neither the curvature nor the competition indices were selected as growth predictors in any of the best-fitted models.

| Site | Parameters                      | Wi   |
|------|---------------------------------|------|
| BOV  | 18.66 Age + 3.45 Diam + 2.86 Tm | 0.77 |
| OCR  | 7.60 Age + 3.45 Diam + 2.86 Tm  | 0.79 |
| MOR  | 14.99 Age + 9.73 Diam           | 0.78 |

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

329

#### 330 *3.4 Production of cones by treeline trees*

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

336

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

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

341

#### 342 **4. Discussion**

We described the natural ascent of human-shaped treelines in the central Apennines. Black pine is 343 344 expanding upwards in formerly treeless areas, particularly on steep slopes and where seed availability depends on downslope pine plantations. The irregularage structures found at all sites 345 could also be affected by un-stationary mortality caused by climate extreme events, e.g. frosts, 346 347 winter drought (Camarero et al. 2015, Barros et al. 2017), or other factors such as pathogens or mass wasting processes (e.g. rock fall, debris flow, land slide). We observed a patchy pattern 348 349 (Figure 4) of treeline shift driven by both changes in microtopography and availability of suitable regeneration sites for black pine. Our results show that most tree seedlings were located on debris 350 ground-cover and steeper slopes, avoiding grass competition. The relative lower number of trees on 351 352 flat and grass-cover areas could be a consequence of herbs competition and snow accumulation on 353 late winter, particularly in convex areas (Treml and Chuman 2005). However, recruits that overcome grass competition on less steep sites grew successfully, as confirmed by the abundance of 354 saplings on those sites. Indeed, debris microsites on steeper slopes most frequently hosted pine 355 seedlings (Figure 3), and tree encroachment was also favored at shorter distances from the pine 356 plantations (Table 4). Herbaceous vegetation, which is often dominant at many treeline ecotones, 357 exerts an important and mostly limiting impact on the establishment of tree seedlings (Loranger et 358 al. 2017). Studies on Scots pine (Pinus sylvestris) encroachment in Mediterranean mountain 359 360 grasslands showed that the physical barrier created by the herbaceous layer could hamper pine regeneration and limit potential forest expansion (Castro et al. 2002). Bare soil or very sparse 361 vegetation are favourable substrates for pine recruitment (Loranger et al. 2017). Sites with 362 363 prevailing shrub cover and rocky outcrops were considered safe for establishment and development of black pine (Piermattei et al. 2016) and for mountain pine (Pinus uncinata) recruitments 364 (Camarero and Gutiérrez 2007, Batllori et al. 2009). Abrupt treeline physiognomy and a decreasing 365 number of new trees (but no changes in height or age) as elevation increases are typical features of 366 367 anthropogenic treelines (Batllori and Gutiérrez 2008).

368 These results compare well with other treelines that have been studied in the central Apennines,369 where the density of newly established trees decreased with elevation (Piermattei et al. 2016).

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

We observed that tree density decreased with elevation due to the increasing distance of 375 upslope encroached trees from pine plantations. This fits with a general theory where the shorter the 376 377 distance to old trees (the plantations in our case), the higher the reforestation rate (Tasser et al. 378 2007, Stueve et al. 2011). The higher availability of seeds is the main driver of pine colonization since it helps propagules ascend higher, and potentially favors the establishment of new pine 379 380 individuals. Moreover, the results based on the negative binomial GLMs showed a positive slope influence on tree density at least at the BOV and MOR sites (Table 3). Similar recruitment patterns 381 were found in the Southern United States where increased density was found to relate to slope and 382 proximity to the forest (Coop and Givnish 2007). 383

Our tree growth models showed the dominant role played by tree age and size in determining 384 385 growth rates (BAI) at the treeline, whereas spring temperatures had secondary importance. Elevation, curvature and the competition index were not included in the best-fitted growth models 386 (Table 4). Tree density was relatively low in the study sites, likely excluding the competition effect 387 388 from the best models. The newly established pines are not growth-limited at high elevations indicating that they have not reached the uppermost climatic threshold for tree growth. We did not 389 assess the role of wind disturbance and radiation stress on seedling abundance or tree growth even 390 though they can be additional abiotic constraints at the treeline (McIntire et al. 2016). Linking 391 changes of grazing intensity and individual tree growth is a big challenge since such historical 392 393 pastoral records are often lacking at local to regional scales, but their availability would allow more 394 precise testing of the impact of land-use changes on forest growth at high elevation and treeline395 dynamics.

The fecundity of Mediterranean pines like black pines is particularly important considering 396 that they are significant pioneering and/or invasive species across many world regions (Richardson 397 398 and Rejmánek 2004). Our results showed that tree height or stem diameter were better predictors of cone production than tree age (Table 5), and that similar thresholds for becoming reproductive 399 400 individuals occurred at all sites: ca. 15 cm of basal diameter, ca. 2 m of height and about 15 years of age (Supporting Information, Figure A4). This agrees with Isajev et al. (2004) indicating that black 401 pine maturity is reached at 15 years old. We did not assess either seed production or seed viability 402 403 which can be relevant variables in the understanding of treeline encroachment since slow-growing 404 treeline standing trees or krummholz may form cones, but with few or no viable seeds (Camarero et 405 al. 2017). Generally, trees release many more seeds when conditions are dry and windy, potentially 406 increasing the proportion of long-distance dispersal events (Coutts et al. 2012). A comparison showed that non-native black pine populations had a higher net reproductive rate and higher 407 effective dispersal than native Scots pine, leading to a rapid expansion of black pine into grasslands 408 409 (Debain et al., 2007). If recently encroached trees overcome bottlenecks related to seed viability, the future of these anthropogenic treeline ecotones will depend on the future dynamics of successful 410 high-density tree groups or clustered islands. These trees growing on debris-rich and steep slope 411 sites may become new seed sources and catalyze the recruitment process, increasing the annual seed 412 413 production at closer distances.

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

426

# 427 **5.** Conclusions

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

434

### 435 Acknowledgements

We wish to thank the following institutions and people: Monti Sibillini National Park, SirenteVelino Regional Park, Majella National Park, for providing authorization and logistic support;
Giampiero Ciaschetti, Francesca Lallo, Matteo Cerioni for field sampling and laboratory assistance;
Michele Brunetti for providing the climatic dataset; Angela Sánchez-Miranda and Antonio Gazol
for analysis support; Patricia Crotty (www.expressolanguageservices.it) for English language
revision. We also thank two anonymous reviewers for their constructive comments during the
revision process.

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# Supporting Information - Appendix A



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



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



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



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