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(Article begins on next page)

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

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4 Alessandro Vitali^{1*}, Matteo Garbarino², J. Julio Camarero³, Francesco Malandra¹, Elvin Toromani⁴,
5 Velibor Spalevic⁵, Milić Čurović⁶, Carlo Urbinati¹

6

7 ¹Department of Agricultural, Food and Environmental Sciences, Marche Polytechnic University,
8 Ancona, Italy

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

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

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

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

13 ⁶University 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)

23 Abstract

24

25 Worldwide treelines seem to share a twofold condition: over 50% of them are advancing and 50%
26 appear to be static. In this study we compared the encroachment patterns of four pine species across
27 anthropogenic treelines in Southern Europe. Using a synchronic approach, we studied structure and
28 recent spatio-temporal patterns of pine recruitment at upper treeline ecotones in Albania, Italy,
29 Montenegro and Spain. Within altitudinal transects we mapped and sampled 964 living individuals
30 of *Pinus heldreichii*, *Pinus peuce*, *Pinus sylvestris* and *Pinus uncinata* growing above the current
31 forest line. We measured their basal diameter, total height, and counted the number of seed cones.
32 We differentiated seedlings (height < 0.5 m) from saplings (0.5 m ≤ height < 2 m) and trees (height
33 ≥ 2 m). From individuals with basal stem diameter >4 cm we extracted one increment core for cambial
34 age determination and tree-ring width measurements. On smaller specimens, we estimated the age
35 by counting annual internodes (terminal bud scars) along the whole stem. We compared the ground
36 cover around each pine, applied point pattern analyses, modelled the probability of seed cone
37 production and estimated the average distance of seed dispersal. The four pine species exhibited
38 heterogeneous density values (87-1552 N° ha⁻¹). The overall averaged means ranged 2-7 cm for
39 basal diameter, 54-106 cm for total height and 9-20 years for cambial age, suggesting a recent
40 encroachment process. None of these structural variables decreased with increasing relative altitude
41 and distribution patterns exhibited a few higher density spots but not cohort spatial structure. Ground
42 cover differed between species and more significantly between size classes. Grass was the most
43 frequent type at all sites except for *P. sylvestris* where shrubs prevailed (> 50%). Further differences
44 appeared when discriminated by height thresholds, with larger share of saplings and trees
45 neighboring shrubs and rocks. Basal area increments increased from 1990 and stabilized in recent
46 years at all species except for *P. peuce*. Height and basal diameter predicted cones production better
47 than cambial age. *P. heldreichii* and *P. peuce* dispersed seeds at longer distances than *P. uncinata*
48 and *P. sylvestris*, suggesting different potential for further encroaching. Pine recruitment above the
49 forest lines is quite synchronic at all sites (last 30 years), but in some cases it appeared as a high
50 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

81 al., 2004) and seedlings competition with ground vegetation (Dullinger et al., 2009; Holtmeier and
82 Broll, 2007; Tasser et al., 2007). Seedlings' establishment above the Central Mountain Range
83 (Taiwan) treeline is predicted to be spatially heterogeneous due to topography (Greenwood et al.
84 2015). Batllori et al. (2009) suggested that scarce availability of safe sites control seedlings'
85 recruitment patterns at Pyrenees (Spain) treeline ecotones. However, both spatial and temporal
86 patterns of conifer seedlings' survival suggested that high sunlight exposure may exacerbate low-
87 temperature and water stress, inhibiting their establishment at Snowy Range (USA) treeline
88 (Germino et al., 2002). Finally, short distances between seed sources can have a significant effect
89 on early demographic performance in conifer population at Niwot Ridge (USA) (Castanha et al.,
90 2013).

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

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

102 At different sites in the central Apennines (Italy), we found similar spatio-temporal
103 recolonization patterns of black pine above the current depressed forest line (Piermattei et al.,
104 2016; Vitali et al., 2017). The encroaching pine cohorts generated from high altitude forests planted
105 to control slope erosion. Given the different rates of pastoral abandonment at each study sites and
106 the synchronic pine encroachment process, we considered climate warming as a possible
107 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

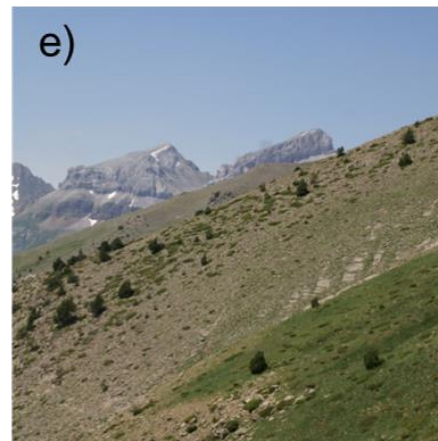
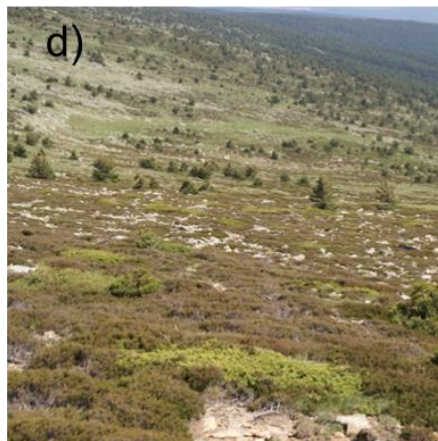
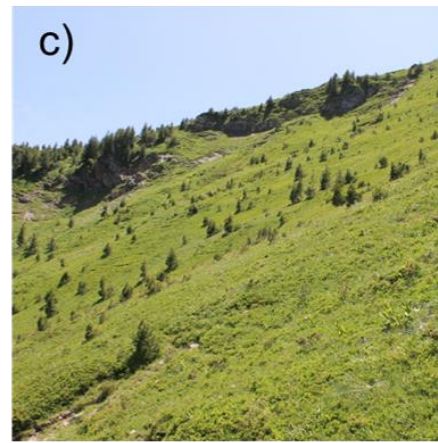
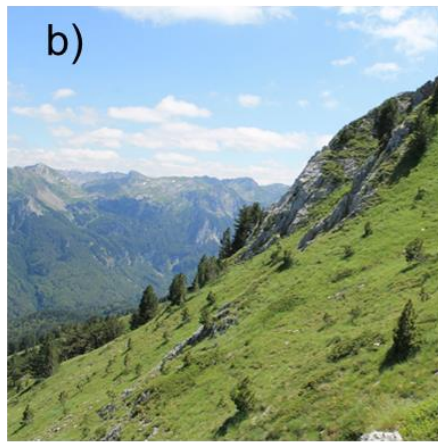
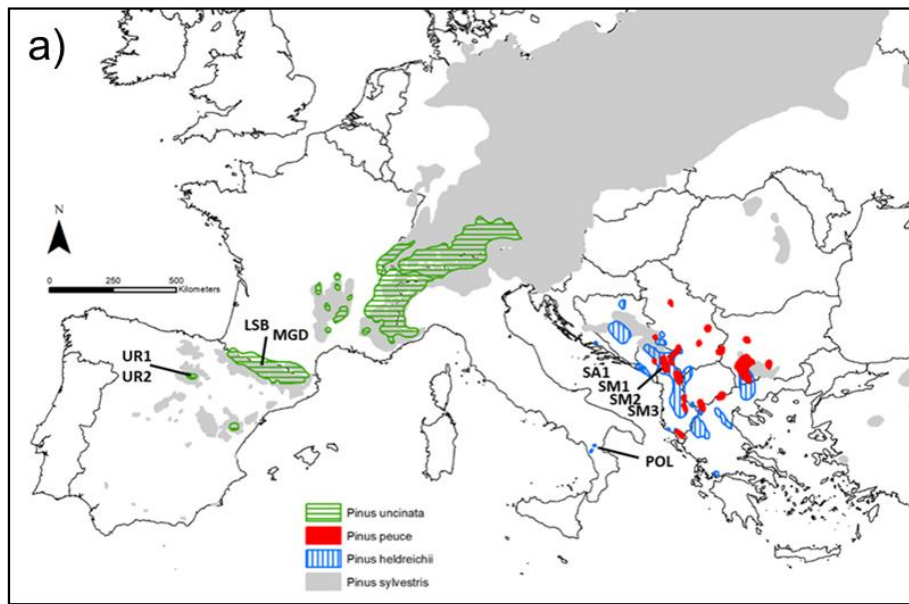
129 **2.1. Study sites**

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

136 useful to select the appropriate sites with evidence of recent abandonment. One site is in the
137 southern Apennines (Italy), four in the Dinaric Alps (at the Albanian and Montenegro border), and
138 four in northern Spain (two in the Pyrenees and two in the Iberian System). The Italian site is on Mt.
139 Pollino (POL) in the southern Apennines, where Bosnian pine (*Pinus heldreichii*) is at its westernmost
140 range limits and widespread naturally above the forest line formed mainly by European beech (*Fagus*
141 *sylvatica* L.). The Balkan sites were selected for the native and widespread presence of *Pinus*
142 *heldreichii* (Fig. 1b) and *Pinus peuce* (Fig. 1c), respectively at Mt. Komovi (Montenegro) and M.
143 Prokletije (Albania). The Spanish sites correspond to the western part of *Pinus sylvestris* distribution
144 range (Picos de Urbi3n, Iberian System) (Fig. 1d) and the Pyrenean core area of *Pinus uncinata*
145 (Pico de la Magdalena) (Fig. 1e). Sampling sites were selected after an accurate literature analysis,
146 aerial photographs assessment and field visits with local experts. Selected sites fulfilled three
147 requirements: i) a forest line (closed canopy forest with cover > 50%) located at ≥ 1500 m above sea
148 level (m a.s.l.); ii) the mountain peaks elevation located higher than 2000 m a.s.l., and iii) the absence
149 of geomorphic constraints to a potential upward tree encroachment. Field data collection occurred
150 in the summers of 2015 (Italy), 2016 (Balkans) and 2017 (Spain) within altitudinal rectangular
151 transects of variable size, extending along the slope from the mountain ridge downward to the closed
152 forest. Tree encroachment involved only one pine species at each transect. The surface areas of
153 transects ranged from 0.05 to 1 ha according to local conditions and accessibility (Table 1).

154



155

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

162

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

Site	Species	Latitude (N)	Longitud e (-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	<i>Pinus heldreichii</i>	39.897	16.206	Italy	2045	2142	NW	38	40 x 240	0.96
SM3	<i>Pinus heldreichii</i>	42.690	19.675	Montenegro	1960	2222	SE	45	20 x 500	1.00
SA1	<i>Pinus peuce</i>	42.505	20.006	Albania	1990	2093	NE	30	10 x 50	0.05
SM1	<i>Pinus peuce</i>	42.508	19.908	Montenegro	2000	2095	NE	43	10 x 170	0.17
SM2	<i>Pinus peuce</i>	42.649	19.849	Montenegro	2050	2092	N	10	10 x 70	0.07
UR1	<i>Pinus sylvestris</i>	42.002	-2.873	Spain	2000	2165	SW	36	20 x 360	0.72
UR2	<i>Pinus sylvestris</i>	42.001	-2.871	Spain	2000	2148	SW	36	20 x 325	0.65
LSB	<i>Pinus uncinata</i>	42.718	-0.570	Spain	1935	2078	W	34	20 x 185	0.37
MGD	<i>Pinus uncinata</i>	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 regenerate 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 ($0.5 \leq \text{height} < 2$ m) and trees (height \geq
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 dividing 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).

269

3. Results

271

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

273

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).

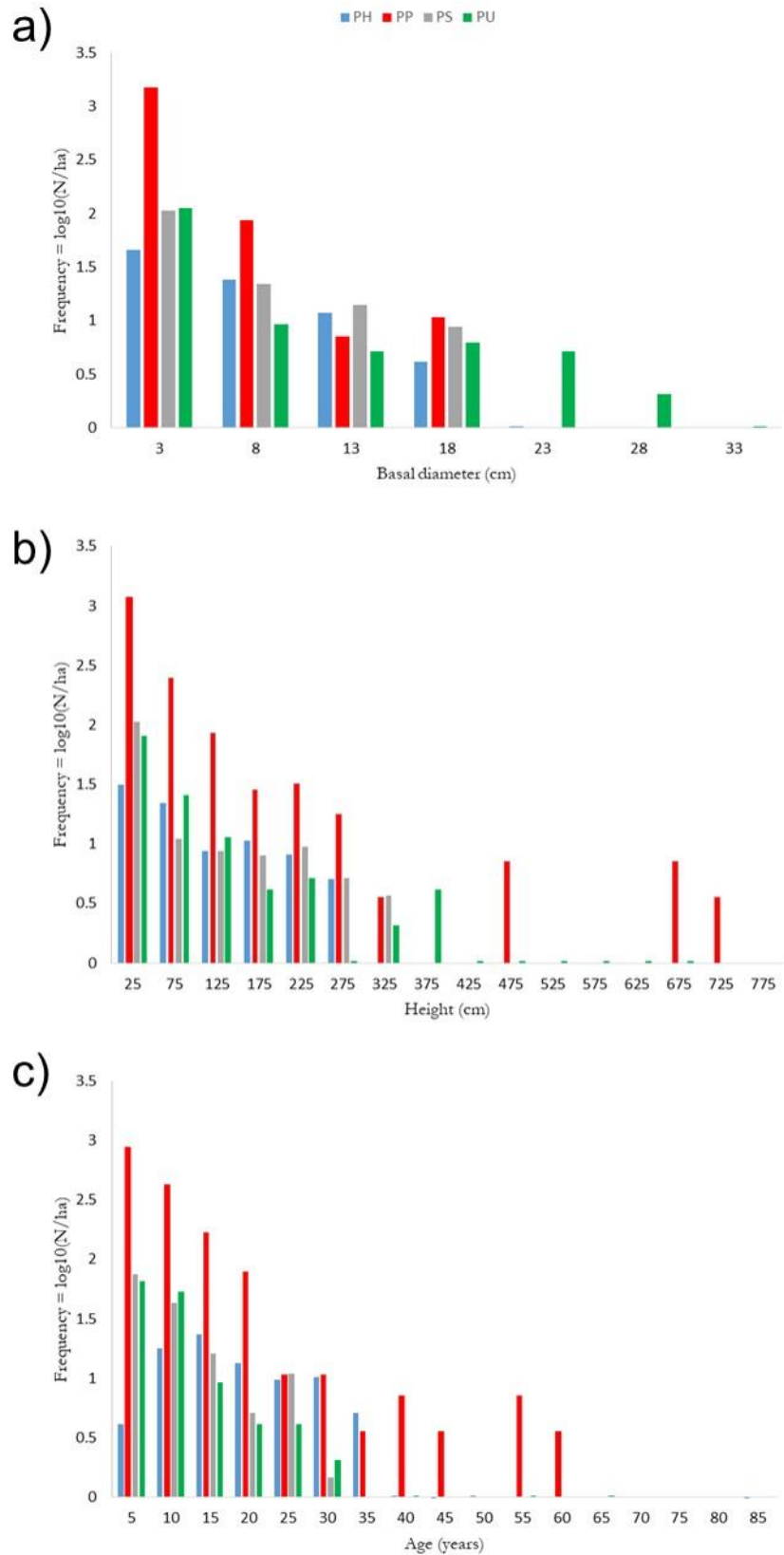
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Table 2. Main structural variables of the sampled encroaching individuals at the nine study sites. Values are means ± standard deviation (SD). We classified pine specimens as seedlings (height < 0.5 m), saplings (0.5 ≤ height < 2 m) and trees (height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

Pine species	No. transects	No. sampled individuals	Density (N° ha ⁻¹)	No. sampled cores	Indivi duals with cones (%)	No. sampled seedlings/ saplings/ trees	Mean basal diameter ± SD (cm)	Mean height ± SD (cm)	Mean age ± SD (years)
<i>P. heldreichii</i>	2	170	87	73	6	57/83/30	7 ± 5	106 ± 81	20 ± 10
<i>P. peuce</i>	3	450	1552	29	2	321/107/22	2 ± 2	54 ± 80	9 ± 7
<i>P. sylvestris</i>	2	207	151	52	7	144/36/27	4 ± 5	67 ± 86	10 ± 6
<i>P. uncinata</i>	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 R², ranging from 0.70 (*P. peuce*) to 0.91 (*P. uncinata*)
296 (Supporting Information, Fig. S1). Lower R² 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 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 ($r = 0.30$, $p \leq 0.01$). Negative
302 correlations for diameter-elevation ($r = -0.30$, $p \leq 0.05$) and height-elevation ($r = -0.35$, $p \leq 0.01$)
303 occurred only for *P. uncinata* at MGD. Age and elevation were never significantly correlated.



304

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

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309 3.2. Spatio-temporal analyses

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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 (≥ 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

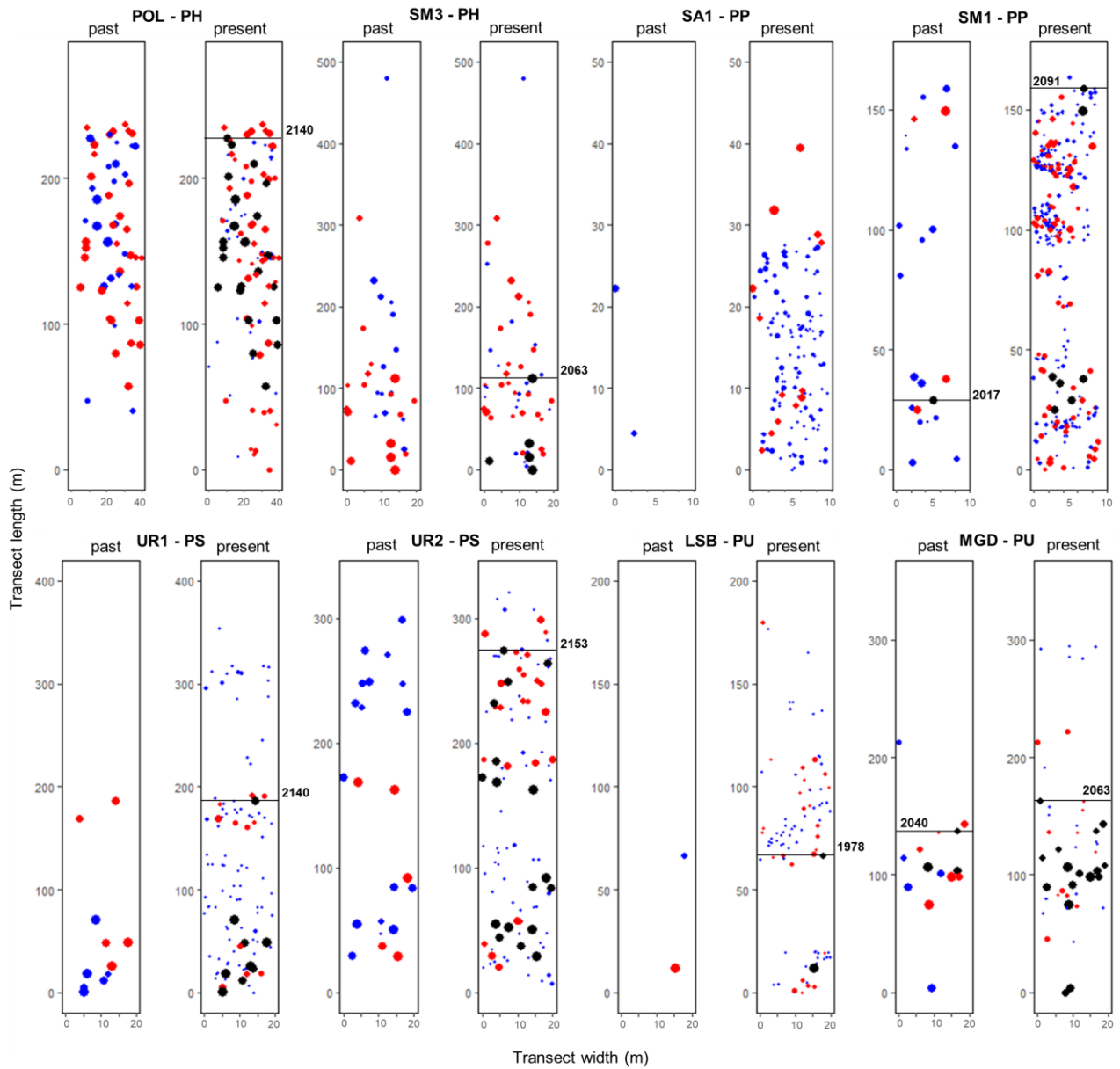
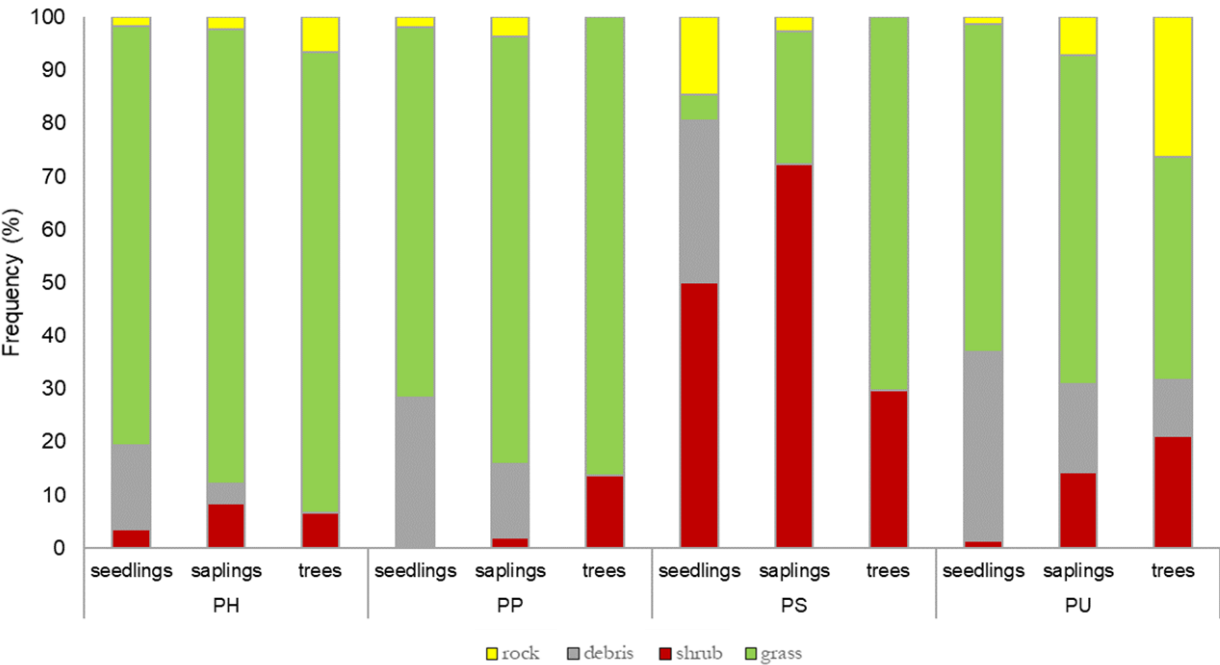


Fig. 3. Mapped point distribution of all pine individuals at the eight study sites (see Tables 1 and 2 for site characteristics) 15 years before the sampling (Past, plots to the left) and at sampling date (Present, plots to the right). The pine heights were reconstructed using species-specific linear regressions (see text). Blue dots are seedlings (height < 0.5 m), red dots saplings ($0.5 \leq \text{height} < 2$ 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

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Ground cover differed significantly 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: $\chi^2 = 12.92\text{--}91.32$, $p < 0.05$). *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).



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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

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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 cm² year⁻¹
357 respectively, whereas *P. heldreichii*, due to the higher mean age, showed the lowest rate (1.8 cm²
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).

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361 3.5. Cone production and seed dispersal simulation

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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-R² values) with height (R² = 0.27–0.59) and basal diameter (R² =
367 0.19–0.62) than age (R² = 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 cm² and 1.32
371 ± 0.10 cm² 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 \pm SD (cm year ⁻¹)	Mean tree ring width \pm SD (mm year ⁻¹)	Mean BAI \pm SD (cm ² year ⁻¹)
PH	POL-SM3	300	7.1 \pm 3.8	1.5 \pm 0.7	1.8 \pm 1.7
PP	SA1-SM1-SM2	300	9.0 \pm 6.9	1.9 \pm 1.2	4.4 \pm 5.6
PS	UR1-UR2	250	11.4 \pm 5.6	2.3 \pm 1.0	2.6 \pm 2.0
PU	LSB-MGD	200	15.3 \pm 7.6	2.5 \pm 1.4	4.6 \pm 5.7

4. Discussion

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 cm² 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 cm² 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

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

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

449 Few studies surveyed natural recruitment patterns of several tree species along elevation
450 ranges including the treeline ecotones. Some aimed to disentangle the different factors affecting
451 occurrence, abundance and growth of recruits (Didier, 2001; Benavides et al., 2016). Others
452 focused more on the influence of climate on these processes (Rabasa et al., 2013; Trant and
453 Hermanutz, 2014). Seed dispersal from encroached trees appeared a crucial aspect for future
454 treeline dynamics considering the relevant importance of seed source availability (Castanha et al.,
455 2013) and differences among species characteristics. The seed-release experiment proved that
456 dispersal characteristics of the four species could play a key role in colonization processes. Seed
457 dispersal features should be also connected to other reproduction traits because the fecundity of

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

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

471

472 **5. Conclusions**

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

486 increasing number of these recent tree cohorts within the treeline ecotones can also induce
487 changes in major biogeochemical cycles, soil properties, and mountain eco-hydrological processes
488 (Rundel et al., 2014), leading to a significant long-term plant diversity decline in species-rich
489 grasslands (Dullinger et al., 2009). Forest densification could improve slope protection against
490 landslides and snow avalanches but also produce more fuel, and together with climate warming,
491 increase the risk of mountain wildfires (Holtmeier & Broll, 2005).

492 Accurate predictions about these new subalpine forests will require better estimation of
493 demographic and dispersal parameters in similar low-density expanding tree populations (Debain
494 et al., 2007). The establishment of permanent transects or plots with the availability of precise
495 geographic positions and structural data of all detected trees, provide a monitoring of pine survival,
496 a general assessment of spatio-temporal regeneration dynamics and the forecast of future treeline
497 pine expansion.

498

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500

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