Pine recolonization dynamics in Mediterranean human-disturbed treeline ecotones

(Article begins on next page)

27 April 2024

1 **Pine recolonization dynamics in Mediterranean human-disturbed treeline ecotones**

2

3

4 Alessandro Vitali[1]*, Matteo Garbarino[2], J. Julio Camarero[3], Francesco Malandra[1], Elvin Toromani[4],

5 Velibor Spalevic[5], Milić Čurović[6], Carlo Urbinati[1]

6

7 [1]Department of Agricultural, Food and Environmental Sciences, Marche Polytechnic University,

8 Ancona, Italy

9 [2]University of Turin, Department of Agricultural, Forest and Food Sciences, Turin, Italy

10 [3]Pyrenean Institute of Ecology (IPE-CSIC), Zaragoza, Spain

11 [4]Agricultural University of Tirana, Faculty of Forestry Sciences, Tirana, Albania

12 [5]University of Montenegro, Faculty of Philosophy - Geography department, Nikšić, Montenegro

13 [6]University of Montenegro, Biotechnical Faculty, Podgorica, Montenegro

14

15 Alessandro Vitali (Corresponding author; alessandro.vitali@univpm.it)

16 Matteo Garbarino (matteo.garbarino@unito.it)

17 J. Julio Camarero (jjcamarero@ipe.csic.es)

18 Francesco Malandra (f.malandra@pm.univpm.it)

19 Elvin Toromani (elvintoromani@gmail.com)

20 Velibor Spalevic (velibor.spalevic@ac.me)

21 Milić Čurović (curovic@ac.me)

22 Carlo Urbinati (c.urbinati@univpm.it)

Abstract

Worldwide treelines seem to share a twofold condition: over 50% of them are advancing and 50% appear to be static. In this study we compared the encroachment patterns of four pine species across anthropogenic treelines in Southern Europe. Using a synchronic approach, we studied structure and recent spatio-temporal patterns of pine recruitment at upper treeline ecotones in Albania, Italy, Montenegro and Spain. Within altitudinal transects we mapped and sampled 964 living individuals of *Pinus heldreichii*, *Pinus peuce*, *Pinus sylvestris* and *Pinus uncinata* growing above the current forest line. We measured their basal diameter, total height, and counted the number of seed cones. We differentiated seedlings (height < 0.5 m) from saplings (0.5 m ≤ height < 2 m) and trees (height ≥ 2 m). From individuals with basal stem diameter >4 cm we extracted one increment core for cambial age determination and tree-ring width measurements. On smaller specimens, we estimated the age by counting annual internodes (terminal bud scars) along the whole stem. We compared the ground cover around each pine, applied point pattern analyses, modelled the probability of seed cone production and estimated the average distance of seed dispersal. The four pine species exhibited heterogeneous density values (87-1552 N° ha^{-1}). The overall averaged means ranged 2-7 cm for basal diameter, 54-106 cm for total height and 9-20 years for cambial age, suggesting a recent encroachment process. None of these structural variables decreased with increasing relative altitude and distribution patterns exhibited a few higher density spots but not cohort spatial structure. Ground cover differed between species and more significantly between size classes. Grass was the most frequent type at all sites except for *P. sylvestris* where shrubs prevailed (> 50%). Further differences appeared when discriminated by height thresholds, with larger share of saplings and trees neighboring shrubs and rocks. Basal area increments increased from 1990 and stabilized in recent years at all species except for *P. peuce*. Height and basal diameter predicted cones production better than cambial age. *P. heldreichii* and *P. peuce* dispersed seeds at longer distances than *P. uncinata* and *P. sylvestris*, suggesting different potential for further encroaching. Pine recruitment above the forest lines is quite synchronic at all sites (last 30 years), but in some cases it appeared as a high altitude tree densification process, whereas in others as a starting treeline advance. The use of

51   permanent transects provides a detailed monitoring of tree survival and a more precise prediction of

52   future treeline expansion.

1. Introduction

At global scale, altitudinal or latitudinal treeline formation and development are mainly controlled by air and soil temperatures, and their changes in structure are sensitive to climate warming (Holtmeier & Broll, 2005; Körner, 2007). For this reason, the dynamics of these marginal ecotones have been studied worldwide with the aim of detecting changes and understanding responses of forest ecosystems to climate warming (Holtmeier & Broll, 2007). Nonetheless, several biotic and abiotic factors should be considered in addition to climate when studying treeline dynamics at multiple spatial scales (Case & Duncan 2014). In many cases, climate and vegetation changes together with reiterated human pressure have shaped the current treeline physiognomy and dynamics (Harsch & Bader, 2011). Former impacts still control the current position and overall structure of treeline ecotones (Holtmeier & Broll, 2005; Liang et al., 2011, 2018).

A worldwide analysis on 166 treeline sites, proved that, regardless of form, location and severity of temperature change experienced over the last century, treelines have either advanced (55%) or remained stable (44%) (Harsch et al., 2009). The share of advancing treelines could be even greater including in the analysis many more sites featuring a notable disturbance history.

Human-shaped treelines are common in mountain landscapes across Eurasia, from Himalaya to Western Europe, including long-term managed Mediterranean high-elevation areas (Vitali et al., 2017). The centuries-long history of transhumant land use of alpine pastures significantly depressed the upper treelines (Wallentin et al., 2008). The natural establishment of trees near alpine treelines was widespread during the 20th century in Europe after a progressive decline of traditional agro-pastoral practices at high elevation (Chauchard et al., 2007; Debussche et al., 1999; Gehrig-Fasel et al., 2007; Gellrich et al., 2007; MacDonald et al., 2000), combined with the absence of relevant geomorphological constraints (Leonelli et al., 2011).

Spatio-temporal patterns of encroaching tree species at the mountain treelines were studied worldwide. Differences are mainly due to local scale influences, as forest line advancement is strongly related to dispersal characteristics of the current treeline species such as production of viable seeds (Juntunen & Neuvonen, 2006), seed dispersal kernels (Clark et al., 1999; Dullinger et

al., 2004) and seedlings competition with ground vegetation (Dullinger et al., 2009; Holtmeier and Broll, 2007; Tasser et al., 2007). Seedlings' establishment above the Central Mountain Range (Taiwan) treeline is predicted to be spatially heterogeneous due to topography (Greenwood et al. 2015). Batllori et al. (2009) suggested that scarce availability of safe sites control seedlings' recruitment patterns at Pyrenees (Spain) treeline ecotones. However, both spatial and temporal patterns of conifer seedlings' survival suggested that high sunlight exposure may exacerbate low-temperature and water stress, inhibiting their establishment at Snowy Range (USA) treeline (Germino et al., 2002). Finally, short distances between seed sources can have a significant effect on early demographic performance in conifer population at Niwot Ridge (USA) (Castanha et al., 2013).

Recent studies of recolonization on abandoned high-elevation grasslands in the central Apennines (Italy) proved that European black pine (*Pinus nigra* Arn.) is expanding upwards in formerly treeless pastures or grasslands. The process is particularly evident on steep rocky slopes and partially controlled by the distance from pine plantations, acting as seed sources (Piermattei et al., 2016; Vitali et al., 2017). Recruitment of tree cohorts above the current treeline is likely to occur only if climatic and edaphic conditions are favorable and if land-use changes are suitable for their establishment and range expansion (Ott et al., 1997; Weisberg et al., 2013).

Here we used the term 'treeline' to refer to the transition zone (ecotone) between the forest line (the margin of the closed forest) and the treeless alpine area above. Differently to climatic treelines, where tree density usually fades upward, human-disturbed treeline ecotones often appear as abrupt shifts from forest to non-forest cover (Harsch & Bader, 2011).

At different sites in the central Apennines (Italy), we found similar spatio-temporal recolonization patterns of black pine above the current depressed forest line (Piermattei et al., 2016; Vitali et al., 2017). The encroaching pine cohorts generated from high altitude forests planted to control slope erosion. Given the different rates of pastoral abandonment at each study sites and the synchronic pine encroachment process, we considered climate warming as a possible facilitation driver (Vitali et al., 2017). In this study, we investigated the occurrence and the

ecological patterns of similar recent processes of four pine species at human-disturbed treeline ecotones across southern Europe.

We hypothesized that, the synergic influences of climate and human abandonment could have triggered comparable encroachment patterns above other naturally formed forest lines on Mediterranean mountains. At all treeline ecotones we found evidence of former pastoral management but given the incomplete availability of official land-use changes data, we avoided to attempt the disentanglement of climate and land-use change effects on the recent treeline ecotone dynamics. We then selected the following pine species naturally occurring at high elevation for understanding their ecotones' structures and dynamics: *Pinus heldreichii* Christ. (PH), *Pinus peuce* Griseb. (PP), *Pinus sylvestris* L. (PS) and *Pinus uncinata* Ram. (PU).

Comparatively for all pine species and their roles in treeline structure and dynamics, we searched answers to the following questions: i) what are the tree structure characteristics (age and size) and their spatio-temporal patterns?; ii) are there differences between seedlings, saplings and tree ground cover (regeneration substrate *sensu* Grubb 1977)?; iii) how is tree growth at these marginal populations?; iv) are there minimum reproductive thresholds for newly encroached pines (e.g. difference in cone production)?; and v) are seed dispersal patterns different? Providing plausible answers, we could shed some light on these widespread trees encroachment processes in human-shaped treelines.

2. Materials and methods

2.1. Study sites

We sampled nine treeline sites situated in southern Europe (Fig. 1a), all featuring a Mediterranean climate influence (i.e. warm and dry summers) and showing signs of anthropogenic disturbances (relatively low elevation of forest lines, evidence of past grazing, open and recent stands dominating the landscape). The lack of homogeneous and suitable data on past management at all study sites, was only partially compensated by information provided by local farmers, that was

useful to select the appropriate sites with evidence of recent abandonment. One site is in the southern Apennines (Italy), four in the Dinaric Alps (at the Albanian and Montenegro border), and four in northern Spain (two in the Pyrenees and two in the Iberian System). The Italian site is on Mt. Pollino (POL) in the southern Apennines, where Bosnian pine (*Pinus heldreichii*) is at its westernmost range limits and widespread naturally above the forest line formed mainly by European beech (*Fagus sylvatica* L.). The Balkan sites were selected for the native and widespread presence of *Pinus heldreichii* (Fig. 1b) and *Pinus peuce* (Fig. 1c), respectively at Mt. Komovi (Montenegro) and M. Prokletije (Albania). The Spanish sites correspond to the western part of *Pinus sylvestris* distribution range (Picos de Urbión, Iberian System) (Fig. 1d) and the Pyrenean core area of *Pinus uncinata* (Pico de la Magdalena) (Fig. 1e). Sampling sites were selected after an accurate literature analysis, aerial photographs assessment and field visits with local experts. Selected sites fulfilled three requirements: i) a forest line (closed canopy forest with cover > 50%) located at ≥ 1500 m above sea level (m a.s.l.); ii) the mountain peaks elevation located higher than 2000 m a.s.l., and iii) the absence of geomorphic constraints to a potential upward tree encroachment. Field data collection occurred in the summers of 2015 (Italy), 2016 (Balkans) and 2017 (Spain) within altitudinal rectangular transects of variable size, extending along the slope from the mountain ridge downward to the closed forest. Tree encroachment involved only one pine species at each transect. The surface areas of transects ranged from 0.05 to 1 ha according to local conditions and accessibility (Table 1).

155
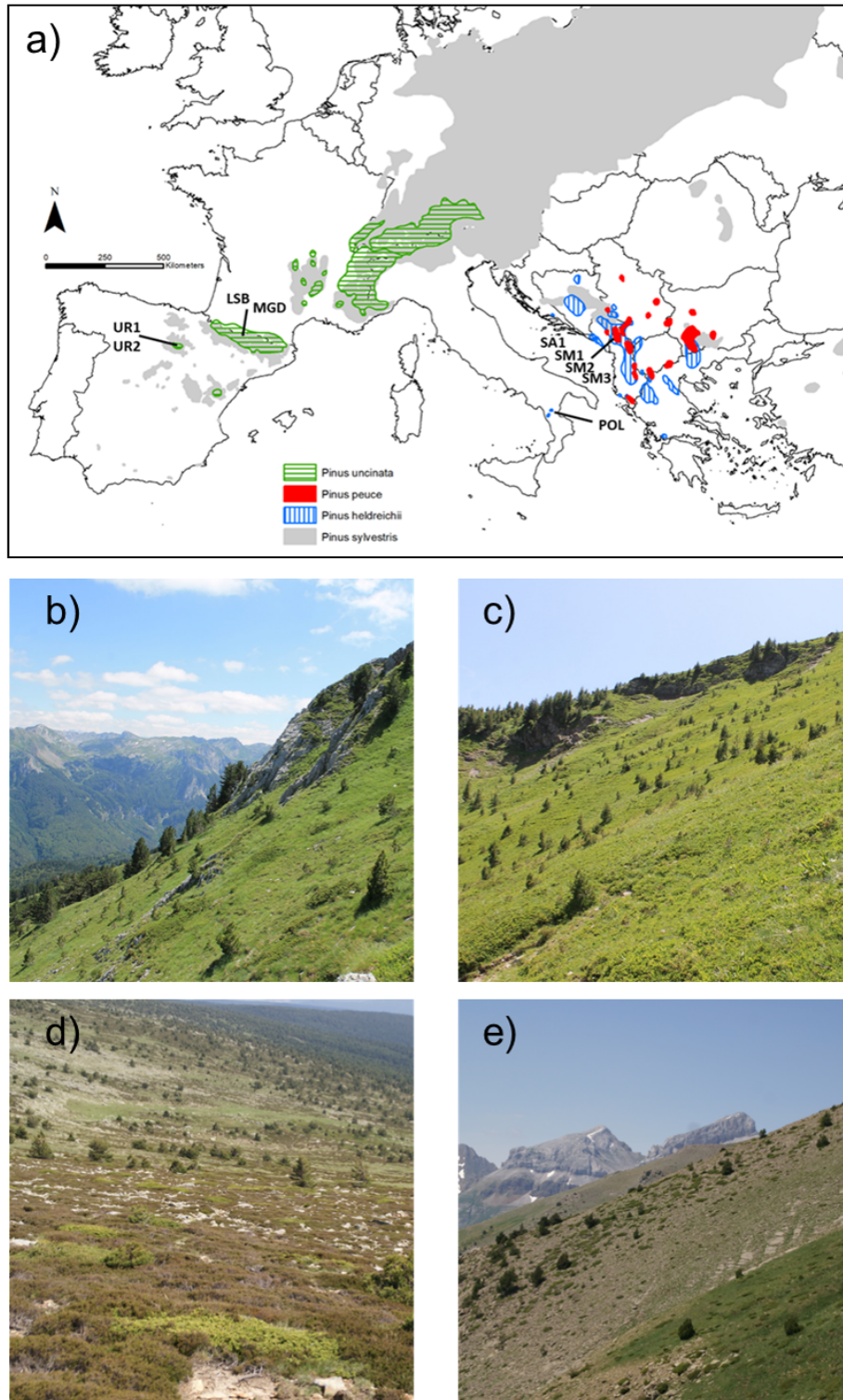
Fig. 1. (**a**) Distribution map of the four studied pine species in the Mediterranean basin [*P. uncinata* (green), *P. heldreichii* (blue), *P. peuce* (red) and *P. sylvestris* (grey)] and position of the nine treeline study sites (see Table 1). The map is a synthesis of the relative chorological maps (from Caudullo et al., 2017; IUCN Red List of Threatened Species 2017). (**b**) Upward pine recruitment of *Pinus heldreichii,* Mt. Komovi (SM3), Montenegro; (**c**) *Pinus peuce* at Mt. Prokletije (SA1), Albania; (**d**) *Pinus sylvestris* at Picos de Urbión (UR1-UR2), Iberian System; (**e**) *Pinus uncinata* at Pico de la Magdalena (MGD), Pyrenees, Spain.

162

Table 1. Main physiographic features of the study sites. Forest line is the upper limit of closed canopy forests located near the transects.

Site	Species	Latitude (N)	Longitude (-W, +E)	Country	Current forest line elevation (m a.s.l.)	Altitude of the uppermost sampled pine (m a.s.l.)	Prevailing exposure	Mean slope (%)	Transect planimetric size width x length (m)	Transect planimetric area (ha)
POL	*Pinus heldreichii*	39.897	16.206	Italy	2045	2142	NW	38	40 x 240	0.96
SM3	*Pinus heldreichii*	42.690	19.675	Montenegro	1960	2222	SE	45	20 x 500	1.00
SA1	*Pinus peuce*	42.505	20.006	Albania	1990	2093	NE	30	10 x 50	0.05
SM1	*Pinus peuce*	42.508	19.908	Montenegro	2000	2095	NE	43	10 x 170	0.17
SM2	*Pinus peuce*	42.649	19.849	Montenegro	2050	2092	N	10	10 x 70	0.07
UR1	*Pinus sylvestris*	42.002	-2.873	Spain	2000	2165	SW	36	20 x 360	0.72
UR2	*Pinus sylvestris*	42.001	-2.871	Spain	2000	2148	SW	36	20 x 325	0.65
LSB	*Pinus uncinata*	42.718	-0.570	Spain	1935	2078	W	34	20 x 185	0.37
MGD	*Pinus uncinata*	42.730	-0.571	Spain	1975	2165	SW	50	20 x 350	0.70

2.2. Tree species profiles

Bosnian pine (*Pinus heldreichii* H. Christ., 1863) grows between 800 and 2600 m a.s.l. (Supporting Information, Table S1). It is an upper montane species forming mixed stands with silver fir (*Abies alba* Mill.) and European beech. At the forest line in the central western part of the Balkan Peninsula and in the southern Apennines (Monte Pollino, Italy) it can form pure stands on steep and dry rocky south-exposed slopes (Vendramin et al., 2008). *P. heldreichii* seed production begins at the age of 15–20 years and the female cones mature in two years. Seeds are wind-dispersed. It grows preferably on dry, sunny sites and is a very frost-hardy species scarcely susceptible to insect attacks (Vendramin et al., 2008).

Macedonian pine (*Pinus peuce* Griseb, 1844) is an endemic species in the Balkans (Table S1), growing at 600-2500 m a.s.l. (Farjon et al., 2017). The cones mature in two years and seeds are mainly wind-dispersed. It grows preferably in cold and humid mountain climates and is adapted to rocky steep slopes. It is highly resistant to pathogens (Alexandrov & Andonovski, 2011).

Scots pine (*Pinus sylvestris* L., 1753) presence in southern Europe is limited to high elevation (up to 2100 m a.s.l. in the Balkans and Spain, and up to 2700 m in the Caucasus). It is a wind-pollinated and monoecious species (Table S1). Female flowering starts at the age of 15 years on solitary trees or 25–30 years in closed stands, whereas abundant male flowering occurs some years later (Mátyás et al., 2004). Across its wide distribution range, it grows naturally in a variety of habitats, and as a pioneer species it is well adapted to nutrient-poor soils and can readily regenerates after major natural or human disturbances (Gardner, 2013; Mátyás et al., 2004).

Mountain pine (*Pinus uncinata* Ram.) grows at 1800-2400 m a.s.l. in scattered populations across southwestern Europe (Table S1). It has small cones maturing in 2 years, hosting small-winged seeds wind-dispersed in spring (Batllori and Gutiérrez, 2008). In the Central and Eastern Pyrenees, it is mainly found in subalpine forests and forming natural treelines up to ca. 2400 m a.s.l. (Camarero et al., 2005; Batllori et al. 2009; Camarero et al., 2009).

2.3. Field sampling protocol

At the nine sites we mapped totally 964 pine specimens all growing above the forest line, with a Trimble Pro 6H GPS antenna (Trimble Inc., Sunnyvale, USA). A post-processing differential correction through Pathfinder Office 4.2 software was necessary for a 0.5-m estimated accuracy. We classified pines as seedlings (height < 0.5 m), saplings (0.5 ≤ height < 2 m) and trees (height ≥ 2 m). For each specimen, we measured the basal stem diameter and total heights and we counted the number of seed cones. We used the term 'pines' to refer to all sizes together. Although individual pines could influence the regeneration substrate throughout their growing process (Vitali et al., 2017), we estimated the ground cover share (% of each class) within circular plots of 1 m diameter around each main pine stem using four cover classes: bare rock, rocky debris, grass and shrub. The

204   shrub cover was of *Juniperus* spp., and *Calluna vulgaris* only in *P. sylvestris* sites. We then averaged

205   the individual ground cover of seedlings, saplings and trees for each species.

206   On specimens with basal stem diameter > 4 cm, we extracted wood cores at basal stem

207   position with a Pressler increment borer (10 cm length) for cambial age determination and tree-ring

208   width measurements. For smaller pines, we estimated the age by counting the number of annual

209   internodes (terminal bud scars) along the whole stem (Camarero and Gutiérrez, 2007).

210   We computed linear regressions for modelling specimens' height as a function of basal

211   diameter and age as a function of basal diameter and height. We used χ^2 tests to compare seedlings,

212   saplings and trees ground cover types. We used Generalized Linear Models (GLM) to predict the

213   probability of cone production as a function of several variables (stem diameter, height and age).

214   The number of cones was normalized per each species to account for interspecific differences. The

215   goodness of fit of the GLMs was assessed using McFadden's pseudo-R^2 values (Venables & Ripley,

216   2002).

217

218   *2.4. Spatio-temporal analyses*

219

220   Univariate point pattern analysis (PPA) techniques were applied using mapped individual data

221   (Moeur, 1993) to detect the pine spatial patterns within the altitudinal transects at different spatial

222   scales. We used the pair-correlation function $g(r)$ (Wiegand & Moloney, 2004), a second-order

223   statistic providing information at multiple scales. The pair-correlation function is non-cumulative and

224   uses only points separated by a certain distance r, allowing specific scales to be identified where

225   significant point–point interactions occur, particularly at small spatial scales (Wiegand & Moloney,

226   2004). We analyzed patterns at a scale of r = 1 to 5 m (half width of the smallest transects) and

227   verified the robustness of each pattern using the Goodness-of-Fit (*GoF*) test.

228   The univariate patterns were contrasted with the Heterogeneous Poisson (HP), which

229   considers that any point of the pattern has not an equal probability of occurring at any location within

230   the plot (Wiegand & Moloney, 2004). The 95% confidence intervals were computed from 999 Monte

231   Carlo simulations (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2004). The spatial pattern was

232 defined as significantly random, clumped or regular (hyperdispersed) if the $g(r)$ values were

233 respectively equal to, greater or lower than the confidence envelopes.

234   To detect temporal patterns of the pine recruitment process we set up a 15 year threshold

235 based on the age frequency distribution of all the available pines which revealed that most of them

236 (96%) were younger than 30-years. The specimen's past heights were reconstructed by species-

237 specific age-height linear regressions of sampled pines. All regressions had significant predictors

238 ($p<0.001$) and adjusted R-squared between 0.3 and 0.7 and allowed to differentiate seedling, sapling

239 and tree life stages.

240

241 *2.5. Tree growth assessment*

242

243   We collected 190 increment cores at basal stem position (see Table 2 for details) and mounted

244 and glued them on wooden supports. We thoroughly polished the cores with progressively finer

245 sandpaper until the tree rings were clearly visible. We used the semi-automatic LINTAB system and

246 WinTSAP software (Rinntech, Heidelberg, Germany) to measure tree-ring width at 0.01 mm

247 precision. Most of the ring width series were shorter than 30 years and they were visually cross-

248 dated. Tree-ring widths were converted into basal area increments (BAI) since this variable reflects

249 more accurately growth changes and trends (Biondi and Qeadan, 2008). We estimated mean BAI,

250 mean tree-ring width and mean longitudinal growth rate, obtained by diving specimen height with

251 estimated age, for all sampled species.

252

253 *2.6. Seed dispersal*

254

255   To determine the contribution of pine seed dispersal to the spatial patterns of tree recruitment

256 at the treeline, we conducted seed-release experiments with the four species following the

257 procedures by Greene and Johnson (1989) and Camarero et al. (2005). Seeds were extracted from

258 cones collected during the same field surveys, except for *P. uncinata* and *P. sylvestris* cones that

259 were collected during previous field trip in 2013-2014 at Spanish treeline sites. In a winter morning,

30 seeds per species were released from a height of 10 m under moderate wind conditions (0.5-3.0 m s^{-1}) on an open field near the Pyrenean Institute of Ecology, Zaragoza, Spain (41.771° N, 0.716° W). The height for seed dispersal was established considering the mean tree height of nearby forest stands measured at all the study sites. During the release experiment, wind blew from north to north-west, while mean air temperature and relative humidity ranged from 6 to 15 °C and 65% to 85%, respectively, but did not change during each experiment. We recorded the distance travelled by each released seed and obtained a frequency distribution of dispersal distances for each species. Seed weight was obtained for each released seed and its mean seed area was estimated by scanning all seeds and by using an image-analysis system (NIH IMAGE ver. 1.63).

3. Results

3.1. Size and age of trees and treeline-ecotone structure

The forest line elevation at the nine sites ranged between 1935 m a.s.l. of *P. uncinata* (LSB, Spain) and 2050 m a.s.l. of *P. peuce* (SM2, Montenegro). The highest elevation of individual trees ranged between 2078 m a.s.l. for *P. uncinata* at LSB and 2222 m a.s.l for *P. heldreichii* at SM3 (Table 1). Pine recruitment at the different treeline ecotones featured scattered patterns, with very heterogeneous tree density values ranging from 87 (*P. heldreichii*) to 1552 (*P. peuce*) trees ha^{-1} (Table 2). On average, the seedlings, saplings and trees share was 57%, 30% and 12% respectively. *P. peuce*, *P. sylvestris* and *P. uncinata* were mainly seedlings (55-71%), whereas *P. heldreichii* mainly saplings (49%) (Table 2). The trees mean size was small, with basal diameters ranging from 2 cm (*P. peuce*) to 7 cm (*P. heldreichii*). The mean height varied between 54 cm (*P. peuce*) and 106 cm (*P. heldreichii*) and the mean age from 9 (*P. peuce*) to 20 years (*P. heldreichii*) (Table 2).

Table 2. Main structural variables of the sampled encroaching individuals at the nine study sites. Values are means ± standard deviation (SD). We classified pine specimens as seedlings (height < 0.5 m), saplings (0.5 ≤ height < 2 m) and trees (height ≥ 2 m).

Pine species	No. transects	No. sampled individuals	Density (N° ha^{-1})	No. sampled cores	Individuals with cones (%)	No. sampled seedlings/ saplings/ trees	Mean basal diameter ± SD (cm)	Mean height ± SD (cm)	Mean age ± SD (years)
P. heldreichii	2	170	87	73	6	**57/83/30**	7 ± 5	106 ± 81	20 ± 10
P. peuce	3	450	1552	29	2	**321/107/22**	2 ± 2	54 ± 80	9 ± 7
P. sylvestris	2	207	151	52	7	**144/36/27**	4 ± 5	67 ± 86	10 ± 6
P. uncinata	2	137	128	36	15	**76/42/19**	5 ± 7	95 ± 132	10 ± 8

We used 5-cm diameter classes and named them with the central interval value. The mode of the diameter frequency distribution was on the first classes for all species, but especially for *P. peuce* with more than 1500 stems ha^{-1} in the class with diameter ≤ 5 cm (Fig. 2a). Tree height and age distributions showed similar patterns, with higher frequency of small and young individuals (Fig. S2b and S2c). *P. uncinata* had the maximum diameter (35 cm), *P. heldreichii* had the maximum age (85 years), while *P. peuce* the maximum height (7.2 m). The tree height-basal diameter linear regressions showed high values of adjusted R^2, ranging from 0.70 (*P. peuce*) to 0.91 (*P. uncinata*) (Supporting Information, Fig. S1). Lower R^2 values occurred when relating tree age with diameter and tree height as predictors (Supporting Information, Fig. S2). In general, none of the tree structural variables (diameter, height and age) decreased with transect length (Supporting Information, Fig. S3, S4 and S5) that being constant at each plot was was used as a proxy of relative elevation. Positive significant correlations between transect relative elevation and pine structural variables (diameter and height) were observed only for *P. peuce* at SA1 (r = 0.30, p ≤ 0.01). Negative correlations for diameter-elevation (r = -0.30, p ≤ 0.05) and height-elevation (r = -0.35, p≤ 0.01) occurred only for *P. uncinata* at MGD. Age and elevation were never significantly correlated.

304
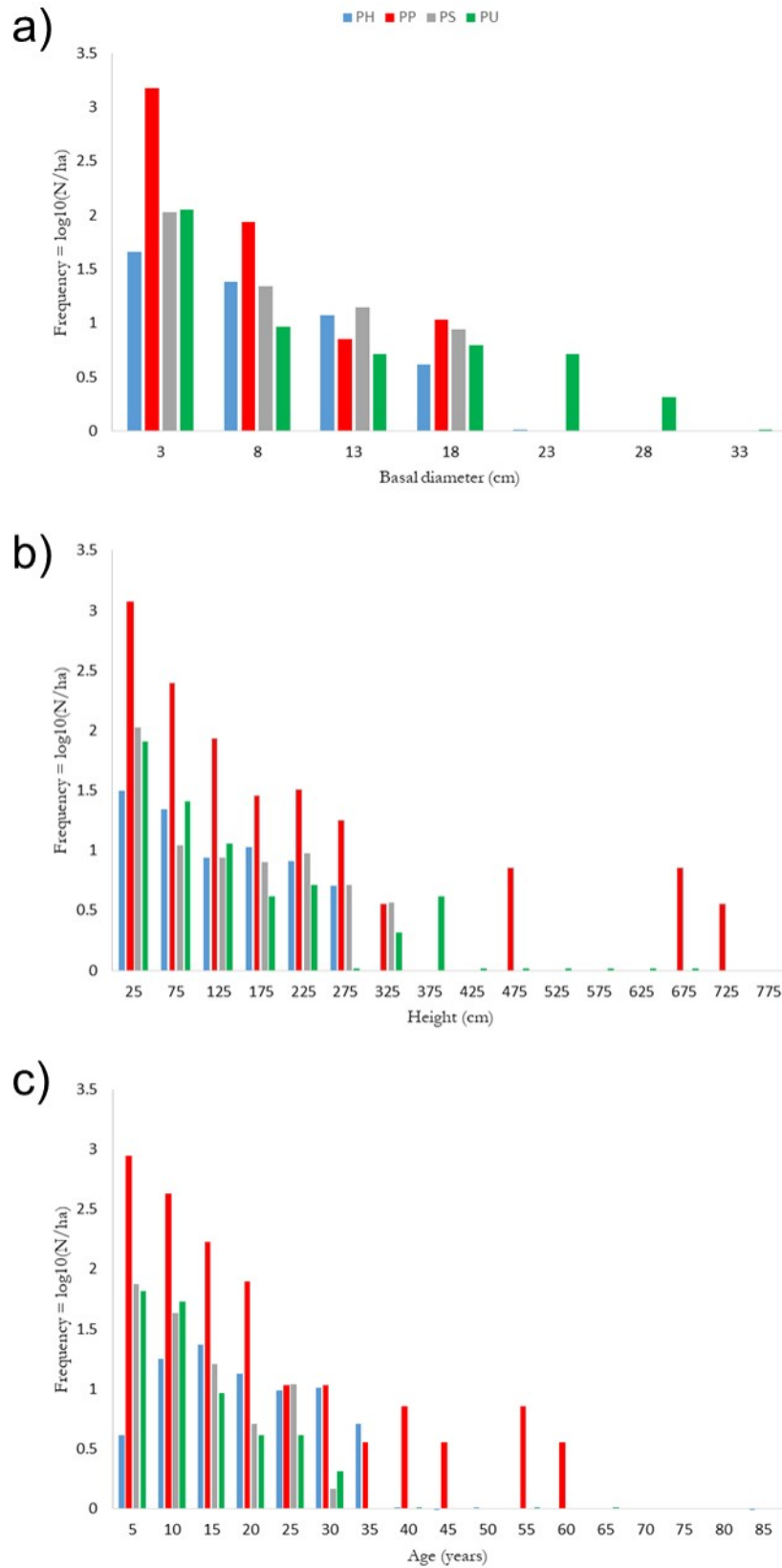
Fig. 2. Log-transformed frequency distribution (No. ha⁻¹) of basal diameter (a), height (b) and estimated age (c) of all the treeline-sampled pines: *P. heldreichii* (PH, blue bars), *P. peuce* (PP, red bars), *P. sylvestris* (PS, grey bars) and *P. uncinata* (PU, green bars). The x-axis values are the central values of each class.

308

3.2. Spatio-temporal analyses

310

At all treeline transects, seedlings, saplings and trees were in general randomly distributed (Fig. 3 - Present plots) and without spatial segregation patterns. In some cases, we found the occurrence of higher density spots (e.g. SM1, UR1, UR2, and LSB sites). The PPAs for all pines showed a significant tendency (GoF: $p \leq 0.05$) towards a clustered distribution only for *P. peuce* at the scale of 1 m at SA1 and at scales from 1 to 4 m at SM1 (Supporting Information, Table S2). The past plots, 15 years before present, revealed the absence of pine trees (≥ 2 m of height) at all sites except SM1 and MGD (Fig. 3 - Past plots). Here we could estimate an upward increase of 74 and 23 m respectively of the "tree species line", the uppermost elevation of individual trees (*sensu* Körner, 1998). On the other hand, the infilling process occurred synchronously at all transects, but less on *P. heldreichii* sites (POL and SM3).
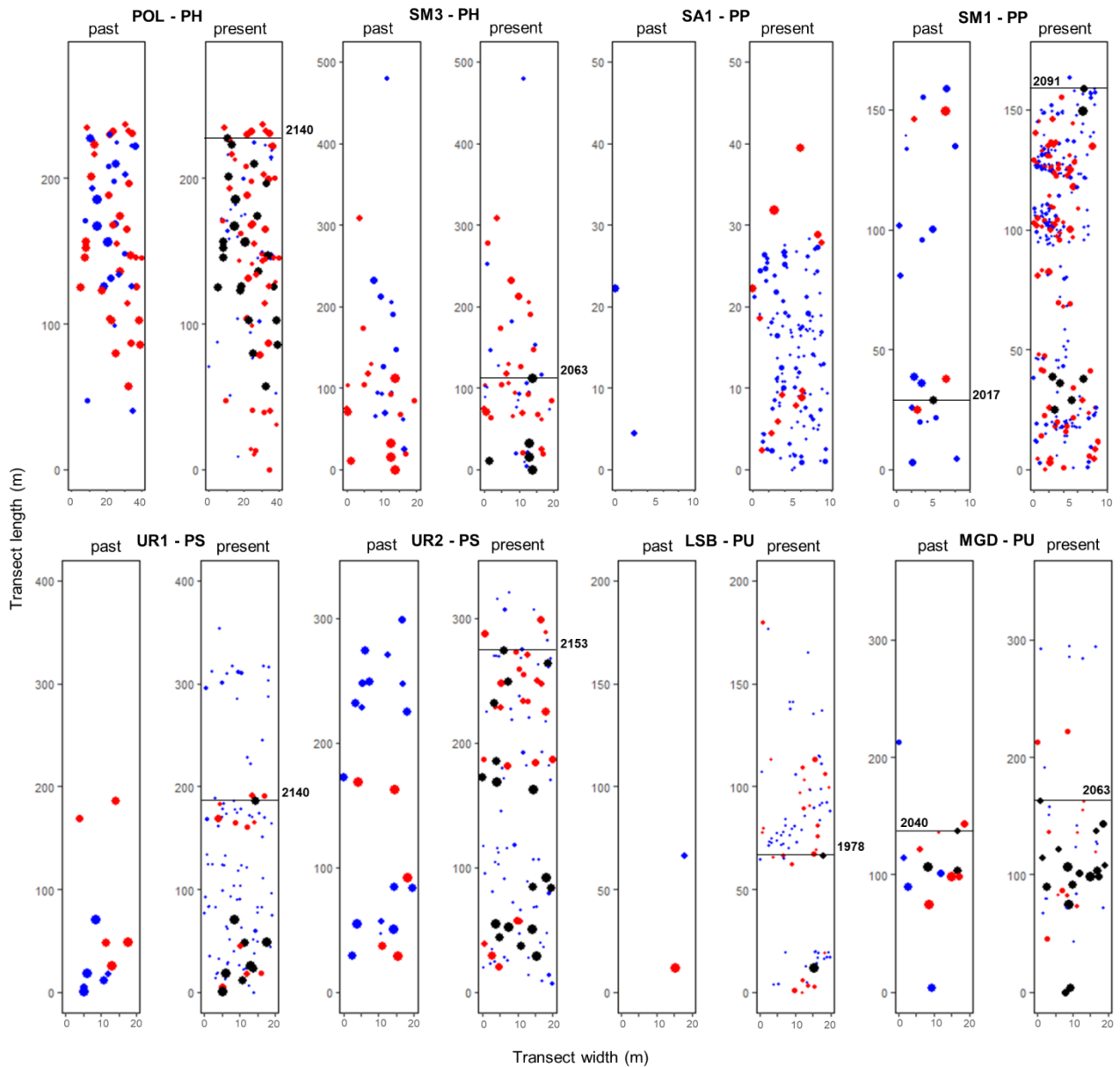
321

Fig. 3. Mapped point distribution of all pine individuals at the eight study sites (see Tables 1 and 2 for site characteristics) 15 years before the sampling (Past, plots to the left) and at sampling date (Present, plots to the right). The pine heights were reconstructed using species-specific linear regressions (see text). Blue dots are seedlings (height < 0.5 m), red dots saplings (0.5 ≤ height < 2 m) and black dots trees (height ≥ 2 m). The dot scale size is proportional to the height range at each pair of plots (study sites). The pine positions are relative planimetric coordinates (meters) from lower (0) to higher relative positions within each transect. Horizontal black lines indicate the highest elevation (m a.s.l.) where a tree (height ≥ 2 m) is located (tree species line) (see text). SM2 (*P. peuce*) was excluded for the very low number of pines present in the transect.

3.3. Regeneration substrate

Ground cover differed significatively among sites: in general grass cover was prevalent (> 50%), except for *P. sylvestris* transects, where more than 50% of the individuals were within or neighboring shrubs. Rock debris and especially bare rock had minor shares but occurred at almost all sites (Fig. 4). More significant differences appeared for all species when discriminating for development class (seedlings, saplings and trees: χ^2 = 12.92–91.32, *p* < 0.05). *P. heldreichii* specimens in general were mostly on grass substrate (>80%) (Fig. 3), with a decreasing proportion on debris from seedlings to trees. Similarly, *P. peuce* grew mostly on grass substrate (60-80%), whereas seedlings and saplings, but not trees, occurred on rock debris. A large share of *P. sylvestris* seedlings (50%) and saplings (70%) were found within *Calluna vulgaris* low shrubs, whereas saplings and trees were never on debris substrate. Most seedlings of *P. uncinata* were on grass (62%) and debris (36%) cover, saplings mainly on grass (62%) and the rest distributed between shrub (14%) and debris (17%), whereas trees largely on rock (26%) and shrub (21%) cover (Fig. 4).
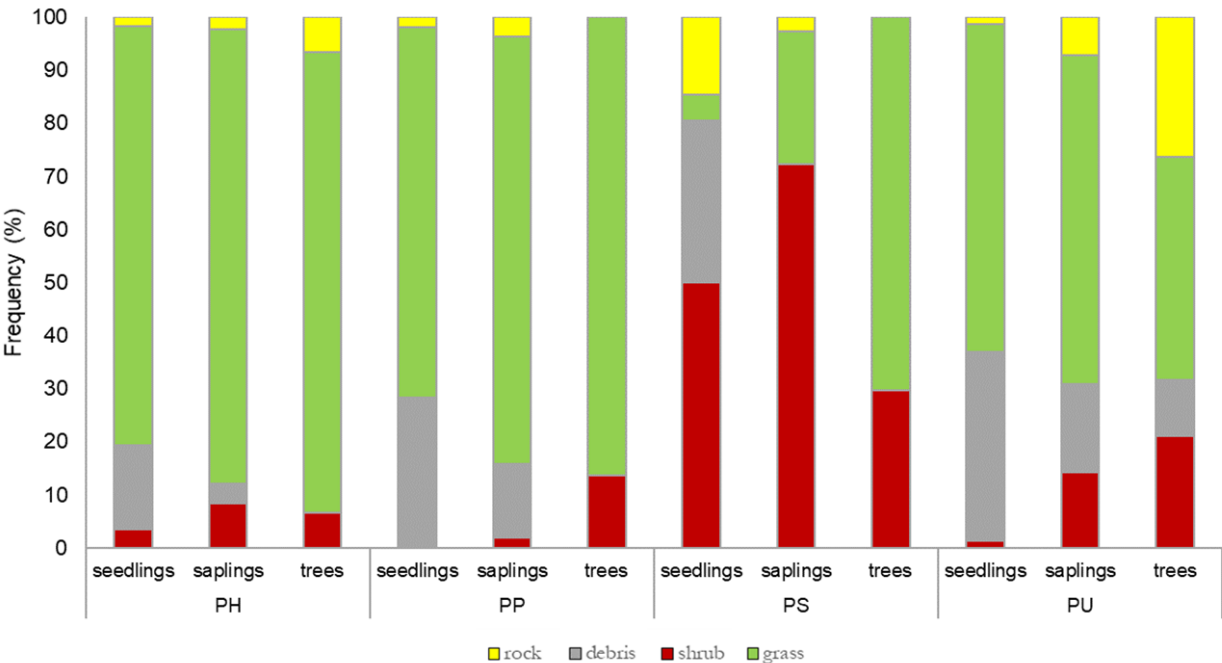
Fig. 4. Frequency distribution of pine seedlings, saplings and trees according to species and ground cover class (rock, debris, shrub and grass).

3.4. Tree growth assessment

352

Radial growth expressed as mean BAI values was similar for all species, except *P. peuce* (Supporting Information, Fig. S6), featuring an initially increasing trend, then a slightly decreasing or a stabilizing one in the last few years. *P. sylvestris* featured much flatter growth curves, raising only after 2005. *P. uncinata* and *P. peuce* reached the highest mean BAI values, 4.6 and 4.4 cm^2 $year^{-1}$ respectively, whereas *P. heldreichii*, due to the higher mean age, showed the lowest rate (1.8 cm^2 $year^{-1}$). The mean longitudinal growth rate estimated from specimen's height and age ranged from 7.1 cm (*P. heldreichii*) to 15.3 cm $year^{-1}$ (*P. uncinata*) (Table 3).

3.5. Cone production and seed dispersal simulation

Pine specimens bearing seed cones ranged from 2% in *P. peuce* to 15% in *P. uncinata* (Table 2). All GLMs were significant at $p<0.001$ (except for *P. heldreichii* in the GLM of cones-age, where $p<0.1$). The GLMs for cone production (Supporting Information, Table S3 and Fig. S7) showed higher correlations (McFadden's pseudo-R^2 values) with height (R^2 = 0.27−0.59) and basal diameter (R^2 = 0.19−0.62) than age (R^2 = 0.04−0.58). All species showed similar size (ca. 200-300 cm of tree height and ca. 10-20 cm of basal diameter) and different age characteristics when they reached a 50% probability of producing cones (Table 3 and Fig. S7).

P. heldreichii and *P. peuce* exhibited the largest seed surface areas, 1.52 ± 0.07 cm^2 and 1.32 ± 0.10 cm^2 respectively, whereas *P. uncinata* and *P. sylvestris* produced the lightest seeds: 12.5 ± 1.9 mg and 15.5 ± 0.3 mg of mean fresh weight (Table S4). The seed-release experiment revealed a heterogeneous mean horizontal dispersal with two species showing longer dispersal distances (*P. heldreichii*, 10.9 m; *P. peuce*, 6.7 m) than the others (*P. sylvestris*, 4.2 m; *P. uncinata*, 3.7 m) (Supporting Information, Fig. S8).

Table 3. Pines height with 50% probability of cones production (resulted from GLMs), mean longitudinal growth rates and radial (tree ring width, BAI) growth rates of species sampled: PH, *P. heldreichii*; PP; *P. peuce*; PS, *P. sylvestris*; PU, *P. uncinata*.

Species	Sites	Height with 0.5 probability of cones production (cm)	Mean longitudinal growth rate ± SD (cm year^{-1})	Mean tree ring width ± SD (mm year^{-1})	Mean BAI ± SD (cm^2 year^{-1})
PH	POL-SM3	300	7.1 ± 3.8	1.5 ± 0.7	1.8 ± 1.7
PP	SA1-SM1-SM2	300	9.0 ± 6.9	1.9 ± 1.2	4.4 ± 5.6
PS	UR1-UR2	250	11.4 ± 5.6	2.3 ± 1.0	2.6 ± 2.0
PU	LSB-MGD	200	15.3 ± 7.6	2.5 ± 1.4	4.6 ± 5.7

380

4. Discussion

382

383   Mountain treelines in the Mediterranean basin were shaped by millennial human activities
384 featuring heterogeneous ecotones composed by different conifer tree species. A suitable
385 comprehension of the ongoing spatio-temporal vegetation dynamics is a challenging but necessary
386 task to suggest plausible predictions of their post-abandonment dynamics and trajectories. A tree
387 recruitment process is occurring at high elevation on most European mountains after a recent
388 decline of pastoral use causing evident land-cover changes (Holtmeier and Broll, 2018). We
389 searched for evidence of treeline advancement that requires seedlings survival above the current
390 treeline elevation (Korner 1998). The results of our study conducted in different human-disturbed
391 treelines of Southern Europe exhibited a widespread pine encroachment on treeless areas above
392 the current forest line. Here we compared the colonization trends of four native pine species at
393 their respective treeline ecotones. At most sites we detected similar temporal patterns of tree
394 encroachment especially during the last 15 years from sampling dates and species-specific
395 responses of their growth, spatial distribution and seed dispersal.
396   The size-age structure distributions highlighted that most of the encroaching pines,
397 regardless of the species, are small and young individuals: the mean basal diameter ranged
398 between 2 and 7 cm, the mean height between 0.54 and 1.06 m and the mean age 9-20 years.
399 Very few individuals were older than 30 years or taller than 2 m, suggesting a tree establishment in
400 recent decades, as reported at Pyrenees treelines (Batllori & Gutiérrez, 2008). In several study
401 regions, young trees were taller in the lower and middle part of the ecotones, revealing an

increasing population density (infilling) rather than a real treeline advancement (Camarero & Gutiérrez, 2004). In our sites recent encroachment occurred up to the mountain ridge and several pines reached the 2 m height threshold during the last 15 years, indicating an upward establishment of trees and maybe a potential treeline upshift. This complex process could require several decades or even centuries to be confirmed (Holtmeier & Broll, 2005).

The recolonization was spatially heterogeneous, featuring very variable tree density values (from 87 to 1552 pines ha^{-1}) and in general unclear spatial patterns. Only at two *P. peuce* sites we found a clustered distribution of seedlings at scales from 1 to 4 m. High elevation, exposure to wind disturbance and snow accumulation are usually considered unfavorable environmental conditions for regeneration. Therefore, the increasing mean BAI (1.8 to 4.6 cm^2 year^{-1}) and the mean height growth (7.1 to 15.3 cm year^{-1}), even with some interspecific differences, were not expected. In a similar study at high elevation on central Apennines (Italy), the growth rates of *Pinus nigra* Arn. (BAI = 5–10 cm^2 year^{-1}) suggested that trees of anthropogenic treelines after pastoral abandonment can respond positively to climate warming (Vitali et al., 2017).

All species shared common minimum reproductive thresholds: a 50% probability of producing cones was attained when specimens reached 2-3 m of height and 10-20 cm of basal diameter. Some interspecific differences occurred on minimum age threshold. Moreover, tree size were better predictors than age for cone production (Krannitz & Duralia, 2004; Ayari & Khouja, 2014; Davi et al., 2016).

P. peuce in Albania and Montenegro had the lowest mean size and age, despite the presence of very few individuals with higher values. Seed dispersal came from closed forest at lower elevation and encroached trees have so far the lowest percentage of seed cones. The presence of trees reaching the minimum size (but not age) thresholds for cone production models indicated that these populations could count on new reproductive individuals. This colonization process was not affected by grass cover competition proving the shade-tolerance of *P. peuce* (Farjon, 2017).

P. heldreichii had similar characteristics but displayed different encroaching processes both at Italian and Balkans sites. These sites host the oldest encroaching populations and the lowest

growth rate recorded. *P. heldreichii* had the least proportion of reproductive trees, suggesting that its encroachment depended both on the availability of seeds from the neighboring forest and on the conspicuous seed dispersal. We observed two dissemination trajectories: i) an upshifting one from the downslope pine forest in the Balkans and ii) an overtopping one from the opposite slope of the mountain in the Apennines. Coherently, the spatial structures were reversed at the two sites, with a decreasing pine density from bottom to top and top to bottom of transects respectively at Mt. Komovi (SM3) and at Mt. Pollino (POL). Generally, *P. heldreichii* was mainly on grass cover but seedlings could also colonize on debris (16%), whereas saplings and trees due their vicinity to shrubs and rocks, could suggest some facilitation effects.

   P. sylvestris and *P. uncinata* featured similar population structures. Their dispersal distances were the shortest one due to their smaller seed projected area. Both species could reach the cone production height thresholds in a shorter time, due to higher growth rate. However, the two species differed for ground cover at different life stages: more than 50% of *P. sylvestris* seedlings and saplings were both found near or inside *Calluna vulgaris* shrubs and 15% of seedlings close to rocks. This is a facilitation strategy to compensate the harsh microclimate conditions until their complete establishment (Camarero & Gutiérrez, 2007). On the other hand, low shrubs forming dense patches seemed to hamper the recruitment of *P. uncinata* in the Pyrenees sites, as confirmed by the greater share of seedlings on debris and on grass cover, where competition for light is lower (Batllori et al., 2009).

   Few studies surveyed natural recruitment patterns of several tree species along elevation ranges including the treeline ecotones. Some aimed to disentangle the different factors affecting occurrence, abundance and growth of recruits (Didier, 2001; Benavides et al., 2016). Others focused more on the influence of climate on these processes (Rabasa et al., 2013; Trant and Hermanutz, 2014). Seed dispersal from encroached trees appeared a crucial aspect for future treeline dynamics considering the relevant importance of seed source availability (Castanha et al., 2013) and differences among species characteristics. The seed-release experiment proved that dispersal characteristics of the four species could play a key role in colonization processes. Seed dispersal features should be also connected to other reproduction traits because the fecundity of

pines is an important trait considering their pioneering and invasive behavior all around the world (Richardson and Rejmánek, 2004). For instance, a comparison between native *P. sylvestris* and non-native *P. nigra* in southern France reported a higher net reproductive rate and more efficient dispersal for black pine (Debain et al., 2007). Seed maturation phenology, masting behavior and timing of cone opening could be other crucial aspects to monitor for assessing the treeline potential upward shift. Longer season for cone opening, as for *Pinus nigra* (Piermattei et al., 2016; Vitali et al., 2017), allows major dispersal and uplifting events with spring winds (Debain et al., 2007).

Treeline advance is confirmed only after successful establishment, growth, and survival of new seedlings (Kambo and Danby, 2018). Tree seedlings establishment is contingent on many abiotic and biotic factors acting at local scales (Lett and Dorrepaal, 2018), like the effect of landform influence (Greenwood et al., 2015). These newly emerged trees must deal with grass cover competition and possibly benefit of facilitation by shrubs or rocks (Liang et al., 2018), highlighting the key role of safe sites availability (Batllori et al., 2009).

5. Conclusions

With this synchronic study, we detected and analyzed a recent encroaching process shared by four locally native pine species at different treeline ecotones in Southern Europe. At most sites the tree recruitment started 30-35 years before sampling dates; only in Montenegro a few *P. heldreichii* specimens were dated at older age (55-60 years). Also, the similarity of structural features together with the spatial distribution patterns of these pine populations seem to indicate a coeval and common trend of recolonizing treeless areas above the forest line. At some sites, it appeared as an infilling dynamic, but at others some trees (taller than 2 m) were found at higher elevation than in the recent past (15 years), acting as new posts of the tree species line (*sensu* Korner). More time and more growing trees are necessary to confirm the occurrence of a treeline advance, but these high elevation pine populations featured a rapid encroachment aptitude regardless of slope steepness or exposure. Microtopography and ground cover type can play an important role in shaping the safer sites for seed germination and seedling establishment. The

increasing number of these recent tree cohorts within the treeline ecotones can also induce

changes in major biogeochemical cycles, soil properties, and mountain eco-hydrological processes

(Rundel et al., 2014), leading to a significant long-term plant diversity decline in species-rich

grasslands (Dullinger et al., 2009). Forest densification could improve slope protection against

landslides and snow avalanches but also produce more fuel, and together with climate warming,

increase the risk of mountain wildfires (Holtmeier & Broll, 2005).

Accurate predictions about these new subalpine forests will require better estimation of

demographic and dispersal parameters in similar low-density expanding tree populations (Debain

et al., 2007). The establishment of permanent transects or plots with the availability of precise

geographic positions and structural data of all detected trees, provide a monitoring of pine survival,

a general assessment of spatio-temporal regeneration dynamics and the forecast of future treeline

pine expansion.

REFERENCES

Ayari, A., Khouja, M.A., 2014. Ecophysiological variables influencing Aleppo pine seed and cone production: a review. Tree Physiology. 34 (4), 426–437. https://doi.org/10.1093/treephys/tpu022

Alexandrov, A.H., Andonovski, V., 2011. EUFORGEN Technical Guidelines for genetic conservation and use of Macedonian pine (Pinus peuce). Bioversity Int. Rome, Italy. 6 pages.

Batllori, E., Camarero, J.J., Ninot, J.M., Gutiérrez, E., 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. Implications and potential responses to climate warming. Glob. Ecol. Biogeogr. 18, 460–472. doi:10.1111/j.1466-8238.2009.00464.x

Batllori, E., Gutiérrez, E., 2008. Regional tree line dynamics in response to global change in the Pyrenees. Journal of Ecology. 96 , 1275–1288.Benavides, R., Escudero, A., Coll, L., Ferrandis, P., Ogaya, R., Gouriveau, F., Peñuelas, J., Valladares, F., 2016. Recruitment patterns of four tree species along elevation gradients in Mediterranean mountains: Not only climate matters. For. Ecol. Manage. 360, 287–296. doi:10.1016/j.foreco.2015.10.043

Biondi, F., Qeadan, F., 2008. A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. Tree-Ring Res. 64, 81–96. doi:10.3959/2008-6.1

Camarero, J.J., Gutiérrez, E., 2007. Response of Pinus uncinata Recruitment to Climate Warming and Changes in Grazing Pressure in an Isolated Population of the Iberian System (NE Spain). Arctic, Antarct. Alp. Res. 39, 210–217. doi:10.1657/1523-0430(2007)39

Camarero, J.J., Gutiérrez, E., Fortin, M.J., Ribbens, E., 2005. Spatial patterns of tree recruitment in a relict population of Pinus uncinata: forest expansion through stratified diffusion. J. Biogeogr. 32, 1979–1992. doi:10.1111/j.1365-2699.2005.01333.x

Camarero, J.J., Gutierrez, E., 2004. Pace and pattern of recent tree line dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. Clim. Change 63: 181-200.

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

536   doi:10.1111/ecog.00280

537   Castanha, C., Torn, M.S., Germino, M.J., B. Weibel, Kueppers, L.M., 2013. Conifer seedling

538   recruitment across a gradient from forest to alpine tundra: effects of species, provenance, and

539   site. Plant Ecology & Diversity. 6 (3–4), 307–318.

540   http://dx.doi.org/10.1080/17550874.2012.716087

541   Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European

542   woody species. Data Br. 12, 662–666. doi:10.1016/j.dib.2017.05.007

543   Chauchard, S., Carcaillet, C., Guibal, F., 2007. Patterns of land-use abandonment control tree-

544   recruitment and forest dynamics in Mediterranean mountains. Ecosystems 10, 936–948.

545   doi:10.1007/s10021-007-9065-4

546   Clark, J.S., Silman, M., Kern, R., Macklin, E., HilleRisLambers, J., 1999. Seed dispersal near and

547   far: patterns across temperate and tropical forests. Ecology, 80, 1475–1494.

548   Davi, H., Cailleret, M., Restoux, G., Amm, A., Pichot, C., Fady, B. 2016. Disentangling the factors

549   driving tree reproduction. Ecosphere. 7(9), e01389. 10.1002/ecs2.1389

550   Debain, S., Chadœuf, J., Curt, T., Kunstler, G., Lepart, J., 2007. Comparing effective dispersal in

551   expanding population of Pinus sylvestris and Pinus nigra in calcareous grassland. Can. J. For.

552   Res. 37, 705–718. doi:10.1139/X06-265

553   Debussche, M., Lepart, J., Dervieux, A., 1999. Mediterranean landscape changes: evidence from

554   old postcards. Glob. Ecol. Biogeogr. 8, 3–15. doi:10.1046/j.1365-2699.1999.00316.x

555   Didier, L., 2001. Invasion patterns of European larch and Swiss stone pine in subalpine pastures in

556   the French Alps. For. Ecol. Manage. 145, 67–77. doi:10.1016/S0378-1127(00)00575-2

557   Dullinger, S., Dirnböck, T., Greimler, J., Grabherr, G., Dirnböck, T., 2009. A resampling approach for

558   evaluating effects of pasture abandonment on subalpine plant species diversity. J. Veg. Sci. 14,

559   243–252. doi:10.1111/j.1654-1103.2003.tb02149.x

560   Dullinger, S., Dirnböck, T., Grabherr, G., 2004. Modelling climate change-driven tree line shifts:

561   relative effects of temperature increase, dispersal and invasibility. J. Ecol. 92, 241-252.

562   Farjon, A., 2017. Pinus peuce. IUCN Red List Threat. Species e.T34193A95751594.

563   doi:http://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T34193A95751594.en

564   Gardner, M., 2013. Pinus sylvestris. IUCN Red List Threat. Species 2013 e.T42418A2978732.

565   doi:http://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T42418A2978732.en

566   Gellrich, M., Baur, P., Koch, B., Zimmermann, N.E., 2007. Agricultural land abandonment and natural

567   forest re-growth in the Swiss mountains: A spatially explicit economic analysis. Agric. Ecosyst.

568   Environ. 118, 93–108. doi:10.1016/j.agee.2006.05.001

569   Gehrig-Fasel, J., Guisan, A., Zimmermann, N.E., 2007. Tree line shifts in the Swiss Alps: climate

570   change or land abandonment? J. Veg. Sci. 18 (4), 571–582.

571   Germino, M.J., Smith, W.K., Resor, A.C., 2002. Conifer seedling distribution and survival in an

572   alpine-treeline ecotone. Plant Ecology. 162, 157–168.

573   Greene, D.F., Johnson, E.A., 1989. A Model of Wind Dispersal of Winged or Plumed Seeds. Ecology

574   70, 339–347.

575   Greenwood, S., Chen, J-C., Chen C-T., Jump, A.S., 2015. Temperature and sheltering determine

576   patterns of seedling establishment in an advancing subtropical treeline. Journal of Vegetation

577   Science. 26, 711–721.

578   Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the

579   regeneration Nnche. Biol. Rev 52, 107–145. doi:10.1111/j.1469-185X.1977.tb01347.x

580   Harsch, M.A., Bader, M.Y., 2011. Treeline form - a potential key to understanding treeline dynamics.

581   Glob. Ecol. Biogeogr. 20, 582–596. doi:10.1111/j.1466-8238.2010.00622.x

582   Harsch, M.A., Hulme, P.E., McGlone, M.S., Duncan, R.P., 2009. Are treelines advancing? A global

583   meta-analysis of treeline response to climate warming. Ecol. Lett. 12, 1040–1049.

584   doi:10.1111/j.1461-0248.2009.01355.x

585   Holtmeier, F.K., Broll, G., 2018. Subalpine Forest and Treeline Ecotone under the Influence of

586   Disturbances: A Review. J. Environ. Prot. (Irvine,. Calif). 09, 815–845.

587   doi:10.4236/jep.2018.97051

588   Holtmeier, F.K., Broll, G., 2007. Treeline advance - driving processes and adverse factors. Landsc.

589   Online 1, 1–33. doi:10.3097/LO.200701

590   Holtmeier, F.K., Broll, G., 2005. Sensitivity and response of northern hemisphere altitudinal and polar

591   treelines to environmental change at landscape and local scales. Glob. Ecol. Biogeogr. 14,

395–410. doi:10.1111/j.1466-822X.2005.00168.x

Kambo, D., Danby, R.K., 2018. Factors influencing the establishment and growth of tree seedlings at Subarctic alpine treelines. Ecosphere 9. doi:10.1002/ecs2.2176

Körner, C., 2007. Climatic treelines: conventions, global patterns, causes. Erdkunde 61, 316–324.

Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia. 115, 445-459

Krannitz, P.G., Duralia, T.E., 2004. Cone and seed production in Pinus Ponderosa: a review. Western North American Naturalist. 64(2), 208–218

Juntunen, V., Neuvonen, S., 2006. Natural regeneration of Scots pine and Norway spruce close to the timberline in northern Finland. Silva Fennica, 40 (3), 443–458.

Leonelli, G., Pelflni, M., Morra Di Cella, U., Garavaglia, V., 2011. Climate warming and the recent treeline shift in the european alps: The role of geomorphological factors in high-altitude sites. Ambio 40, 264–273. doi:10.1007/s13280-010-0096-2

Lett, S., Dorrepaal, E., 2018. Global drivers of tree seedling establishment at alpine treelines in a changing climate. Funct. Ecol. 32, 1666–1680. doi:10.1111/1365-2435.13137

Liang, Y., Duveneck, M.J., Gustafson, E.J., Serra-Diaz, J.M., Thompson, J.R., 2018. How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. Glob. Chang. Biol. 24, e335–e351. doi:10.1111/gcb.13847

Liang E., Wang Y., Eckstein D., Luo T., 2011. Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. New Phytologist. 190, 760-9.

MacDonald, D., Crabtree, J.., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Gutierrez Lazpita, J., Gibon, a, 2000. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. J. Environ. Manage. 59, 47–69. doi:10.1006/jema.1999.0335

Mátyás, C., Ackzell, L., Samuel, C.J.A., 2004. EUFORGEN Technical Guidelines for genetic conservation and use for Scots pine (Pinus sylvestris). Int. Plant Genet. Resour. Institute, Rome, Italy. 6 pages.

Moeur, M., 1993. Characterizing spatial patterns of trees using stem-mapped data. Forest Science. 39, 756-775.

Ott, E., Frehner, M., Frey, H.U., Lüscher, P., 1997. Gebirgsnadelwälder-Ein praxisorientierter Leitfaden füreine standortgerechte Waldbehandlung. Verlag Paul Haupt, Bern.

Piermattei, A., Lingua, E., Urbinati, C., Garbarino, M., 2016. Pinus nigra anthropogenic treelines in the central Apennines show common pattern of tree recruitment. Eur. J. For. Res. 135, 1119–1130. doi:10.1007/s10342-016-0999-y

Rabasa, S.G., Granda, E., Benavides, R., Kunstler, G., Espelta, J.M., Ogaya, R., Peñuelas, J., Scherer-Lorenzen, M., Gil, W., Grodzki, W., Ambrozy, S., Bergh, J., Hódar, J.A., Zamora, R., Valladares, F., 2013. Disparity in elevational shifts of European trees in response to recent climate warming. Glob. Chang. Biol. 19, 2490–2499. doi:10.1111/gcb.12220

Richardson, D.M., Rejmánek, M., 2004. Conifers as invasive aliens: a global survey and predictive framework. Divers. Distrib. 10, 321–331. doi:10.1111/j.1366-9516.2004.00096.x

Rundel, P.W., Dickie, I.A., Richardson, D.M., 2014. Tree invasions into treeless areas: mechanisms and ecosystem processes. Biol. Invasions 16, 663–675. doi:10.1007/s10530-013-0614-9

Stoyan, D., Stoyan, H., 1994. Fractals, random shapes and point fields: methods of geometrical statistics. Wiley, Chichester, UK.

Tasser, E., Walde, J., Tappeiner, U., Teutsch, A., Noggler, W., 2007. Land-use changes and natural reforestation in the Eastern Central Alps. Agriculture Ecosystems and Environment. 118, 115–129.

Trant, A.J., Hermanutz, L., 2014. Advancing towards novel tree lines? A multispecies approach to recent tree line dynamics in subarctic alpine Labrador, northern Canada. J. Biogeogr. 41, 1115–1125. doi:10.1111/jbi.12287

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics With S, Springer. doi:10.1198/tech.2003.s33

Vendramin, G.G., Fineschi, S., Fady, B., 2008. EUFORGEN Tecnical Guidelines for genetic conservation and use for Bosnian pine (Pinus heldreichii). Bioversity Int. Rome, Italy. 6 pages.

Vitali, A., Camarero, J.J., Garbarino, M., Piermattei, A., Urbinati, C., 2017. Deconstructing human-

647 shaped treelines: Microsite topography and distance to seed source control Pinus nigra

648 colonization of treeless areas in the Italian Apennines. For. Ecol. Manage. 406, 37–45.

649 doi:10.1016/j.foreco.2017.10.004

650 Wallentin, G., Tappeiner, U., Strobl, J., Tasser, E., 2008. Understanding alpine tree line dynamics:

651 an individual-based model. Ecological Modelling, 218, 235–246.

652 Weisberg, P.J., Shandra, O., Becker, M.E., 2013. Landscape Influences on Recent Timberline Shifts

653 in the Carpathian Mountains: Abiotic Influences Modulate Effects of Land-Use Change. Arctic,

654 Antarct. Alp. Res. 45, 404–414.

655 Wiegand, T., Moloney, K.A., 2004. Rings, circles, and null-models for point pattern analysis in

656 ecology. Oikos. 104, 209–229.