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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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Keywords

Anthropogenic treeline, black pine, pasture abandonment, pine recruitment, Mediterranean mountains

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.

Abstract

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

1. Introduction

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

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

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

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

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

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

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

2. Materials and Methods

2.1 Study sites

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

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

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

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

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

2.2 Field sampling

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

Site	No. trees	Tree density (N° ha^{-1})	No. sampled cores	Trees with cones (%)	Seedlings / saplings (%)	Mean basal diameter ± SD (cm)	Mean height ± SD (m)	Mean age ± 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 ± 7	1.41 ± 1.23	16 ± 6
MOR	113	25	84	23	54 / 46	11 ± 6	1.81 ± 1.03	16 ± 5

GEN	49	11	35	24	67 / 33	11 ± 9	2.08 ± 2.42	17 ± 8

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

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

2.3 Topographic, climatic and microsite ground-cover data

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

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).

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^2 values (Venables and Ripley 2002).

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

Finally, we fitted negative binomial GLMs to predict the number of pines (the density of pines in 100 m^2 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).

3. Results

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

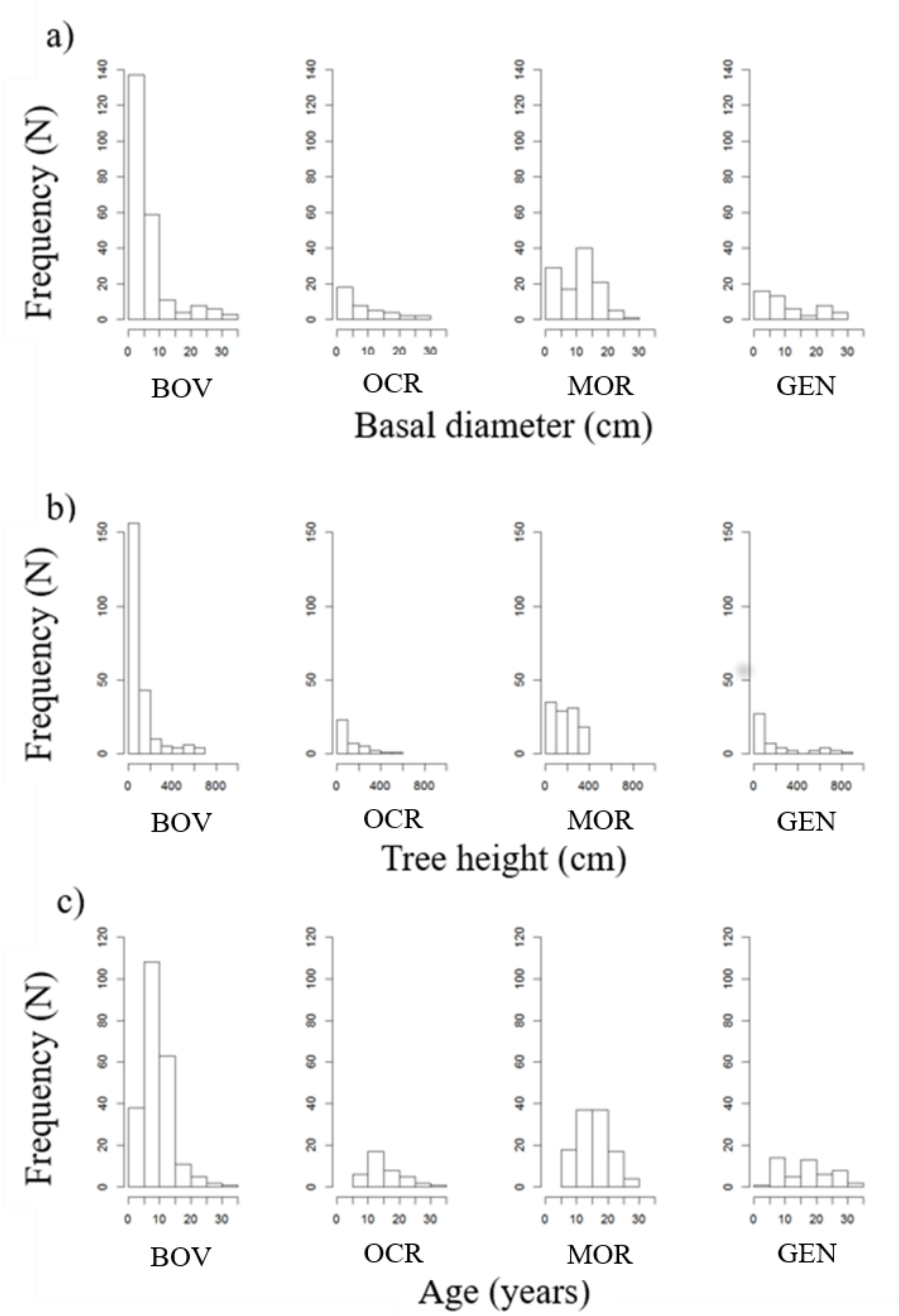

Figure 2. Frequency distribution of basal diameter (a), tree height (b) and estimated age (c) of the treeline black pines (*Pinus nigra*) sampled at each of the four study sites.

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 $r = 0.36$ $p < 0.05$). Generally, the pine encroachment pattern across the treeline ecotones was not spatially structured in cohorts, but some clustered patterns were detected at 200 m intervals. These spots with higher tree density occur usually with increasing slope and consequently debris cover. Whereas in moderate slopes the grass-cover treeless areas increased.

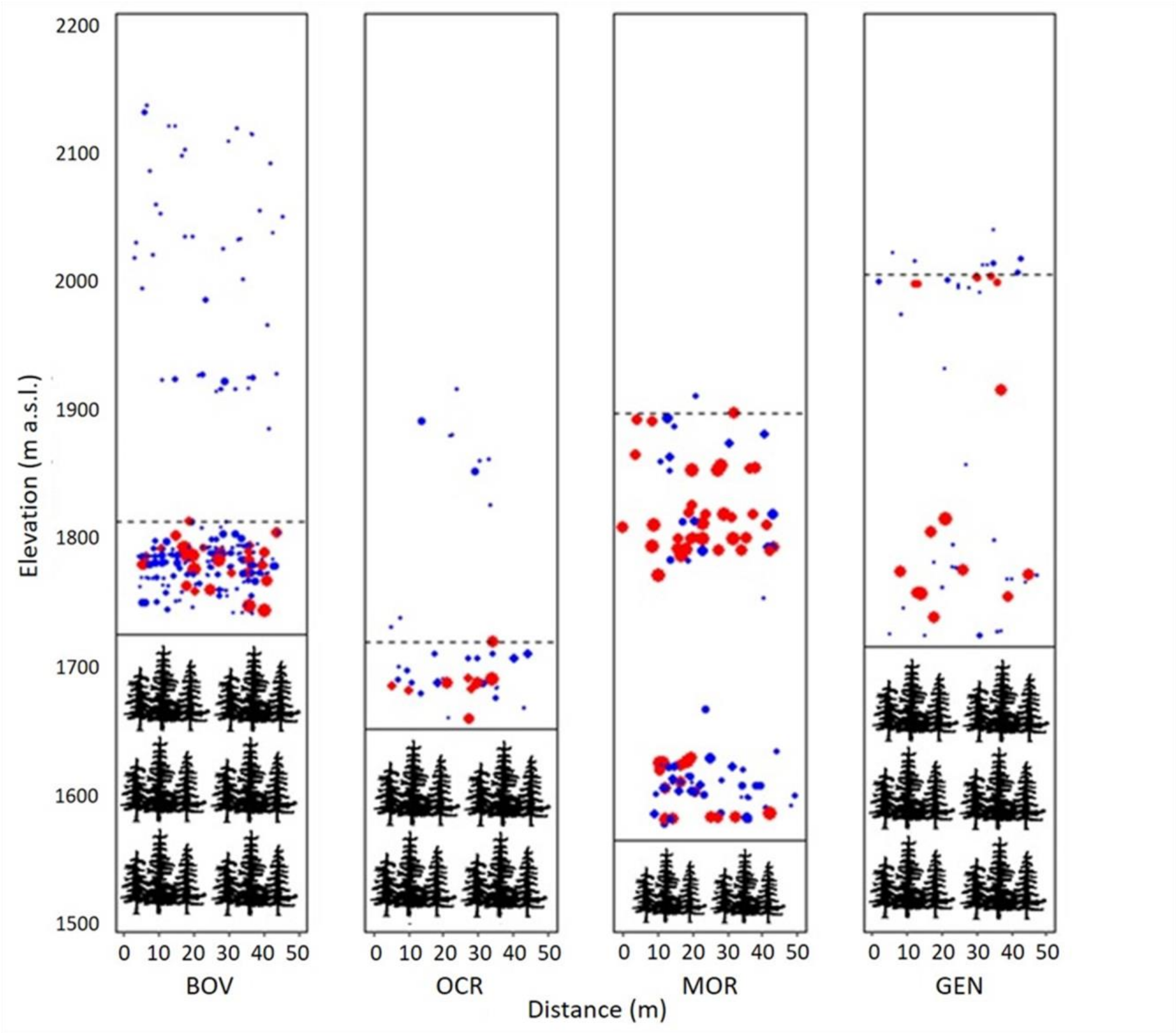

Figure 3. Mapped point patterns of black pine individuals at the four Apennines treeline ecotones (see Tables 1 and 2 for site characteristics). Blue dots are seedlings (tree height < 2 m) and red dots are saplings (height ≥ 2 m.). The dot scale size is proportional to the tree height. Solid and dashed 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

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; °°, not-significant parameters

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

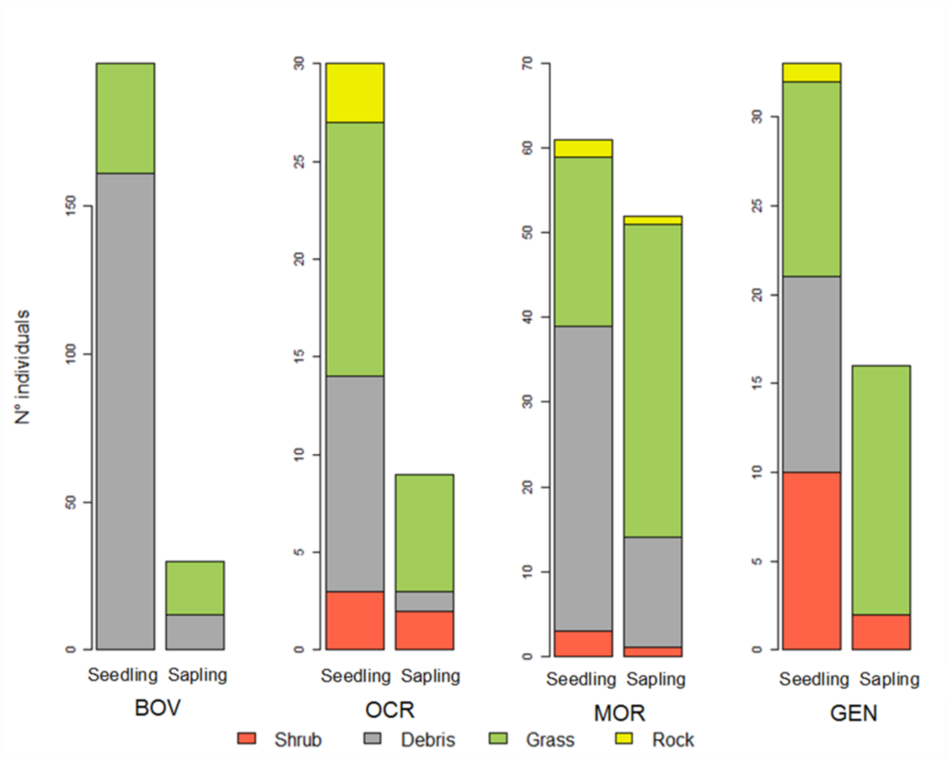

Figure 4. Number of black pine recruits sampled at each treeline ecotone (BOV, OCR, MOR and GEN sites) and classified as a function of their height (seedling and sapling; see Figure 3) and microsite types (shrub, debris, grass and rock).

3.3 Growth trends

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

Site	Parameters	*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

GEN	12.95 Diam + 9.82 Age + 3.73 Tm	0.80

Table 4. Summary of the linear mixed-effect models of tree growth (basal area increment) fitted as a function of site, topographic variables (elevation and curvature index), tree variables (age, basal diameter, and competition index), and climate variables. All regression intercepts are significant. The last column shows the relative Akaike weights (*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.

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^2 values with basal diameter (R^2 = 0.38−0.55) or height (R^2 = 0.37−0.75) as predictors rather than using age (R^2 = 0.12−0.47) (Table 5).

		McFadden's pseudo-R^2		
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

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.

4. Discussion

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

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

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

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

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

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

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

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.

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Supporting Information - Appendix A

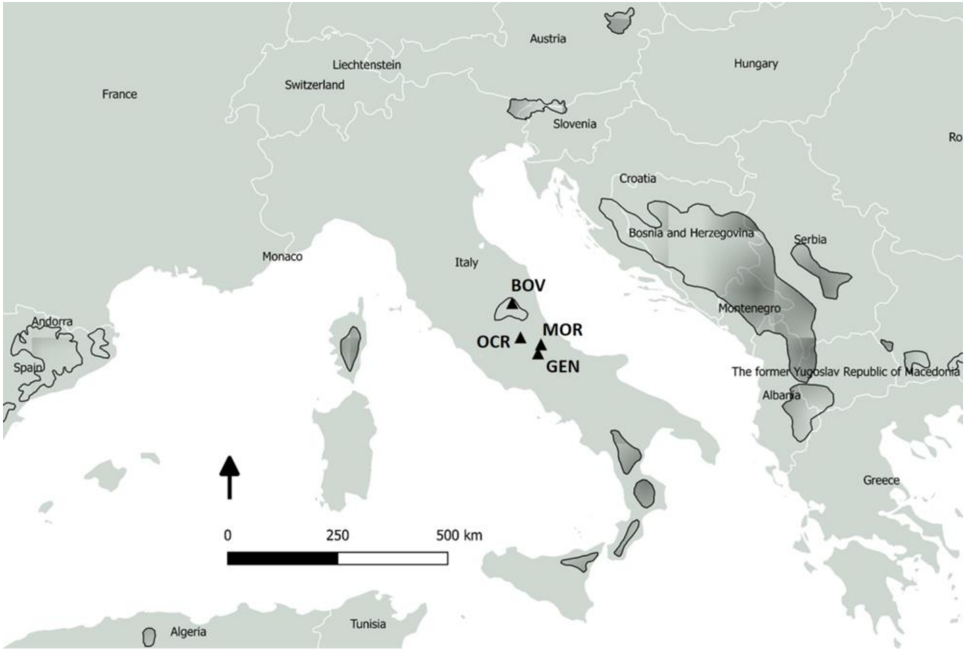

Figure A1. Natural distribution range of European black pine (*Pinus nigra* and sub-species) in the circum-mediterranean areas (black contours); locations of the four study treeline sites at the central Apennines, Italy (black triangles).

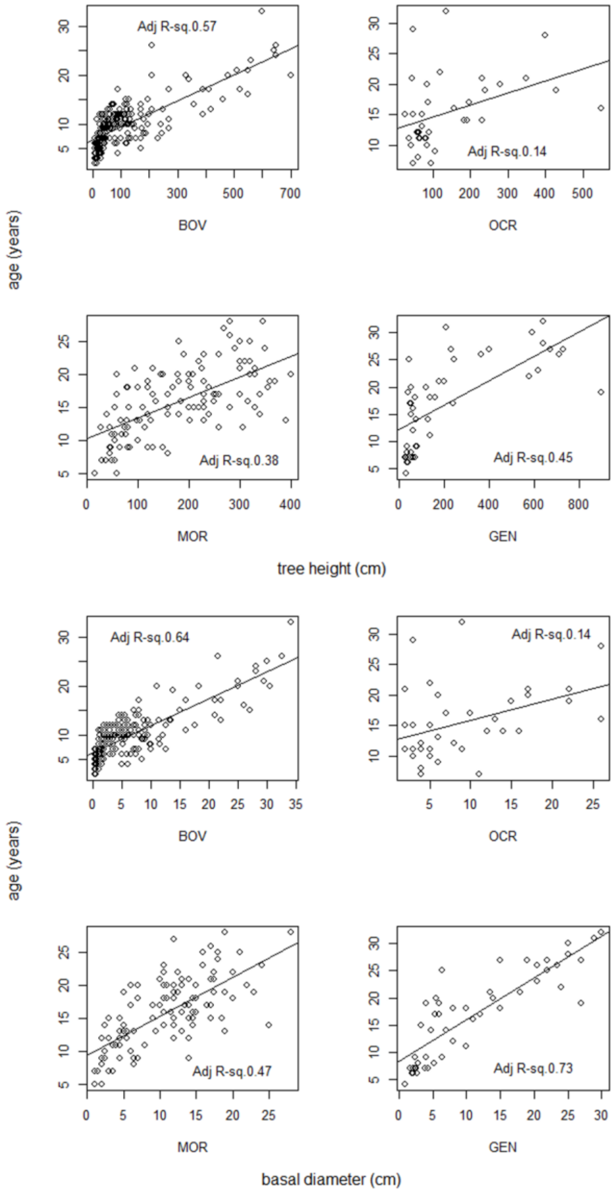

Figure A2. Adjusted R^2 values and linear regressions calculated for models of tree age as a function of basal diameter and tree height in the four black pine treeline sites.

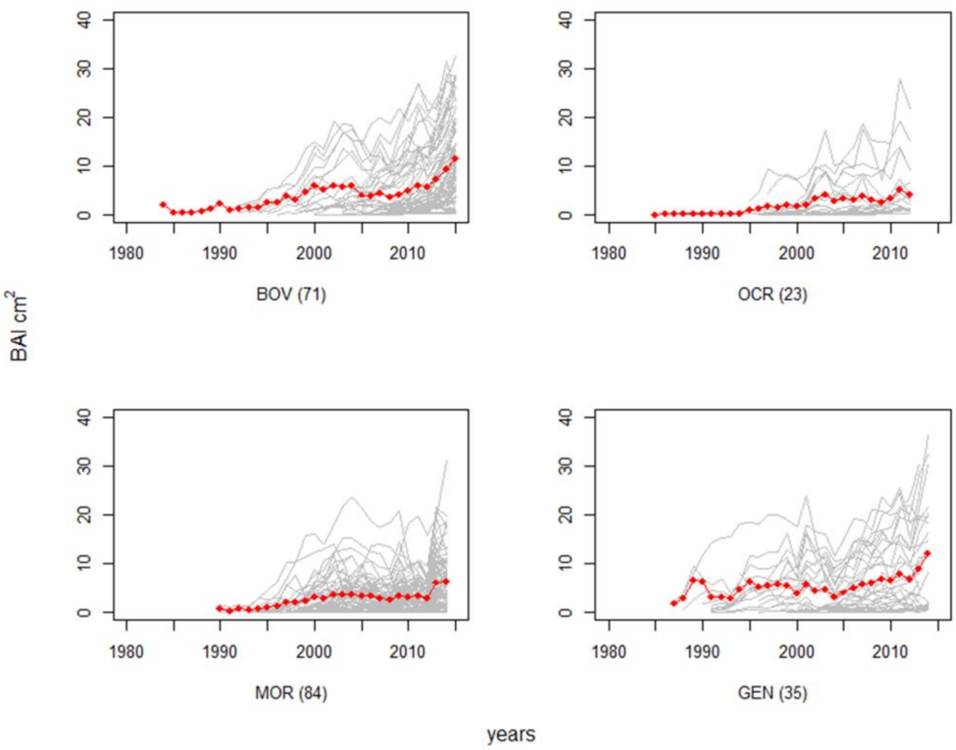

Figure A3. Radial-growth trends of black pine (*Pinus nigra*) at the four treeline sites expressed as basal area increment (BAI). Grey lines are individual series and red lines are the means of each. The numbers in brackets on the x-axis label are the number of analyzed cores at each site.

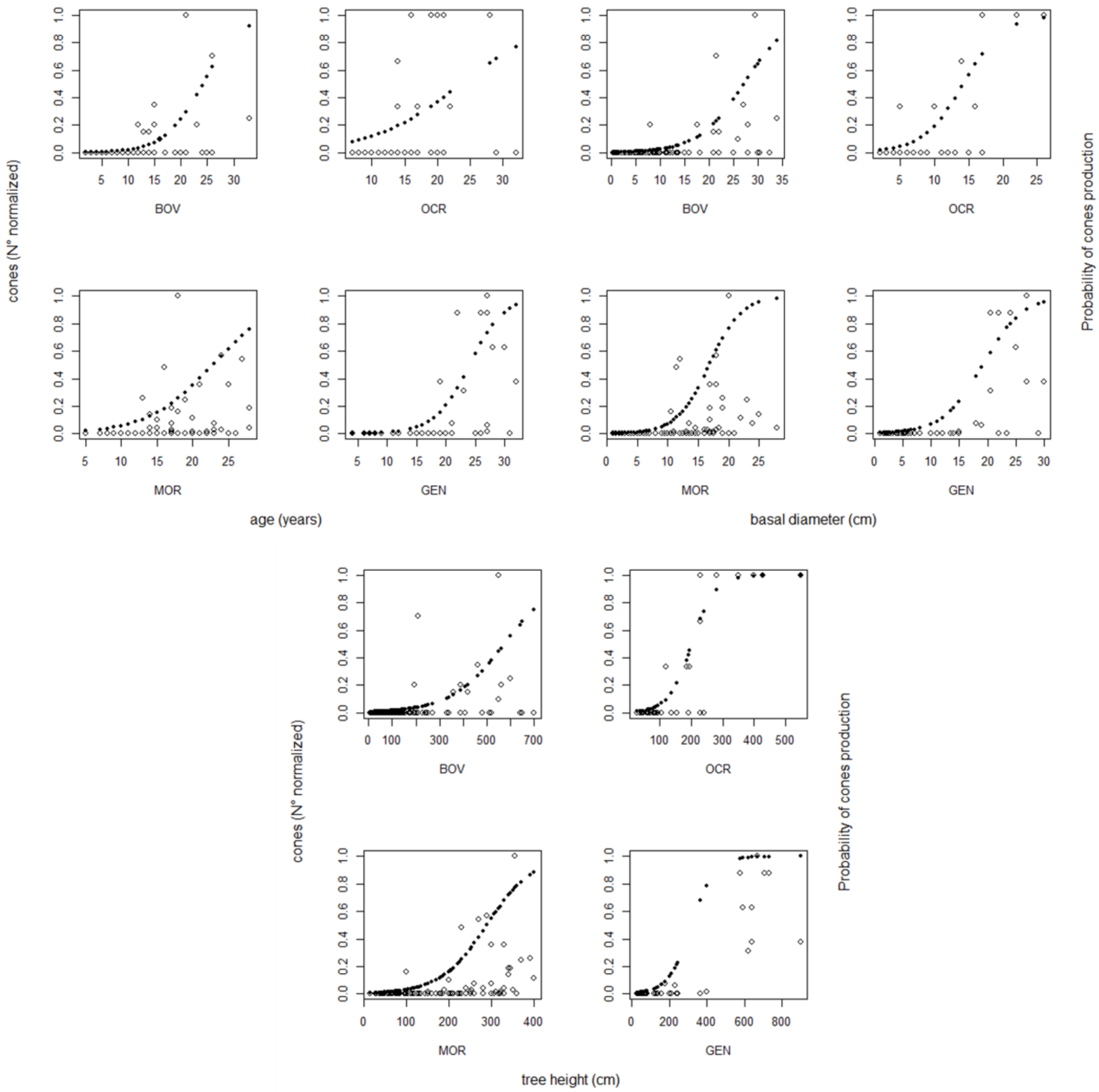

Figure A4. Generalized Linear Models (GLMs, black symbols) fitted to cone numbers (normalized values) to predict the probability of cone production in treeline black pine trees as a function of tree age, basal diameter and height.