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Pine recolonization dynamics in Mediterranean human-disturbed treeline ecotones

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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

108   ecological patterns of similar recent processes of four pine species at human-disturbed treeline

109   ecotones across southern Europe.

110   We hypothesized that, the synergic influences of climate and human abandonment could

111   have triggered comparable encroachment patterns above other naturally formed forest lines on

112   Mediterranean mountains. At all treeline ecotones we found evidence of former pastoral

113   management but given the incomplete availability of official land-use changes data, we avoided to

114   attempt the disentanglement of climate and land-use change effects on the recent treeline ecotone

115   dynamics. We then selected the following pine species naturally occurring at high elevation for

116   understanding their ecotones' structures and dynamics: *Pinus heldreichii* Christ. (PH), *Pinus peuce*

117   Griseb. (PP), *Pinus sylvestris* L. (PS) and *Pinus uncinata* Ram. (PU).

118   Comparatively for all pine species and their roles in treeline structure and dynamics, we

119   searched answers to the following questions: i) what are the tree structure characteristics (age and

120   size) and their spatio-temporal patterns?; ii) are there differences between seedlings, saplings and

121   tree ground cover (regeneration substrate *sensu* Grubb 1977)?; iii) how is tree growth at these

122   marginal populations?; iv) are there minimum reproductive thresholds for newly encroached pines

123   (e.g. difference in cone production)?; and v) are seed dispersal patterns different? Providing

124   plausible answers, we could shed some light on these widespread trees encroachment processes

125   in human-shaped treelines.

126

127   **2. Materials and methods**

128

129   *2.1. Study sites*

130

131   We sampled nine treeline sites situated in southern Europe (Fig. 1a), all featuring a

132   Mediterranean climate influence (i.e. warm and dry summers) and showing signs of anthropogenic

133   disturbances (relatively low elevation of forest lines, evidence of past grazing, open and recent

134   stands dominating the landscape). The lack of homogeneous and suitable data on past management

135   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).

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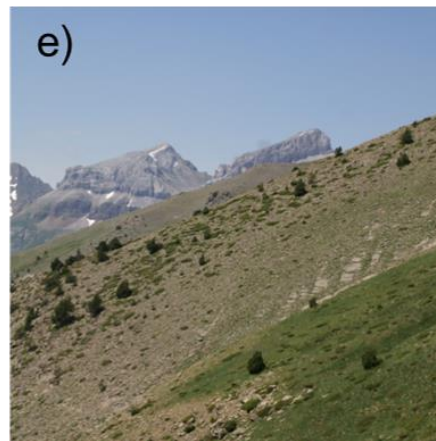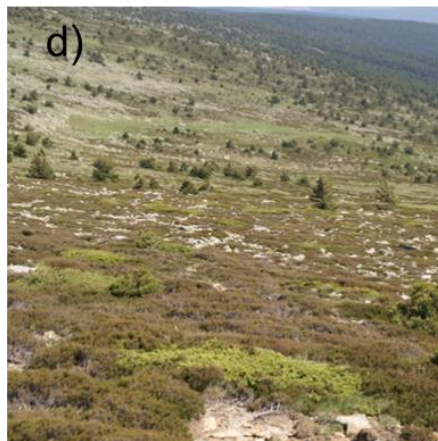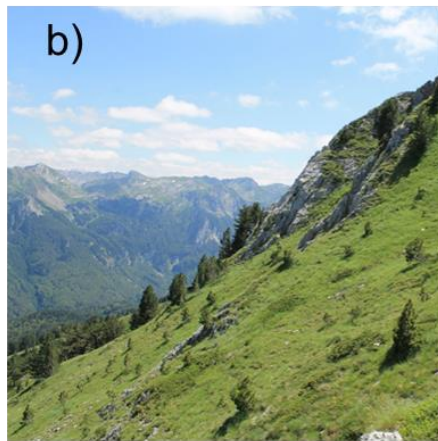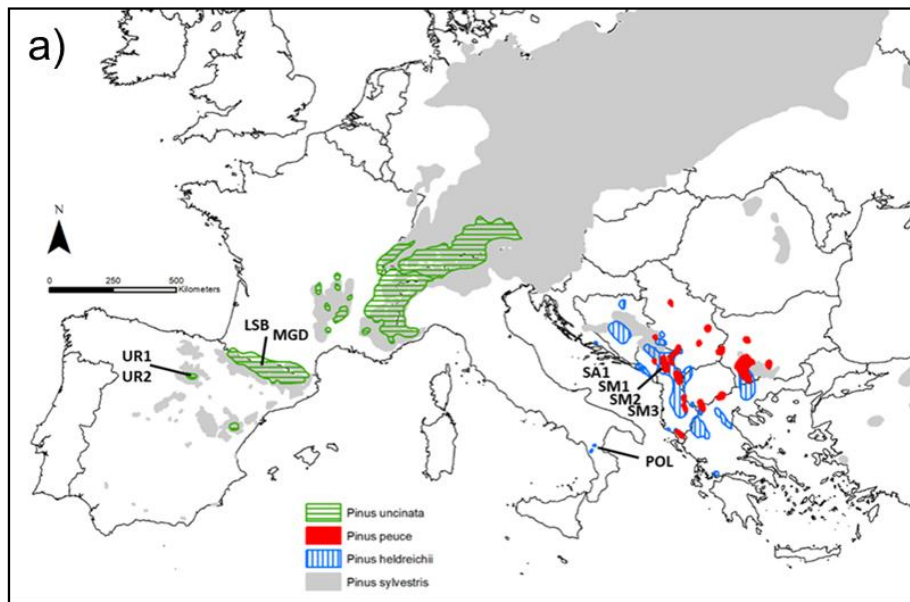
Fig. 1. (**a**) Distribution map of the four studied pine species in the Mediterranean basin [*P. uncinata* (green),
P. heldreichii (blue), *P. peuce* (red) and *P. sylvestris* (grey)] and position of the nine treeline study sites (see
Table 1). The map is a synthesis of the relative chorological maps (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.

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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

165

166 *2.2. Tree species profiles*

167

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

176   Macedonian pine (*Pinus peuce* Griseb, 1844) is an endemic species in the Balkans (Table S1),

177   growing at 600-2500 m a.s.l. (Farjon et al., 2017). The cones mature in two years and seeds are

178   mainly wind-dispersed. It grows preferably in cold and humid mountain climates and is adapted to

179   rocky steep slopes. It is highly resistant to pathogens (Alexandrov & Andonovski, 2011).

180   Scots pine (*Pinus sylvestris* L., 1753) presence in southern Europe is limited to high elevation

181   (up to 2100 m a.s.l. in the Balkans and Spain, and up to 2700 m in the Caucasus). It is a wind-

182   pollinated and monoecious species (Table S1). Female flowering starts at the age of 15 years on

183   solitary trees or 25–30 years in closed stands, whereas abundant male flowering occurs some years

184   later (Mátyás et al., 2004). Across its wide distribution range, it grows naturally in a variety of habitats,

185   and as a pioneer species it is well adapted to nutrient-poor soils and can readily regenerates after

186   major natural or human disturbances (Gardner, 2013; Mátyás et al., 2004).

187   Mountain pine (*Pinus uncinata* Ram.) grows at 1800-2400 m a.s.l. in scattered populations

188   across southwestern Europe (Table S1). It has small cones maturing in 2 years, hosting small-

189   winged seeds wind-dispersed in spring (Batllori and Gutiérrez, 2008). In the Central and Eastern

190   Pyrenees, it is mainly found in subalpine forests and forming natural treelines up to ca. 2400 m a.s.l.

191   (Camarero et al., 2005; Batllori et al. 2009; Camarero et al., 2009).

192

193   *2.3. Field sampling protocol*

194

195   At the nine sites we mapped totally 964 pine specimens all growing above the forest line, with

196   a Trimble Pro 6H GPS antenna (Trimble Inc., Sunnyvale, USA). A post-processing differential

197   correction through Pathfinder Office 4.2 software was necessary for a 0.5-m estimated accuracy.

198   We classified pines as seedlings (height < 0.5 m), saplings (0.5 ≤ height < 2 m) and trees (height ≥

199   2 m). For each specimen, we measured the basal stem diameter and total heights and we counted

200   the number of seed cones. We used the term 'pines' to refer to all sizes together. Although individual

201   pines could influence the regeneration substrate throughout their growing process (Vitali et al.,

202   2017), we estimated the ground cover share (% of each class) within circular plots of 1 m diameter

203   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,

260   30 seeds per species were released from a height of 10 m under moderate wind conditions (0.5-3.0

261   m s^{-1}) on an open field near the Pyrenean Institute of Ecology, Zaragoza, Spain (41.771º N, 0.716°

262   W). The height for seed dispersal was established considering the mean tree height of nearby forest

263   stands measured at all the study sites. During the release experiment, wind blew from north to north-

264   west, while mean air temperature and relative humidity ranged from 6 to 15 °C and 65% to 85%,

265   respectively, but did not change during each experiment. We recorded the distance travelled by each

266   released seed and obtained a frequency distribution of dispersal distances for each species. Seed

267   weight was obtained for each released seed and its mean seed area was estimated by scanning all

268   seeds and by using an image-analysis system (NIH IMAGE ver. 1.63).

269

270   **3. Results**

271

272   *3.1. Size and age of trees and treeline-ecotone structure*

273

274   The forest line elevation at the nine sites ranged between 1935 m a.s.l. of *P. uncinata* (LSB,

275   Spain) and 2050 m a.s.l. of *P. peuce* (SM2, Montenegro). The highest elevation of individual trees

276   ranged between 2078 m a.s.l. for *P. uncinata* at LSB and 2222 m a.s.l for *P. heldreichii* at SM3 (Table

277   1). Pine recruitment at the different treeline ecotones featured scattered patterns, with very

278   heterogeneous tree density values ranging from 87 (*P. heldreichii*) to 1552 (*P. peuce*) trees ha^{-1}

279   (Table 2). On average, the seedlings, saplings and trees share was 57%, 30% and 12% respectively.

280   *P. peuce*, *P. sylvestris* and *P. uncinata* were mainly seedlings (55-71%), whereas *P. heldreichii*

281   mainly saplings (49%) (Table 2). The trees mean size was small, with basal diameters ranging from

282   2 cm (*P. peuce*) to 7 cm (*P. heldreichii*). The mean height varied between 54 cm (*P. peuce*) and 106

283   cm (*P. heldreichii*) and the mean age from 9 (*P. peuce*) to 20 years (*P. heldreichii)* (Table 2).

284

285   **Table 2.** Main structural variables of the sampled encroaching individuals at the nine study sites. Values are

286   means ± standard deviation (SD). We classified pine specimens as seedlings (height < 0.5 m), saplings (0.5

287   ≤ 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

288

289   We used 5-cm diameter classes and named them with the central interval value. The mode of

290 the diameter frequency distribution was on the first classes for all species, but especially for *P. peuce*

291 with more than 1500 stems ha^{-1} in the class with diameter ≤ 5 cm (Fig. 2a). Tree height and age

292 distributions showed similar patterns, with higher frequency of small and young individuals (Fig. S2b

293 and S2c). *P. uncinata* had the maximum diameter (35 cm), *P. heldreichii* had the maximum age (85

294 years), while *P. peuce* the maximum height (7.2 m). The tree height-basal diameter linear

295 regressions showed high values of adjusted R^2, ranging from 0.70 (*P. peuce*) to 0.91 (*P. uncinata*)

296 (Supporting Information, Fig. S1). Lower R^2 values occurred when relating tree age with diameter

297 and tree height as predictors (Supporting Information, Fig. S2). In general, none of the tree structural

298 variables (diameter, height and age) decreased with transect length (Supporting Information, Fig.

299 S3, S4 and S5) that being constant at each plot was was used as a proxy of relative elevation.

300 Positive significant correlations between transect relative elevation and pine structural variables

301 (diameter and height) were observed only for *P. peuce* at SA1 (r = 0.30, p ≤ 0.01). Negative

302 correlations for diameter-elevation (r = -0.30, p ≤ 0.05) and height-elevation (r = -0.35, p≤ 0.01)

303 occurred only for *P. uncinata* at MGD. Age and elevation were never significantly correlated.

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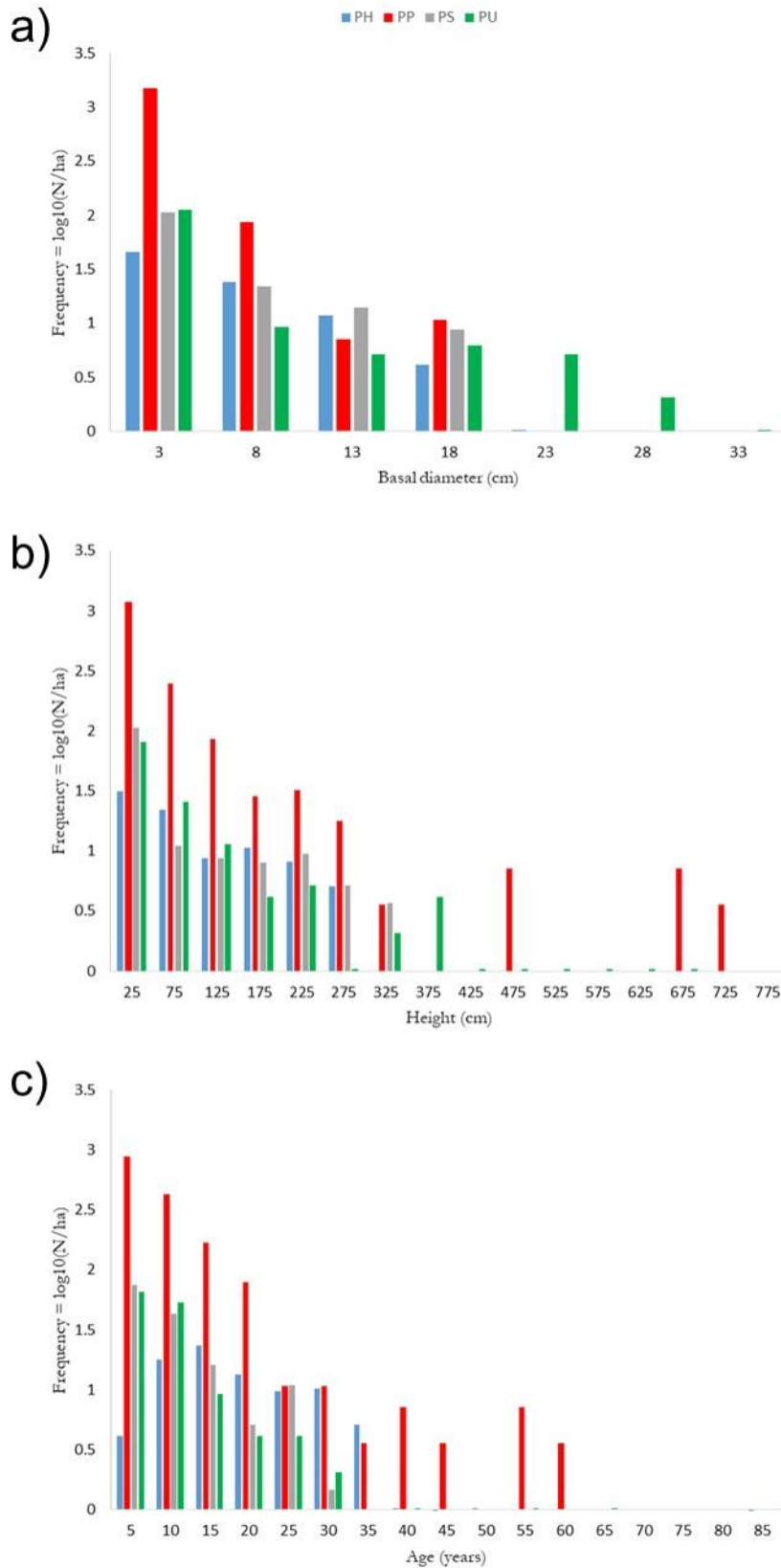
Fig. 2. Log-transformed frequency distribution (No. ha^{-1}) of basal diameter (a), height (b) and estimated age (c) of all the treeline-sampled pines: *P. heldreichii* (PH, blue bars), *P. peuce* (PP, red bars), *P. sylvestris* (PS, grey bars) and *P. uncinata* (PU, green bars). The x-axis values are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

308

309   *3.2. Spatio-temporal analyses*

310

311   At all treeline transects, seedlings, saplings and trees were in general randomly distributed

312   (Fig. 3 - Present plots) and without spatial segregation patterns. In some cases, we found the

313   occurrence of higher density spots (e.g. SM1, UR1, UR2, and LSB sites). The PPAs for all pines

314   showed a significant tendency (GoF: $p \leq 0.05$) towards a clustered distribution only for *P. peuce* at

315   the scale of 1 m at SA1 and at scales from 1 to 4 m at SM1 (Supporting Information, Table S2). The

316   past plots, 15 years before present, revealed the absence of pine trees ($\geq$ 2 m of height) at all sites

317   except SM1 and MGD (Fig. 3 - Past plots). Here we could estimate an upward increase of 74 and

318   23 m respectively of the "tree species line", the uppermost elevation of individual trees (*sensu*

319   Körner, 1998). On the other hand, the infilling process occurred synchronously at all transects, but

320   less on *P. heldreichii* sites (POL and SM3).

321
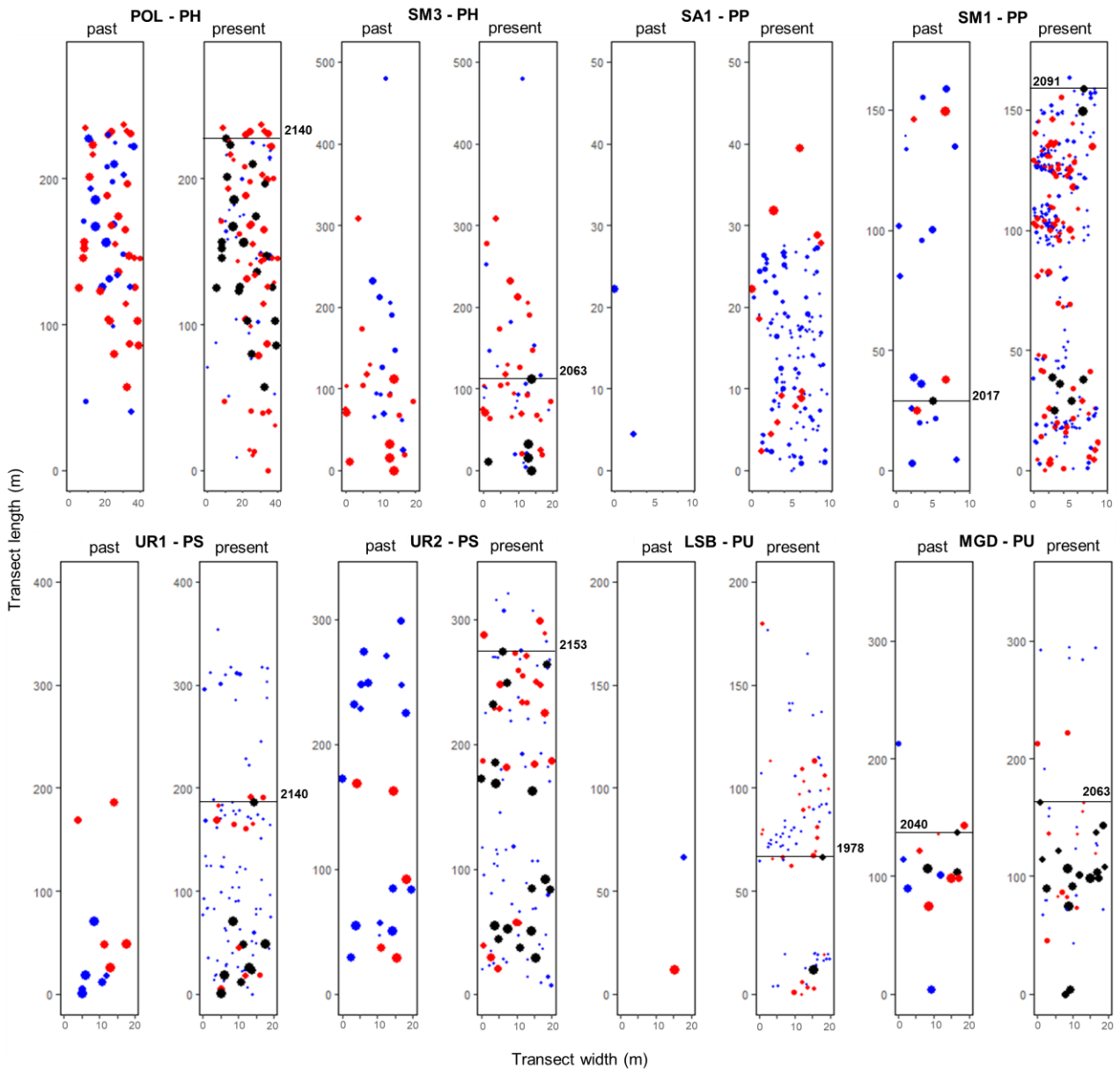
Fig. 3. Mapped point distribution of all pine individuals at the eight study sites (see Tables 1 and 2 for site characteristics) 15 years before the sampling (Past, plots to the left) and at sampling date (Present, plots to the right). The pine heights were reconstructed using species-specific linear 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).
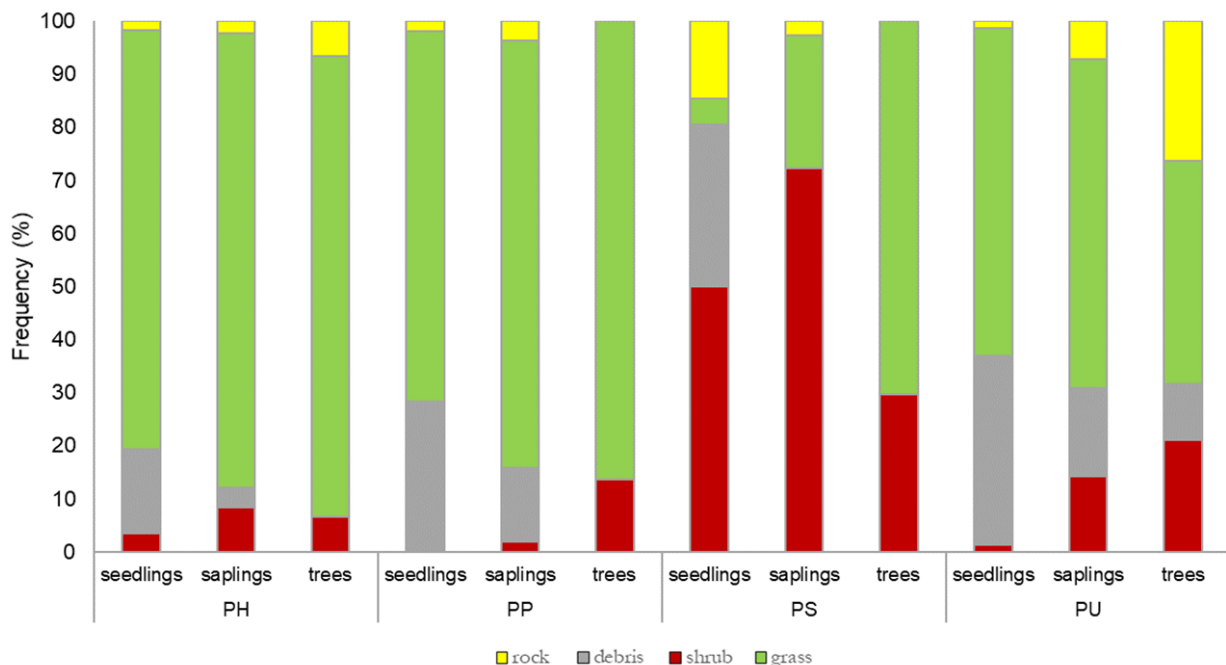
Fig. 4. Frequency distribution of pine seedlings, saplings and trees according to species and ground cover class (rock, debris, shrub and grass).

3.4. Tree growth assessment

352

353   Radial growth expressed as mean BAI values was similar for all species, except *P. peuce*

354   (Supporting Information, Fig. S6), featuring an initially increasing trend, then a slightly decreasing or

355   a stabilizing one in the last few years. *P. sylvestris* featured much flatter growth curves, raising only

356   after 2005. *P. uncinata* and *P. peuce* reached the highest mean BAI values, 4.6 and 4.4 cm^2 $year^{-1}$

357   respectively, whereas *P. heldreichii*, due to the higher mean age, showed the lowest rate (1.8 cm^2

358    $year^{-1}$). The mean longitudinal growth rate estimated from specimen's height and age ranged from

359   7.1 cm (*P. heldreichii*) to 15.3 cm $year^{-1}$ (*P. uncinata*) (Table 3).

360

361   *3.5. Cone production and seed dispersal simulation*

362

363   Pine specimens bearing seed cones ranged from 2% in *P. peuce* to 15% in *P. uncinata* (Table

364   2). All GLMs were significant at $p<0.001$ (except for *P. heldreichii* in the GLM of cones-age, where

365    $p<0.1$). The GLMs for cone production (Supporting Information, Table S3 and Fig. S7) showed higher

366   correlations (McFadden's pseudo-R^2 values) with height ($R^2 = 0.27-0.59$) and basal diameter ($R^2 =$

367    $0.19-0.62$) than age ($R^2 = 0.04-0.58$). All species showed similar size (ca. 200-300 cm of tree height

368   and ca. 10-20 cm of basal diameter) and different age characteristics when they reached a 50%

369   probability of producing cones (Table 3 and Fig. S7).

370   *P. heldreichii* and *P. peuce* exhibited the largest seed surface areas, 1.52 ± 0.07 cm^2 and 1.32

371   ± 0.10 cm^2 respectively, whereas *P. uncinata* and *P. sylvestris* produced the lightest seeds: 12.5 ±

372   1.9 mg and 15.5 ± 0.3 mg of mean fresh weight (Table S4). The seed-release experiment revealed

373   a heterogeneous mean horizontal dispersal with two species showing longer dispersal distances (*P.*

374   *heldreichii*, 10.9 m; *P. peuce*, 6.7 m) than the others (*P. sylvestris*, 4.2 m; *P. uncinata*, 3.7 m)

375   (Supporting Information, Fig. S8).

376

377   **Table 3.** Pines height with 50% probability of cones production (resulted from GLMs), mean longitudinal growth

378   rates and radial (tree ring width, BAI) growth rates of species sampled: PH, *P. heldreichii*; PP; *P. peuce*; PS,

379   *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

Mountain treelines in the Mediterranean basin were shaped by millennial human activities featuring heterogeneous ecotones composed by different conifer tree species. A suitable comprehension of the ongoing spatio-temporal vegetation dynamics is a challenging but necessary task to suggest plausible predictions of their post-abandonment dynamics and trajectories. A tree recruitment process is occurring at high elevation on most European mountains after a recent decline of pastoral use causing evident land-cover changes (Holtmeier and Broll, 2018). We searched for evidence of treeline advancement that requires seedlings survival above the current treeline elevation (Korner 1998). The results of our study conducted in different human-disturbed treelines of Southern Europe exhibited a widespread pine encroachment on treeless areas above the current forest line. Here we compared the colonization trends of four native pine species at their respective treeline ecotones. At most sites we detected similar temporal patterns of tree encroachment especially during the last 15 years from sampling dates and species-specific responses of their growth, spatial distribution and seed dispersal.

The size-age structure distributions highlighted that most of the encroaching pines, regardless of the species, are small and young individuals: the mean basal diameter ranged between 2 and 7 cm, the mean height between 0.54 and 1.06 m and the mean age 9-20 years. Very few individuals were older than 30 years or taller than 2 m, suggesting a tree establishment in recent decades, as reported at Pyrenees treelines (Batllori & Gutiérrez, 2008). In several study regions, young trees were taller in the lower and middle part of the ecotones, revealing an

402 increasing population density (infilling) rather than a real treeline advancement (Camarero &

403 Gutiérrez, 2004). In our sites recent encroachment occurred up to the mountain ridge and several

404 pines reached the 2 m height threshold during the last 15 years, indicating an upward

405 establishment of trees and maybe a potential treeline upshift. This complex process could require

406 several decades or even centuries to be confirmed (Holtmeier & Broll, 2005).

407   The recolonization was spatially heterogeneous, featuring very variable tree density values

408 (from 87 to 1552 pines ha^{-1}) and in general unclear spatial patterns. Only at two *P. peuce* sites we

409 found a clustered distribution of seedlings at scales from 1 to 4 m. High elevation, exposure to wind

410 disturbance and snow accumulation are usually considered unfavorable environmental conditions

411 for regeneration. Therefore, the increasing mean BAI (1.8 to 4.6 cm^2 year^{-1}) and the mean height

412 growth (7.1 to 15.3 cm year^{-1}), even with some interspecific differences, were not expected. In a

413 similar study at high elevation on central Apennines (Italy), the growth rates of *Pinus nigra* Arn.

414 (BAI = 5–10 cm^2 year^{-1}) suggested that trees of anthropogenic treelines after pastoral

415 abandonment can respond positively to climate warming (Vitali et al., 2017).

416   All species shared common minimum reproductive thresholds: a 50% probability of

417 producing cones was attained when specimens reached 2-3 m of height and 10-20 cm of basal

418 diameter. Some interspecific differences occurred on minimum age threshold. Moreover, tree size

419 were better predictors than age for cone production (Krannitz & Duralia, 2004; Ayari & Khouja,

420 2014; Davi et al., 2016).

421   *P. peuce* in Albania and Montenegro had the lowest mean size and age, despite the

422 presence of very few individuals with higher values. Seed dispersal came from closed forest at

423 lower elevation and encroached trees have so far the lowest percentage of seed cones. The

424 presence of trees reaching the minimum size (but not age) thresholds for cone production models

425 indicated that these populations could count on new reproductive individuals. This colonization

426 process was not affected by grass cover competition proving the shade-tolerance of *P. peuce*

427 (Farjon, 2017).

428   *P. heldreichii* had similar characteristics but displayed different encroaching processes both

429 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.

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