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Vegetation dynamics and regeneration of *Pinus pinea* forests in Mount Lebanon: Towards the progressive disappearance of pine

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1 **Title:**

2 “Vegetation dynamics and regeneration of *Pinus pinea* forests in Mount Lebanon: towards
3 the progressive disappearance of pine”
4
5

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16

17 **Keywords:** Vegetation dynamics, pine regeneration, floristic composition, Mount Lebanon,
18 dendrometric characteristics.
19

20 **Highlights**

- 21 - Stone pine has great economic and ecological importance in Lebanon
- 22 - We proposed a classification of pine forests in five ecological groups
- 23 - Pine regeneration is almost absent in the understory while oak species prevail
- 24 - In the absence of management, oaks will progressively replace pine forests

25 **Abstract**

26 *Pinus pinea* is a species of great economic and ecological importance in Lebanon, but
27 there is a lack of knowledge about the distribution of the pine forests, their vegetation
28 dynamics and regeneration. Our study aims to produce the first classification of the pine
29 stands according to their floristic composition and the abiotic factors of the Mount
30 Lebanon region and to analyse natural pine recruitment. Floristic composition,
31 environmental and soil factors as well as stand dendrometric characteristics and woody
32 seedling regeneration were recorded on fifty plots distributed in the main stone pine
33 stands of the study area. Using canonical correspondence and clustering analyses, we
34 classified pine stands into five groups which were mainly influenced by physiographic
35 factors (altitude, slope, temperature, rainfall), nature of the bedrock, and evidence of
36 human interventions. Most, stone pine stands in Mount Lebanon were dense (849
37 stems.ha⁻¹), old (81 years) with a high basal area (49 m².ha⁻¹). Pine regeneration was
38 particularly scant, and the understory was dominated by the oak species: *Q. calliprinos*,
39 mainly and *Q. infectoria*, secondarily. Based on these results, we concluded that the
40 presence of stone pine and its persistence are linked to human actions. In the absence of
41 human intervention, the stone pine stands will progressively disappear and be replaced
42 by oak formations. Thus, an urgent management plan is required to favour pine
43 regeneration to allow for the renewal of the pine stands in the Mount-Lebanon region.

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50 **1-Introduction**

51 Ecosystem dynamics are formed by biological resources, specifically natural vegetation where
52 floristic and faunistic life are present (Balcha, 2008). Plant communities' composition, species
53 persistence and plant richness are largely controlled by environmental factors, spatial
54 heterogeneity and perturbations (Keddy, 1992; Ricklefs and Schulter, 1993; Bennett *et al.*,
55 2006; Dufour *et al.*, 2006).

56 In forest systems, vegetation composition is also the result of complex and mutual relationships
57 between the overstory and the understory although the influence of the overstory is determinant
58 as it controls the availability of resources on the forest floor (Scheller and Mladenoff, 2002;
59 Burrascano *et al.*, 2011; Burton *et al.* 2011; Cutini *et al.* 2015). Therefore, the understory
60 composition can be considered as an indicator of overstory dynamics. It varies with the structure
61 and composition of the dominant canopy that controls light availability (Bartemucci *et al.*,
62 2006; Yu et Sun, 2013), water (Ewers *et al.*, 2002; Barbier *et al.*, 2009), soil nutrients (Augusto
63 *et al.*, 2002; Prescott, 2002), and litter characteristics with physical and chemical soil proprieties
64 (Augusto *et al.*, 2003 ; Barbier *et al.* , 2008). In fact, the current spatial distribution of a plant
65 species is the result of various environmental, anthropogenic and biotic factors (Lacoste and
66 Salanon, 1978). Vegetation diversity and distribution are highly affected by slope (Maestre *et*
67 *al.*, 2003; Bennie *et al.*, 2008) and altitude (Kira and Shidei, 1967; Mayhead, 1973). In addition,
68 soil characteristics can affect vegetation composition (Debelis *et al.*, 2005; Jafari *et al.*, 2009)
69 which is particularly influenced by soil carbon and nitrogen content (Marcuzzo *et al.*, 2013;
70 Noumi, 2015), soil texture (Monier and Wafaa, 2003), and available nutrients (Wales, 1967;
71 Pregitzer *et al.*, 1983). In addition to physiographic factors, Mediterranean vegetation in
72 particular is the product of a long history of anthropogenic disturbances, such as fire, grazing
73 or wood exploitation, which have deeply modified major site factors and shaped the vegetation
74 composition (Quézel, 1998; Mekideche *et al.*, 2018).

75 The existence of a plant community is also highly related to its regeneration potential under
76 different environmental conditions, which means that the long-term sustainability of a forest
77 depends on successful regeneration (Malik and Bhatt, 2016). In fact, regeneration and particular
78 habitat conditions determine future species composition and geographical distribution in a
79 forest (Grubb, 1977). In addition, regeneration capacity often determines the resilience of the
80 ecosystem and its capacity for recovery after a disturbance (Pandey and Shukla, 2001). The
81 successful regeneration of a species entails that there is a sufficient number of seedlings,
82 saplings and trees of this species in a given forest (Dutta and Devi, 2013) that may vary spatially
83 according to forest structure and physiographic conditions (Ward *et al.*, 2006). Overstory and
84 the spatial repartition of dominant trees have a direct effect on natural regeneration as well as
85 soil surface conditions (Bailey and Covington, 2002; Sánchez-Meador *et al.*, 2009).

86 *Pinus pinea* L. (stone pine) forests covered about 750 000 ha around the Mediterranean basin
87 (Fady *et al.*, 2004) and are mainly distributed in Spain, Turkey, Portugal, Italy and in lower
88 proportions in Greece, Lebanon and France (Varol and Tel, 2010). This tree was largely planted
89 in these areas for its timber but especially for its production of edible seeds generating important
90 economic benefits for the local population (Calama *et al.*, 2007). Stone pine forests are also of
91 great ecological interest as they are well adapted to water-limited environment and heavy sandy
92 soils, i.e. under conditions that could be limiting for other tree species (Manso *et al.*, 2013).
93 They also play a major role in preventing erosion of sandy coasts in Mediterranean countries
94 (Raddi *et al.*, 2009) and are often used for recreational purposes (Tomao *et al.*, 2018).

95 In Lebanon, the majority of coniferous forests is covered by stone pine with 12740 ha (Roukoz,
96 2005) which is mainly found in western Mount Lebanon, beginning with its coastal zone up to
97 1650 meters (Baltaxe, 1966). In addition, stone pine is one of the most important recommended
98 trees for plantation in the National Reforestation Plan that was created by the Ministry of
99 Environment in Lebanon in 1993 aiming to increase forest cover from 13 to 20% in 30 years

100 (MoE, 2014). In this country, the stone pine was largely planted (FAO, 2010) for its market
101 value, i.e. nuts production (Sfeir, 2011), while its conservation value received a low interest
102 from most of the stakeholders (Sarkissian *et al.*, 2018). The status of the stone pine in Lebanon
103 is controversial: some authors think that the species has been introduced while it is an endemic
104 species for others (Mikesell, 1969; Chouchani *et al.*, 1975; Abi Saleh *et al.*, 1976; Abi Saleh,
105 1978). For the latter, stone pine represents the terminal stage of plant succession, from open
106 formations to forest, and is therefore capable of natural recruitment. In this study, we ask
107 whether pine stands can sustain themselves in the landscapes through natural regeneration or
108 not. To answer this question, we developed a twofold approach.

109 1- In the absence of prior field surveys, we first characterise pine stands in terms of forest
110 structure and floristic composition in relation to the main environmental factors. On this
111 basis, we want to establish a first classification of these stands and we hypothesize that,
112 depending on the vegetation and site-related factors, some stands may present natural
113 pine regeneration.

114 2- We then analyse more specifically pine regeneration and the recruitment of other tree
115 species at the stand level. We hypothesise that some local factors such as the litter depth
116 and neighbouring vegetation may be detrimental to pine seedlings establishment. In
117 contrast, some non-pine tree species may establish preferentially in the understory.

118 This approach constitutes a preliminary step for the sustainable management of these systems
119 in Lebanon (Gaudin, 2015).

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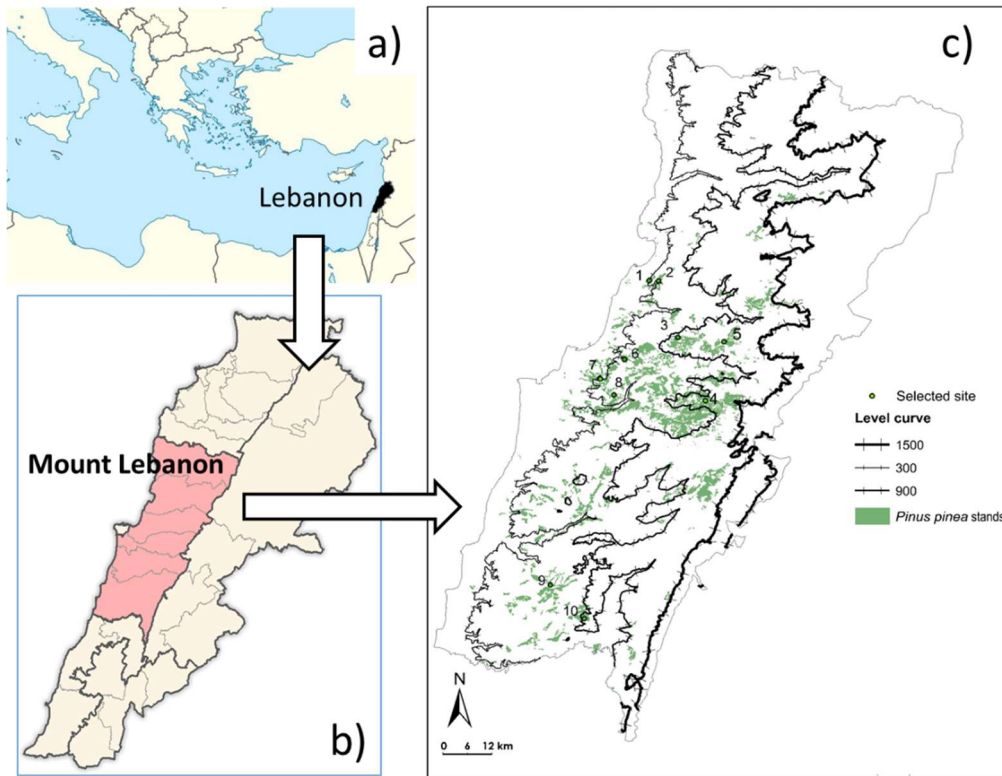
125 **2-Material and Methods**

126 **2.1. Study area: Mount-Lebanon**

127 Mount Lebanon is in the eastern part of the Mediterranean Sea between 33°22' and 34°40' (Fig.
128 1a and b). It is a mountain range of 30 km in width and 170 km in length with a SSW-NNE
129 orientation. It extends from the coast to 3088 m with a mean altitude of 2000 m.

130 This area is characterized by a typical Mediterranean climate. Temperatures vary with altitude
131 starting from an annual average of 20.7°C at coastal zones which decreases by 0.6°C each 100
132 m of altitude. The same pattern is observed for annual precipitation starting with an average of
133 700 to 900 mm at coastal zones that increases with altitude up to 1200 mm at the highest point
134 in Lebanon at 3088 m. Dry season extends over six months from May to October (Sanlavile,
135 1977). Soils are of various types but Red Mediterranean soils, rendzina soils, sandy and mixed
136 soils are the most represented (Geze, 1956).

137 Vegetation is typically Mediterranean and, according to Abi Saleh and Safi (1988), is composed
138 of three components: pines (*Pinus pinea* L.) mainly on sandstone, oak (*Quercus calliprinos*
139 Webb. and *Quercus infectoria* G. Olivier) on limestone, and a coniferous level (*Abies cilicica*
140 (Antoine & Kotschy) Carrière and *Cedrus Libani* A. Rich.) at higher altitude (1200 to 2000 m).
141 Stone pine forests are among the most abundant coniferous forests in Mount Lebanon (Baltaxe,
142 1966) where 80% of pine nut production in Lebanon occurs (Abi Saleh *et al.*, 1996).



143

144 **Fig. 1.** a) The location of Lebanon in the eastern part of the Mediterranean basin. b) The location
 145 of Mount Lebanon in the country. c) The distribution of *Pinus pinea* stands in Mount Lebanon,
 146 the selected sites are indicated (1 to 10).

147

148 2.2. Sampling design

149 Topographic variability such as altitude and slope are considered to be key factors influencing
 150 vegetation cover and development (Coblentz and Riitters, 2004; Coblentz and Keating, 2008;
 151 Zhao *et al.*, 2010) as well as soil characteristics (Peng *et al.*, 2012).

152 In a first step, we used maps of the distribution of stone pine in the massif (Fig. 1c), variation
 153 in slope, altitude and the distribution of soil types. Slope percentage was divided into 5 classes
 154 (0-5; 5-8; 8-30; 30-60; and >60%), altitude into 4 classes (0-300; 300-900; 900-1500; >1500
 155 m) and 28 soil types were recorded.

156 The stone pine map was intersected using ArcGis 9.0 software with slope, altitude and soil
 157 maps in order to obtain a map of the distribution of *Pinus pinea* in Mount Lebanon as a function

158 of all these abiotic factors. We identified 16 major combinations resulting from 2 classes of
 159 altitude, 2 classes of slope and 4 major types of soil (Table 1). Among these combinations, 10
 160 sites in which the cover of stone pine was most abundant were selected (Table 1). In each
 161 selected site, five plots of 15 m x 15 m (pine stands) were sampled in representative ecological
 162 conditions. We also avoided selecting pine stands showing pronounced signs of disturbances
 163 i.e. no grazing, intense logging, or fires. However, since most Lebanon's forests have been
 164 subjected to a some degree of human activity, we systematically found evidence of present or
 165 past human activities. In particular, the presence or absence of terraces, indicating a previous
 166 agricultural use, was recorded as well as evidence of cutting in the overstory and shrub clearing
 167 in the understory.

168

169 **Table 1:** Surface of stone pine stands in km² according to soil, altitude and slope classes.

170 Sampled stands are indicated in grey.

Altitude (m)		300 – 900		900 – 1500	
Slope (%)		8 - 30	30 - 60	8 - 30	30 - 60
Stand surface as a function of soil type (km²)	Sandy soils	15.93	10.93	10.13	6.26
	Mixed soils (discontinuous, especially in mountains) on marl, limestone and siliceous sandstone	7.18	5.88	3.24	3.04
	Discontinuous red soils on compact limestone	9	7.5	1.8	0.36
	Mixed discontinuous soils on marl with white limestone	-	4.17	5.83	3.89

171

172 **2-3 Measurements**

173 2.3.1. Floristic composition.

174 In each plot, all vascular species of the canopy, understory, and herbaceous layer were identified
175 by consulting taxonomic references (Mouterde, 1970; Blamey and Grey-Wilson, 1993). Each
176 species was given a coefficient of abundance-dominance according to the procedure of Braun-
177 Blanquet (1932).

178

179 2.3.2. Environmental factors

180 The altitude, slope and aspect were measured in each plot and the local topography was
181 described according to general observations of the plot (see Table S1 for description of the
182 factors). We also used the climatic data for each site provided by the Lebanese Agricultural
183 Research Institute (LARI) such as annual mean temperature and rainfall by referring to recorded
184 values in the last 10 years at the nearest stations to selected sites (see Table S2 for more details).
185 The nature of the bedrock was noted in the field, the types observed were sandstone (a soft,
186 grey or ochre rock, barely cemented by some limonite), siliceous sandstone (with presence of
187 quartz grains), marl (fossiliferous green marl) and limestone (Dubertret, 1955).

188 To detect the presence of lime in the upper layer, a field test of fine earth reaction to HCl (diluted
189 at 10%) was carried out (presence or absence of reaction) in each plot.

190 Two pits were randomly dug, and two soil samples of 400 g were collected for each pit,
191 corresponding to the first two soil horizons, these were used to measure pH, the ratio C/N and
192 to estimate the soil texture. Soil texture in each plot was estimated by sedimentation tests in
193 addition to the feel method on the collected samples (Jaja, 2016; FAO, 2006). Soil texture was
194 coded by giving a coefficient of 0 (absent), 1 (present) or 2 (dominant) for the proportion of
195 sand, silt and clay (Ripert and Vennetier, 2002). The water content (mm water/cm of soil)
196 associated to each texture was then determined using the soil textural triangle and the data given

197 by Jamagne *et al.* (1977). Lastly, the soil water reserve was computed for each plot by
198 multiplying the water content by soil depth considering the proportion of coarse elements. Soil
199 pH in the first layer was measured according to the French Standard ISO 10390 (ISO, 2005).
200 Ten grams of air-dried soil sieved at 2 mm were put in 50 mL of demineralized water, agitated
201 for 1h and left for 1h. Then, pH was measured using a pH meter calibrated with buffer solutions
202 (pH= 4 and 7) for a total of 50 samples. The C/N ratio was measured by weighting between 30
203 and 40 mg of air-dried sieved soil (n = 50) which had been milled into a fine powder (Retsch
204 brand MM400 oscillating mill vibrator). Then subsamples of 30 to 40 mg were placed in tin
205 capsules for analysis by a CHNS-O elemental analyser which is based on the total combustion
206 of the analytical sample at 950° C under oxygen flow and under pressure.

207

208 2.3.3. Dendrometric and regeneration measurements

209 The circumference at breast height was measured for all living trees (pine and other trees or
210 tree-like species) superior to 1.30 m in height, and pine density, pine basal area and mean girth
211 were computed. In addition, the height of 4-5 dominant pines was measured in each plot and
212 on three dominant pines, 2 cores were extracted from each tree at 1.30 m height in two
213 perpendicular directions using an increment borer. Cores were dried, mounted and finely sanded
214 until the annual rings could be identified. Tree rings were counted using WinDendro software
215 (Regent Instruments Inc.) in order to determine tree age. We could not accurately cross-date
216 the series due to numerous anomalies and reading difficulty (e.g. missing rings, inclusion of
217 resin). Therefore, our measurements could only be considered as an estimate of tree age.
218 However, to have a conservative and cautious approach, we discarded more than 20% of the
219 cores (i.e. only 238 cores on 300 were used).

220 To study the regeneration of the woody species in the understory we used nine 1m×1m subplots
221 per plot distributed along 3 parallel transects. In each subplot, the number of pine and other

222 woody seedlings was counted. Litter thickness was also measured and the herbaceous, shrub
223 and overstory pine covers were estimated.

224

225 **2-4 Data analysis**

226 Two arrays were produced: a floristic array (50 plots × 117 species) and an array of
227 environmental factors (50 plots × 12 factors). These data were analysed using a canonical
228 correspondence analysis (CCA) (R, package ADE4, function `pcaiv`).

229 CCA is a direct gradient analysis in which species composition is directly related to measured
230 environmental variables (Palmer, 1993). It extracts synthetic ecological gradients that
231 maximize the niche separation among species from measured environmental variables (ter
232 Braak and Verdonschot, 1995). CCA is a powerful tool for forest classification and can be
233 complemented with other techniques such as hierarchical clustering (Gégout and Houiller,
234 1996; Javad *et al.*, 2017; Rahman *et al.*; 2017).

235 In this study, hierarchical clustering was performed using Ward's criterion (Ward, 1963) on the
236 selected principal components of the CCA. The number of groups of pine stands was
237 determined by examining the variation of inertia according to the number of clusters.

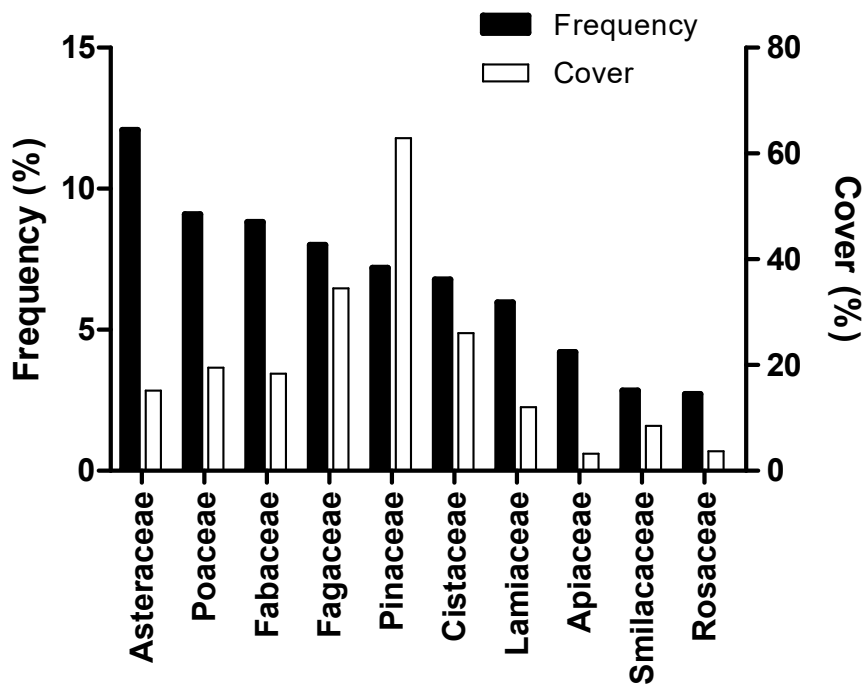
238 Variation in dendrometric characteristics and plant cover of the main tree and shrub species
239 among the different groups were analysed using ANOVA followed by Tukey post-hoc tests
240 after checking for the assumptions of normality and variance homoscedasticity. When
241 necessary, mathematical transformations were applied to meet these conditions.

242 Regeneration of pine in the subplots according to the local vegetation factors was analysed
243 using general linear mixed models with a Poisson distribution (R package `lme4`, function
244 `glmer`). The dependent variable was the number of pine seedlings, the fixed factors were the
245 litter cover and its thickness, the cover in herbs and in shrubs, and the overstory cover. Subplots
246 nested in plots were considered as random factors.

247 **3-Results**

248 **3-1- Floristic composition**

249 We found a total of 117 species belonging to 31 plant families. The three most abundant
250 families, based on plant cover, after *Pinaceae* were *Fagaceae* (35%), *Cistaceae* (26%) and
251 *Poaceae* (19%) while *Asteraceae*, *Poaceae*, *Fabaceae* and *Pinaceae* where the most abundant
252 families based on species occurrence (Fig. 2). The most abundant tree or tree-like species after
253 *Pinus pinea* L. were *Quercus calliprinos* Webb. (28.05% in cover), *Quercus infectoria* G.
254 Olivier (6.45%), *Pistacia palaestina* Boiss. (6.1%). Shrub species were abundant, in particular
255 *Cistus salviifolius* L. (15.3%), *Smilax aspera* L. (8.5%), *Callicotome villosa* (Poir.) Link
256 (6.95%), *Cistus creticus* L. (6.85%), while for herbaceous plants the most abundant species
257 were *Bromus rigidus* Roth. (4.9%), *Hordeum spontaneum* L. (4.5%), *Cyclamen persicum* Mill.
258 (4.2%).



259

260

261 **Fig. 2.** Percentage frequency (based on species occurrence) and percentage cover (based on
262 species cover) of the main plant families.

263 **3-2- Results of the Canonical correspondence analysis and classification**

264 Canonical correspondence analysis (CCA) was used to explore the relationships between the
 265 vegetation composition and the environmental variables. The two first axes of the CCA
 266 explained 27.62 % of the total variance (Fig. 3A). The first axis (Fig. 3B) reveals a positive
 267 correlation with limestone (r = 0.53) and marl bedrocks (r = 0.52), and terraces (Anthro.Terr, r
 268 = 0.44), and a negative correlation with perturbed terraces (Anthro.Terr.Hint, r = -0.475),
 269 calcareous sandstone bedrock (r = -0.59) and absence of limestone in fine earth of the upper
 270 soil layer (HCl.A.No, r = -0.76). This axis therefore depicts edaphic conditions, mainly
 271 controlled by the nature of the bedrock, and anthropogenic disturbances. In contrast, the second
 272 axis is strongly related to altitude (r = -0.96) and to climatic variables: rainfall (r = -0.62) and
 273 temperature (r = 0.84). Less marked correlations were also observed between slope (r = 0.53),
 274 limestone bedrock (r = 0.42), presence of terraces (Anthro.Terr r = -0.57) and soil C/N ratios
 275 (r=0.40).

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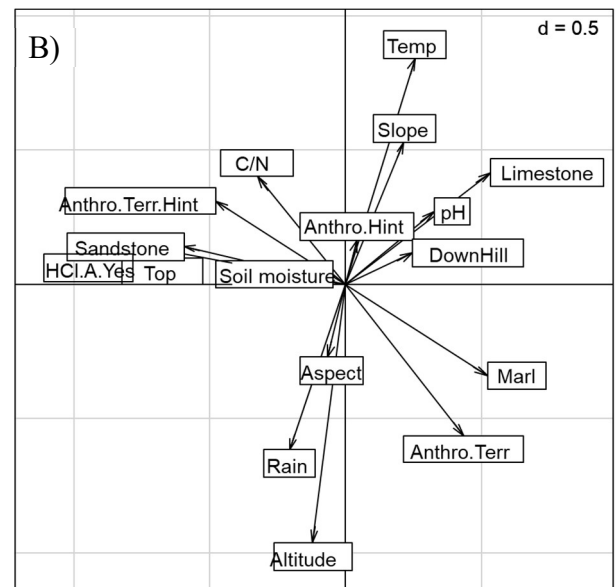
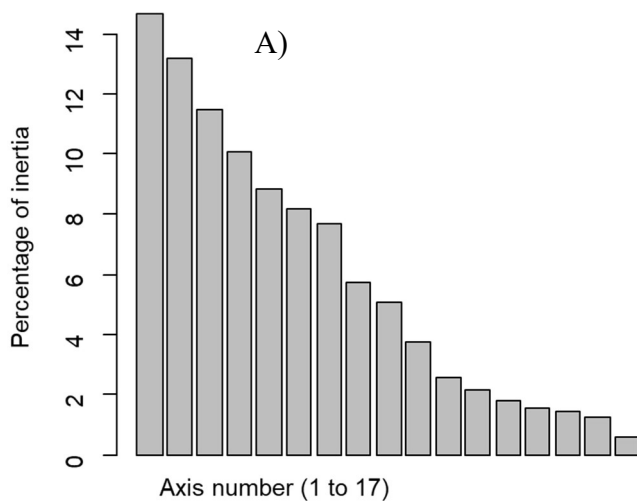
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287 **Fig.3.** Results of the CCA. A) Percentage of inertia for each axis, B) projection of the measured
288 factors, the scale of the graph is given by a grid, the size of which is indicated in the upper right
289 corner (d=0.5). Abbreviations (see also Table S1): Anthro.Terr (presence of terraces);
290 Anthro.Terr.Hint (no terraces but human intervention); HCl.A.Yes (reaction with HCl of the
291 upper soil layer); Limestone, marl, sandstone (bedrock geology); Temp (mean annual site
292 temperature); Rain (mean annual site rainfall); Downhill, Top (general topography); Aspect
293 (plot exposure); Soil moisture (Soil water holding capacity); Altitude (mean site elevation).

294

295 The clustering analysis applied on the CCA results revealed 5 groups (Fig. 4A). The projection
296 on the factorial map of plots classified within these 5 groups as well as major plant species are
297 indicated Fig. 4B.

298 The first group (Group 1) is the largest as it includes 20 plots from 4 sites. Pine stands of this
299 group are found on various types of bedrock and topographic conditions but are located at low
300 altitudes ($416 \text{ m} \pm 37$) and on steep slopes ($22.50\% \pm 1.4$). Topsoil layers are not carbonated,
301 and evidence of other human activities are rare, no terraces are found. This group is
302 characterized by species like *Salvia fruticosa* Mill., *Myrtus communis* Linn., *Cyclamen*
303 *persicum* Mill., *Galium verum* L., *Hypericum thymifolium* Banks et Sol., *Oxalis pes-caprae* L.,
304 and *Smilax aspera* L.

305 The second group (Group 2) includes 10 plots from 2 sites located at a medium altitude (815m
306 $\pm 48\text{m}$) on moderate slopes (12.6 ± 2.3). Carbonate soils developed on marl and limestone and
307 terraces are frequently observed. The main species are *Helichrysum sanguineum* L. (Kostel),
308 *Trifolium purpureum* Loisel., *Lotus corniculatus* L. var. *brachyodon* Boiss., *Alcea digitata*
309 (Boiss.) Alef., *Hordeum bulbosum* L., *Phlomis fruticosa* L., *Convolvulus arvensis* L., *Torilis*
310 *arvensis* (Huds.) Link and *Cirsium vulgare* (Savi) Tenore.

311 The third group (Group 3) includes only 5 plots from the same site located at high altitude (1022
312 m) on a low slope. Soils are not carbonate and developed on a limestone substrate. The presence
313 of clay in the lower soil layer explains its high-water storage capacity (107 mm) compared to
314 the other groups (between 40 and 60 mm). No evidence of past or recent human activities were
315 recorded. The vegetation composition was characterized by the presence of *Lavandula stoechas*
316 L. and *Hordeum spontaneum* L. The Group 4 includes 10 plots from 2 sites located at high
317 altitude (1050-1200 m) on moderate slopes (14.2 ± 1.3). Soils are not carbonate and mostly
318 developed on siliceous sandstone. There was little evidence of past human activities, and
319 terraces were only observed on 3 plots. The main species are *Juniperus oxycedrus* L.,
320 *Asphodelus ramosus* Salzm., *Lolium multiflorum* Gaud., *Anchusa strigosa* Labill., and
321 *Trifolium repens* L. The last group (Group 5) is made up of only 5 plots, located at low altitude
322 (330 m) on low slopes (7.2 %). The bedrock is composed of sandstone and in all plots evidence
323 of past (terraces) and recent human activities were recorded. The main species are *Plantago*
324 *lagopus* L., *Carduus argentatus* L., *Avena sterilis* L., and *Veronica persica* Poir.

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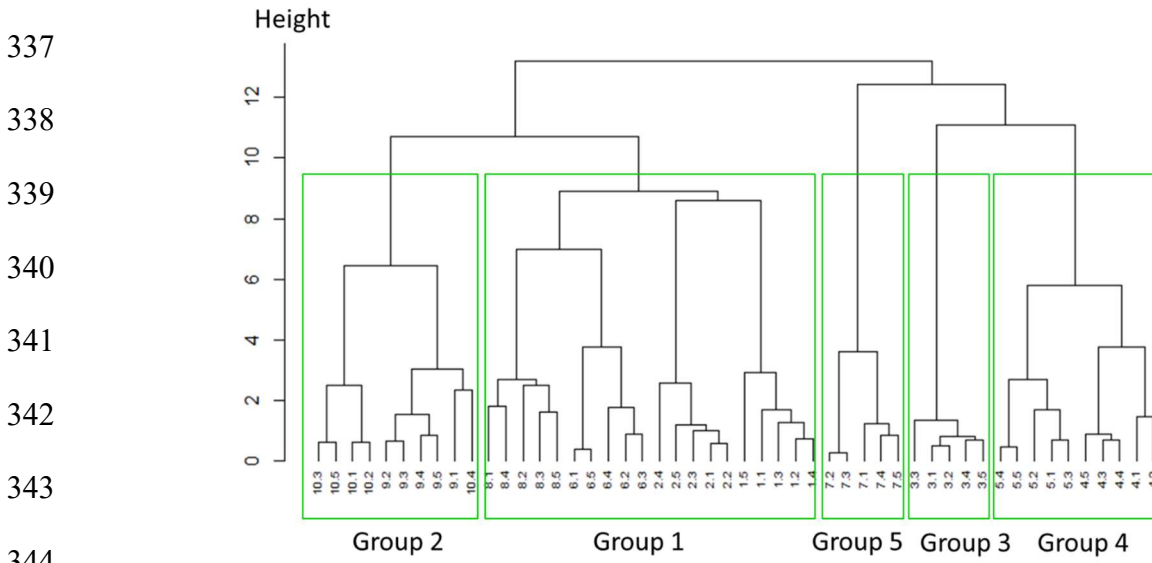
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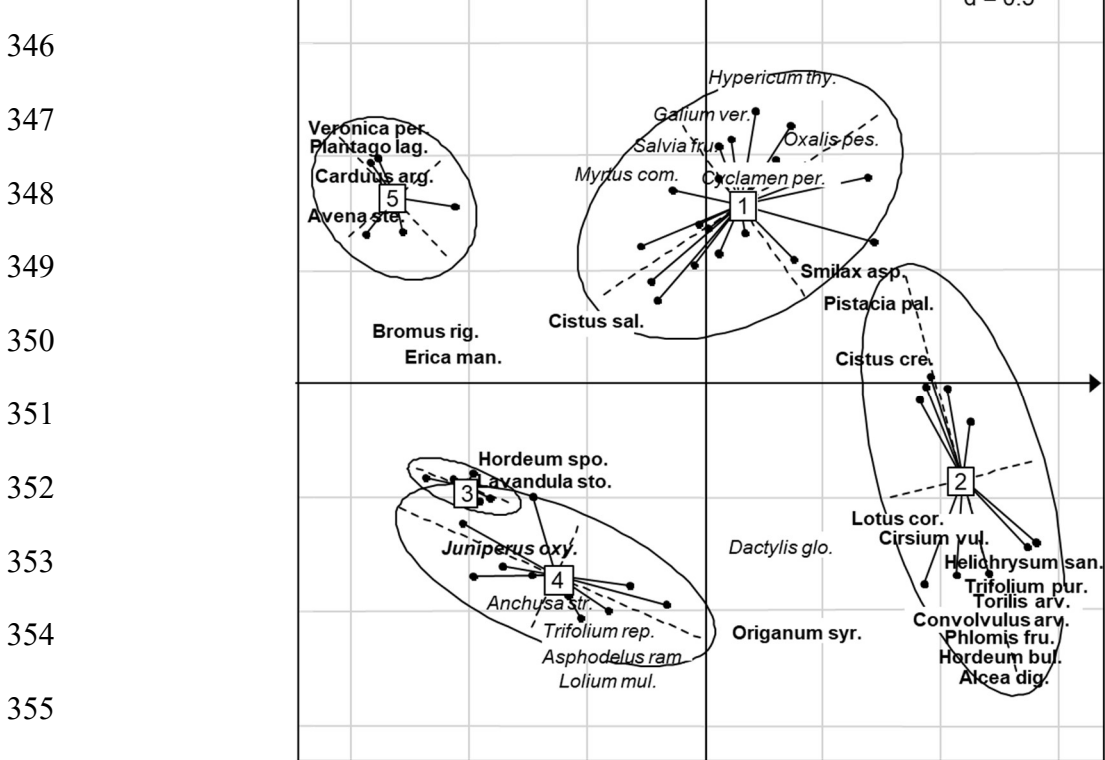
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336 A)



344

345 B)



356

357 **Fig. 4.** A) Results of the clustering analysis based on CCA results. B) The projection of species
358 and plots on the factorial map of the CCA. The five groups resulting from the clustering analysis
359 are indicated by the ellipses (1 to 5). Only plants with a contribution superior to 1.5 of the mean

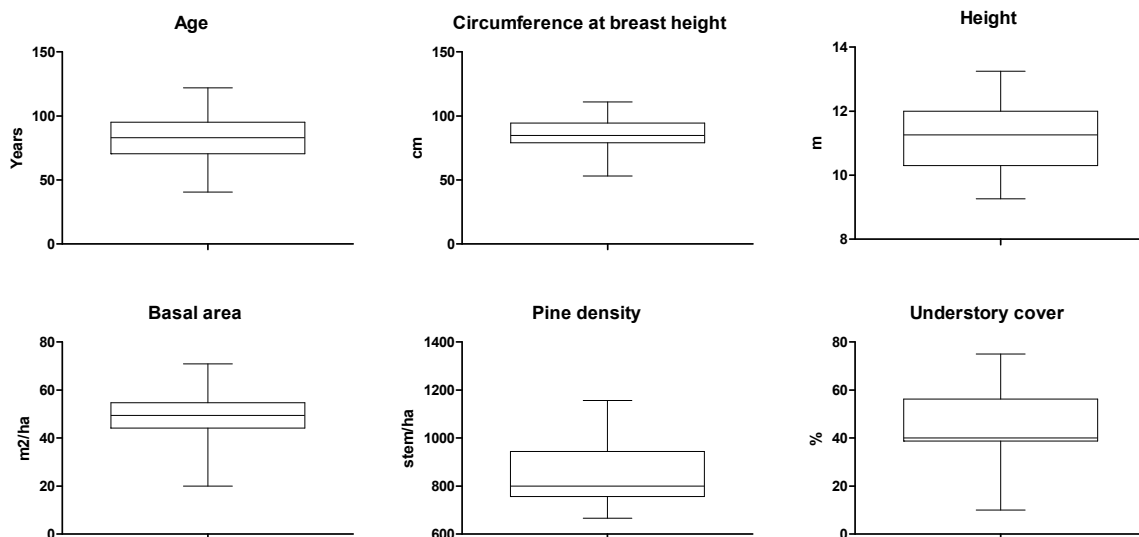
360 contribution were indicated, in bold italics for axis 1 and italics for axis 2. The scale of the
361 graph is the same as Fig. 3B which shows the projection of environmental factors.

362

363 3-3- Stand characteristics

364

365 The main dendrometric characteristics of the pine stands in the study area indicated that stands
366 were old ($80.8 \text{ years} \pm 0.4$) and mature (girth at breast height $84.9 \text{ cm} \pm 0.24$) but with a
367 relatively low mean height ($11.1 \text{ m} \pm 0.02$) (Fig. 5). The stands were also dense ($849 \text{ stems} \cdot \text{ha}^{-1}$)
368 ¹) with a high basal area ($49 \text{ m}^2 \cdot \text{ha}^{-1} \pm 0.21$).



369

370 **Fig.5.** Box and Whiskers plots of main dendrometric characteristics of the pine stands (all data)
371 indicating min, max, median and fourth quartiles.

372

373 When examining the dendrometric attributes of each group in greater detail (Table 2), we note
374 that the youngest stands with the lowest dominant tree height were found in Group 2 (45.4 years
375 and 9.7 m respectively). In contrast, Group 5 included the oldest stands (90.4 years) with the
376 greatest girth (97.8 cm) and basal area ($60.7 \text{ m}^2 \cdot \text{ha}^{-1}$). The other groups (1.2 and 4) exhibited a
377 comparable age although stands of Group 1 were the densest ($940 \text{ stems} \cdot \text{ha}^{-1}$) with the lowest

378 mean girth (75.4 cm). Lastly, the highest understory cover was found in stands of Group 4
 379 (58%) while the lowest herbaceous cover was recorded in Group 3 (22%).

380

381 **Table 2.** Variation in the main stand characteristics (mean \pm se) according to the different
 382 groups. Different letters indicate statistical differences among groups ($P < 0.05$).

383

Groups	1	2	3	4	5
Age	89.4 \pm 3.15 (a)	45.4 \pm 1.14 (b)	84.8 \pm 6.23(a)	84.9 \pm 4.18 (a)	90.4 \pm 5.24 (a)
Circumference					
(cm)	75.4 \pm 2.51 (a)	86.1 \pm 1.52 (a,b)	86.0 \pm 1.95 (a,b)	95.7 \pm 2.11 (b)	97.8 \pm 2.20 (b)
Height	11.5 \pm 0.19 (a,b)	9.7 \pm 0.15 (c)	10.8 \pm 0.45 (b,c)	11.1 \pm 0.33 (a,b)	12.4 \pm 0.22 (a)
Basal area	43.7 \pm 2.57 (a)	48.2 \pm 2.10 (a,b)	51.3 \pm 2.27 (a,b)	54.1 \pm 2.29 (b)	60.7 \pm 3.10 (b)
Pine density	940.0 \pm 28.53 (a)	804.4 \pm 12.31 (b)	862.2 \pm 33.26 (a,b)	7333 \pm 21.21 (b)	791.1 \pm 16.63 (b)
Understory					
cover (%)	46.3 \pm 2.99 (a,b)	34.5 \pm 2.52 (b)	51.0 \pm 4.85 (ab)	58.0 \pm 4.73 (a)	29.0 \pm 5.57 (b)
Herbaceous					
cover (%)	54.0 \pm 4.11 (a)	43.0 \pm 4.90 (a,b)	22.0 \pm 2.55 (b)	43.5 \pm 7.07 (a,b)	52.0 \pm 3.39 (a)

384

385

386 **3-4- Regeneration of pine seedlings and tree saplings**

387

388 Only 15 pine seedlings were recorded over the 450 subplots. We found that the number of
 389 seedlings follow a Poisson law of parameter $\lambda = 0.033$ (Fisher's exact test for count data,
 390 $P = 0.42$). In addition, the results of the GLMM showed that the number of pine seedlings was
 391 significantly negatively correlated with shrub cover and herb cover (Table 3).

392

393 **Table 3.** Results of the GLMM (fixed factors only) giving the number of pine seedlings
 394 according to local vegetation factors.

	Estimate	Std. Error	Z value	P-value
(Intercept)	-5.995	4.669	-1.284	0.199
Litter cover	0.005	0.024	0.226	0.821
Litter thickness	-0.016	0.709	-0.023	0.981
Herb cover	-0.059	0.026	-2.257	0.024 *
Shrub cover	-0.045	0.022	-2.093	0.036 *
Pine cover	0.024	0.026	0.906	0.365

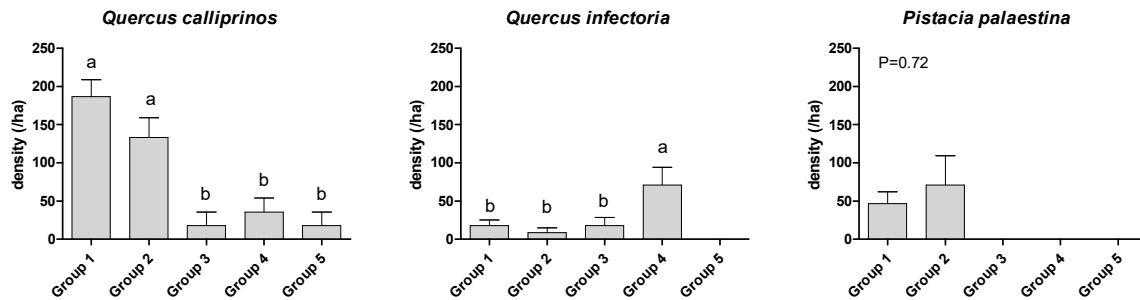
395

396

397 The oak species *Quercus calliprinos* Webb. was by far the most abundant in the understory
 398 (57% of the stems) followed by *Pistacia palaestina* Boiss. (17%), *Quercus infectoria* G. Olivier
 399 (13%) and other species (13%) such as *Ceratonia siliqua* L., *Acer syriacum* Boiss. & Gaill. and
 400 *Arbutus andrachne* L.

401 *Quercus calliprinos* was found in all groups (Fig. 6) but its density was significantly higher in
 402 groups 1 and 2. Similarly, *Quercus infectoria* was frequently observed but in lower abundance
 403 except for in Group 4. *Pistacia palaestina* was only recorded in Groups 1 and 2.

404



405
 406 **Fig. 6.** The density of the three main tree species in each group. Different letters indicate
 407 statistical differences ($P < 0.05$) among groups (no letters = not significant).

408

409

410 4- Discussion

411 This floristic study showed that *Pinus pinea* forests in Lebanon are dense with overstories
 412 dominated by stone pine and understories dominated by *Quercus calliprinos* Webb. and to a
 413 lesser extent *Quercus infectoria* G. Olivier. Shrub species are also abundant in particular *Cistus*
 414 *salviifolius* L., *Callicotome villosa* (Poir.) Link and *Cistus creticus* L.

415

416 4.1. Classification of pine stands

417 The cluster analysis following the CCA produced five groups differentiating themselves by
 418 environmental factors and species composition. Understory species showed strong responses to
 419 altitude, slope, temperature, rain, bedrock, human intervention and C/N.

420 In this study, groups 1 and 5 were located at the lowest altitudes but on very contrasted slope
 421 conditions as the steepest slopes were observed in Group 1 while Group 5 had the lowest slopes.

422 Topographic variability such as elevation and slope are considered as key factors influencing
 423 vegetation cover due to their effect on specific microclimates (Coblentz and Riitters, 2004;

424 Coblentz and Keating, 2008; Zhao *et al.*, 2010). Altitude has been noted for its role in
 425 influencing the distribution of plant communities (Alessandro and Marcello, 2003; Lososova *et*

426 *al.*, 2004; Fisher and Fuel, 2004; Rahman *et al.*, 2017). Altitude is the main factor affecting
427 habitat temperature (Coblentz and Riitters, 2004) and can affect productivity rates in natural
428 forests (Kira and Shidei, 1967; Mayhead, 1973). For instance, Kira and Shidei (1967) showed
429 that elevation can induce variation in the composition of accompanying species and affect the
430 growth of natural forests.

431 On other hand, slope was considered as an important factor controlling plant species'
432 distribution (Abadi and El-Sheikh, 2002; Grongroft *et al.*, 2003; Badano *et al.*, 2005; Boll *et*
433 *al.*, 2005). Increasing slope steepness can decrease soil depth, nutrients and moisture, making
434 plant establishment more difficult (Campo *et al.*, 1999). In our study, the steep slopes were
435 associated with the absence of evidence of present or past human activities, in particular no
436 terraces were found in Group 1 in contrast to Group 2 and 5. Anthropogenic factors have been
437 reported to directly affect the structure and biodiversity of forest ecosystems as well as plant
438 richness and diversity (Shaheen *et al.*, 2001; Ruprecht *et al.*, 2009; Linares *et al.*, 2011; Blanco
439 and Pereira, 2015). Human disturbances can change plant community distribution by negatively
440 affecting soil fertility (Ko *et al.*, 2011; Heydari *et al.*, 2017; Sfair *et al.*, 2018). Terraces were
441 often cultivated before abandonment and many previous studies have recorded better soil
442 fertility on abandoned croplands in particular, lower C/N ratio values, higher P values and better
443 nitrification (Prévosto *et al.*, 2004; Koerner *et al.*, 1997). It was noticeable that the highest C/N
444 ratio were recorded in the Group 1 (32.9 ± 1.22) indicating lower fertility whereas the lowest
445 C/N ratios were recorded in group 2 (24.2 ± 1.73) as the result of a moderate slope and the
446 frequent presence of terraces. In fact, the C/N ratio is a determinant factor in herbaceous plant
447 establishment and an increase of this ratio results in a decrease in nitrogen availability to plants
448 (Christine and McCarthy, 2005). In contrast, the relatively high C/N ratio recorded in Group 5
449 (30.0 ± 2.45) on terraces can be explained by ongoing human disturbances (brushing, local
450 cutting) which could have decreased soil fertility as has been observed in other Mediterranean

451 habitats (Heydari *et al.*, 2017; Javad *et al.*, 2017). However, now more soil chemical analyses
452 (e.g. nutrients, cation exchange capacity) would be needed to further explore the impact of
453 human activities on soil fertility.

454 Groups 3 and 4 are located on medium slopes at high altitude. As frequently observed in many
455 studies, altitude plays an important role in determining plant distribution as this factor is also
456 highly correlated to a gradient of temperature and rainfall (Went, 2003; Hatfield and Prueger,
457 2015; Padilla and Pugnaire, 2007). These two groups exhibit a relatively similar floristic
458 composition, but the former is located exclusively on sandstone bedrock whereas the latter is
459 mostly on siliceous sandstone. The influence of the nature of the geological substratum on soil
460 properties and plant distribution has been widely proven and studied (Just, 1947; Cole, 1982;
461 Searcy *et al.*, 2003). In this study, each group was characterized by a specific bedrock except
462 for Group 1 being present in various types of substratum. Surprisingly, the influence of the soil
463 water reserve was weak: it did not vary among the groups (values ranging from 43 to 53 mm)
464 except for Group 3 which showed a high value (107 mm). In fact, this group was the only one
465 where clay texture was detected whereas the sandy texture was dominant in all other groups.
466 Besides, soil depth did not vary, and all sampled pine stands were located on deep soils (>80cm,
467 the maximum depth reached in this study) indicating that soil water holding capacity was
468 probably not a limiting factor in our study conditions.

469

470 *4.2. Stand characteristics and regeneration*

471 The dendrometric analysis showed that pine stands were relatively dense with a high basal area
472 and mostly old (85-90 years old) except for group 2 (45 years old) which was mostly distributed
473 on privately owned land that had probably been more recently cultivated for pine nuts
474 production. The high basal area can be explained by the absence of thinning or cutting which
475 was also reflected by the lack of pine regeneration. Historically, some *Pinus pinea* plantations

476 have occurred between 1930 and 1940 on sandy soils in Lebanon (Sfeir, 2011) mostly for seeds
477 and not for wood production. Regeneration in these stands was particularly low and can be
478 considered as a rare event. It was restricted to some sites with anthropogenic disturbances
479 especially in Group 5 where disturbances linked to human activity has allowed for the
480 establishment of very few seedlings. This widespread lack of regeneration is probably linked to
481 the reduced light availability under the closed overstory cover which is often a crucial factor
482 for seedling survival in most pine species (Lucas-Borja *et al.*, 2011; Calama *et al.*, 2017)
483 including stone pine (Adili *et al.*, 2013). In fact, previous studies have shown that natural
484 regeneration of stone pine stands must be linked to a strong reduction in tree density (e.g.
485 Calama *et al.*, 2017; Freire *et al.*, 2019). In this study, the influence of litter thickness, which
486 is often detrimental for regeneration (Facelli and Pickett, 1991), was not observed but we found
487 a negative effect of both the shrub and the herb layers. The shrub layer was found to negatively
488 affect pine emergence (Prévosto *et al.*, 2015) and probably survival due to an even more reduced
489 light availability. Developed covers in herbaceous plants, especially grass species, are also
490 particularly detrimental to seedling survival due to competition for both nutrients and water
491 (Diwold *et al.*, 2010; García-Palacios *et al.*, 2012). In contrast, we found clear oak dynamics
492 specifically for *Quercus calliprinos* which was present in all *Pinus pinea* stands and secondarily
493 for *Quercus infectoria*. In Lebanon forests, *Quercus calliprinos* was identified as the most
494 common tree species whereas *Quercus infectoria* was of a less frequent occurrence (Beydoun
495 and Stephan, 2005). In Mediterranean woodlands, oaks were in fact commonly considered as
496 late successional species that followed the pioneer pine stage (Barbero *et al.*, 1998). Pine stands
497 are favourable habitats for oak dissemination as the pine canopy modifies shade, moisture and
498 temperature conditions, as well as promoting oak development (Lookingbill and Zavala, 2000;
499 Gomez, 2004; Pons and Pausas, 2006; Pons and Pausas, 2007). These stands also support a
500 variety of understory shrub vegetation, playing a significant role in these forest ecosystems (like

501 *Cistus* spp.) and some tree-like species (*Pistacia palaestina*.Boiss., *Ceratonia siliqua* L.,
502 *Arbutus andrachne* L.) which could contribute to the diversification of these stands in the future.

503

504 4.3. Lessons and main implications for management

505 This study is the first field study on *Pinus pinea* L. stands in Lebanon which, despite their
506 extensive distribution and important role in the forest economic sector of the country, has
507 received little attention up until now. Pine stands are distributed according to various site
508 conditions, we proposed a first classification of these forests based on environmental factors
509 and plant composition. Most of the stands are old and dense with naturally low pine recruitment
510 emphasising the fact that the conservation of the species in the future is compromised. This
511 finding supports the view that stone pine is an introduced species in Lebanon and cannot form
512 'climatic' forests (i.e. capable of regenerating) as it was stated by some authors (Chouchani et
513 al., 1975; Abi Saleh et al., 1976; Abi Saleh, 1978). In the absence of any forest management
514 intervention and with the ageing of stone pine forests, these stands will progressively disappear
515 in the next few decades and will be replaced by oak species which naturally establish in the
516 understory. Therefore, management action is needed in order to assure either the artificial or
517 natural regeneration of stone pine in relation to the main objectives attributed to these
518 formations (e.g. nut production, wood supply) and future threats to these ecosystems (in
519 particular fire risk and drought). To promote natural regeneration, we recommend reducing tree
520 density (Calama *et al.*, 2012; Freire et al., 2019) and introducing soil disturbances such as soil
521 scarification or prescribed burning (Lucas-Borja *et al.*, 2012; Karlsson, 2000; Prévosto *et al.*
522 2012). These treatments can promote seed-soil contact and improve seedling establishment,
523 while the greater availability of light provided by reduced canopy will promote longer-term
524 seedling growth and survival .

525

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530

531

532 **References**

533

540 Abbadi, A.M., and El-Sheikh, G.A., 2002. Vegetation analysis of Failaka Island (Kuwait).
541 Journal of Arid Environment. 50: 153–165.

542 Abi Saleh, B., Barbero, M., Nahal, I., and Quézel, P., 1976. Les séries forestières de végétation
543 au Liban Essai d'interprétation schématique. Bulletin de la Société Botanique de France.
544 123(9): 541-560. DOI: 10.1080/00378941.1976.10835710

545 Abi Saleh B., 1978. Etude phytosociologique, phytodynamique et écologique des peuplements
546 sylvatiques du Liban. Thèse (PhD), Université Aix-Marseille, 184p.

547 Abi Saleh, B, and Safi, S., 1988. Carte de la végétation du Liban. Ecologia Mediterranea. 14.

548 Abi Saleh, B., Nasser, N., Rami, H., Salt, N., Safi, S., and H., Tohme, 1996. Biological
549 Diversity of Lebanon: La Flore Terrestre. Lebanese Ministry of Agriculture and UNEP.

550 Adili, B., and Balandier, P., 2013. Influence of Stand and tree attributes and silviculture on cone
551 and seed productions in forests of *Pinus pinea* L. in northern Tunisia. 105.

552 Alessandro, P., and Marcello, T., 2003. Ecological profiles of wetland plant species in the
553 northern Apennines (N. Italy). Journal of Limnology. 62(1): 71–78.

554 Augusto, L., Ranger, J., Binkley, D., and Rothe, A., 2002. Impact of several common tree
555 species of European temperate forests on soil fertility. Annals of Forest Science, 59(3): 233-
556 253.

557 Augusto, L., Dupouey, J. L., and Ranger, J., 2003. Effects of tree species on understory
558 vegetation and environmental conditions in temperate forests. Annals of Forest Science,
559 60(8): 823-83.

563 Badano, E.I., Cavieres, L.A., Molinga-Montenegro, M.A., and Quiroz, C.L., 2005. Slope aspect
564 influences association pattern in the Mediterranean natural of central Chile. Journal of Arid
565 Environment. 62: 93-108.

566 Bailey, J.D., and Covington, W.W., 2002. Evaluating ponderosa pine regeneration rates
567 following ecological restoration treatments in northern Arizona, USA. Forest Ecology and
568 Management. 155: 271-278.

569 Balcha, G., 2008. Biological diversity and current *ex situ* conservation practices in Ethiopia.
570 Institute of Biodiversity Conservation and Research, Addis Ababa.

571 Baltaxe, R., 1966. Carte forestière du Liban, 1:200.000. FAO and Lebanese Government.

572 Barbero, M., Loisel, R., Quezel, P., Richardson, D., and Romane, F., 1998. Pines of the
573 Mediterranean Basin. In Richardson, D.M., ed. Ecology and biogeography of *Pinus*, p. 153-
574 170. Cambridge, UK, Cambridge University Press.

575 Barbier, S., Gasselin, F., and Balandier, P., 2008. Influence of tree species on understory
576 vegetation diversity and mechanisms involved: A critical review for temperate and boreal
577 forests. Forest ecology and management. 254(1): 1-15.

578 Barbier, S., Balandier, P. and Gasselin, F., 2009. Influence of several tree traits on rainfall
579 partitioning in temperate and boreal forests: a review. Annals of Forest Science. 66(6): 1-11.

- 580 Bartemucci, P., Messier, C., and Canham, C.O., 2006. Overstory influences on light attenuation
581 patterns and understory plant community diversity and composition in southern boreal
582 forests of Quebec. *Canadian Journal of Forest Research*. 36(9): 2065-2079.
- 583 Bennett, A.F., Radford, J.Q., and Haslem, A., 2006. Properties of land mosaics: implications
584 for nature conservation in agricultural environments. *Biological Conservation*. 133: 250-
585 264.
- 586 Bennie, J., Huntleya, B., Wiltshirea, A., Hill, M.O., and Baxtera, R., 2008. Slope, aspect and
587 climate: Spatially explicit and implicit models of topographic microclimate in chalk
588 grassland. *Ecological Modelling*. 216, 47-59.
- 589 Beydoun, G.Y., and Stephan, J., 2005. National Forest Assessment Program Lebanon. Data
590 Analysis Report by Genane Youness Beydoun – FAO Data Analysis Expert & Jean Stephan
591 Agricultural Engineer, MOA.
- 592 Blamey, M., and Grey-Wilson, C., 1993. *Mediterranean Wild Flowers*. HarperCollins
593 Publishers.
- 594 Blanco, L., and Pereira, V., 2015. Anthropogenic disturbances and the natural vegetation
595 regeneration: A case study of forest fragment located in a cuesta relief area, state of São
596 Paulo, Brazil. *Open Journal of Forestry*. 5: 621–635.
- 597 Boll, T., Svenning, J.C., Vormisto, J., Normand, S., Grandez, C., and Balslev, H., 2005. Spatial
598 distribution and environmental preferences of the piassaba palm *Aphandra Natalia*
599 (*Arecaceae*) along the Pastaza and Urituyacu rivers in Peru. *Forest Ecology and*
600 *Management*. 213, 175-183.
- 601 Braun-Blanquet, J., 1932. *Plant Sociology*. McGraw-Hill Book Company, New York.
- 602 Burrascano, S., Sabatini, F.M., and Blasi, C., 2011. Testing indicators of sustainable forest
603 management on understory composition and diversity in southern Italy through variation
604 partitioning. *Plant Ecology*. 212: 829-841.
- 605 Burton, J.I., Mladenoff, D.J., Clayton, M.K., and Forrester, J.A., 2011. The roles of
606 environmental filtering and colonization in the fine-scale spatial patterning of ground-layer
607 plant communities in north temperate deciduous forests. *Journal of Ecology*. 99: 764-776.
- 608 Calama, R., Madrigal G., Candela J.A. and Montero G., 2007. Effects of fertilization on the
609 production of an edible forest fruit: stone pine (*Pinus pinea* L.) nuts in south-west Andalusia.
610 *Investigación Agraria. Sistemas Y Recursos Forestales*. 16(3): 241-252.
- 611 Calama, R., Madrigal, G., Manso, R., Garriga, E., Gordo, F.J., and Pardos, M., 2012.
612 Germinación, emergencia y supervivencia de regenerado en *Pinus pinea* L. In: Gordo, J.,
613 Calama, R., Pardos, M., Bravo, F., and Montero, G., 2012. La regeneración natural de los
614 pinares en los arenales de la Meseta Castellana. Instituto Universitario de Investigación en
615 Gestión Forestal Sostenible (Universidad de Valladolid-INIA), Valladolid.
- 616 Calama, R., Manso, R., Lucas-Borja, M., Espelta, J., Piqué, M., Bravo, F., del Peso, C., and
617 Pardos, M., 2017. Natural regeneration in Iberian pines: A review of dynamic processes and
618 proposals for management. *Forest Systems*. 26(2): 20.
- 619 Campo, J.G., Alberto, F., Hodgson, J., Garcia-Ruiz, J., and Montserrat-Marti, G., 1999. Plant
620 community patterns in a gypsum area of NE Spain, interactions with topographic factors and
621 soil erosion. *Journal of Arid Environment*. 41: 401-410.
- 622 Chouchani, B., Khouzami, M., and Quezel, P., 1975. A propos de quelques groupements
623 forestiers au Liban. *Ecologia Mediterranea*. 1: 63-77.
- 624 Christine, S., and McCarthy, C., 2005. Relationship of understory diversity to soil nitro-gen,
625 topographic variation and stand age in an eastern Oak forest, USA. *Forest Ecology and*
626 *Management*. 217: 229-243.
- 627 Coblenz, D., and Riitters, K.H., 2004. Topographic controls on the regional-scale biodiversity
628 of the South-Western USA. *Journal of Biogeography*. 31: 1125-1138.

629 Coblenz, D., and Keating, P.L., 2008. Topographic controls on the distribution of tree islands
630 in the high Andes of South-Western Ecuador. *Journal of Biogeography*. 35: 2026-2038.

631 Cole, M., 1982. The Influence of Soils, Geomorphology and Geology on the Distribution of
632 Plant Communities in Savanna Ecosystems. *In*: Huntley B.J., Walker B.H. (eds) *Ecology of*
633 *Tropical Savannas*. Ecological Studies (Analysis and Synthesis). 42. Springer, Berlin,
634 Heidelberg.

635 Cutini, A., Chianucci, F., Giannini, T., Manetti, M.C., and Salvati, L., 2015. Is anticipated seed
636 cutting an effective option to accelerate transition to high forest in European beech (*Fagus*
637 *sylvatica* L.) coppice stands? *Annals of Forest Sciences*. 72: 631-640.

638 Debelis, P. Bozzo, A., Barrios, B., and Bujan, A., 2005. The relationship between soil
639 characteristics and vegetation as a function of landform position in an area of the Flooding
640 Pampa. *Spanish Journal of Agricultural Research*. 3(2): 232-242.

641 Diwold, K., Dullinger, S., and Dirnböck, T., 2010. Effect of nitrogen availability on forest
642 understorey cover and its consequences for tree regeneration in the Austrian limestone Alps.
643 *Plant Ecology*. 209: 11-22.

644 Dubertret, L., 1955. Beirut. Carte Géologique du Liban au 1/200000. République Libanaise,
645 Ministère Des Travaux Publics. Beyrouth.

646 Dufour, A., Gadallah, F., Wagner, H.H., Guisan, A., and Buttler, A., 2006. Plant species
647 richness and environmental heterogeneity in a mountain landscape: effects of variability and
648 spatial configuration. *Ecography*. 29: 573-584.

649 Dutta, G., and Devi, A., 2013. Plant diversity, population structure, and regeneration status in
650 disturbed tropical forests in Assam, northeast India. *Journal of Forestry Research*. 24(4):715-
651 720.

652 Ewers, B.E., Mackay, O.S., Gower, S.T., Ahl, O.E., Burrows, S.N., and Samanta, S. S., 2002.
653 Tree species effects on stand transpiration in northern Wisconsin. *Water Resources Research*.
654 38(7), 8-1.

655 Facelli, J.M., and Pickett, S.T.A., 1991. Plant litter: its dynamics and effects on plant
656 community structure. *Botanical Review*. 57: 1-32.

657 Fady, B., Fineschi, S., and Vendramin, G.G., 2004. EUFORGEN technical guidelines for
658 genetic conservation and use for Italian stone pine (*Pinus pinea*). International Plant Genetic
659 Resources Institute, Rome.

660 FAO, 2006. Guidelines for soil description. ISBN 92-5-105521-1.

661 FAO, 2010. Global forest resources assessment 2010 country report Lebanon, FAO, Rome,
662 2010.

663 Fisher, M.A., and Fuel, P.Z., 2004. Changes in forest vegetation and arbuscular mycorrhizae
664 along a steep elevation gradient in Arizona. *Forest Ecology and Management*. 200: 293-
665 311.

666 Freire, J.A., Rodrigues, G.C., Tomé, M., 2019. Climate change impacts on *Pinus pinea* L.
667 Silvicultural system for cone production and ways to contour those impacts: A review
668 complemented with data from permanent plots. *Forests* 10, 169.

669 García-Palacios, P., Maestre, F., Bardgett, R., and de Kroon, H., 2012. Plant responses to soil
670 heterogeneity and global environmental change. *Journal of Ecology*. 100: 1303-1314.

671 Gaudin, S., 2015. La typologie des peuplements : un outil pour mieux connaître l'état des
672 chênaies à l'échelle régionale. *Forêt.Nature*. 135: 32-39.

673 Gégout, J., and Houillier, F., 1996. Canonical correspondence analysis for forest site
674 classification. A case study. *Annales des sciences forestières, INRA/EDP Sciences*, 1996.
675 53 (5): 981-990.

676 Geze, B., 1956. Carte de Reconnaissance des Sols du Liban au 1/2000000. Notice Explicative.
677 Lebanese Ministry of Agriculture.

678 Gomez, J.M., 2004. Bigger is not always better: conflicting selective pressures on seed size in
679 *Quercus ilex*. *Evolution*. 58:71-80.

680 Grongroft, A., Petersen, A., and Miehlich, G., 2003. Edaphical diversity and biodiversity in
681 mutual dependency project, ID: 01 LC 0024; BIOTA AFRICA So2.

682 Grubb, P.J., 1977. The maintenance of species-richness in plant communities: The importance
683 of the regeneration niche. *Biological Review*. 52:107-145.

684 Heydari, M., Omidipour, R., Abedi, M., and Baskin, C., 2017. Effects of fire disturbance on
685 alpha and beta diversity and on beta diversity components of soil seed banks and above
686 ground vegetation. *Plant Ecology and Evolution*. 150(3): 247-256.

687 ISO, 2005. ISO 10390:2005(fr), Qualité du sol, détermination du pH.,
688 <https://www.iso.org/obp/ui/#iso:std:iso:10390:ed-2:v1:fr>

689 Jafari, M., Biniiaz, M., Janfaza, E., Nematollahi, J., and Karimpour Reyhan, M., 2009.
690 Relationship between Soil Characteristics and Vegetation Types in Damghan. *Desert*. 17:
691 129-135.

692 Jaja, N., 2016. Understanding the Texture of Your Soil for Agricultural Productivity.
693 Publication CSES-162P. Virginia State University.

694 Jamagne M., Bétrémieux R., Bégon J.C., and Mori A., 1977. Quelques données sur la variabilité
695 dans le milieu naturel de la réserve en eau des sols. *Bulletin Technique d'Information*. 324-
696 325: 627-641.

697 Javad, M., Mehdi, H., and Prévosto, B., 2017. Effects of vegetation patterns and environmental
698 factors on woody regeneration in semi-arid oak-dominated forests of western Iran. *Journal*
699 *of Arid Land*. 9(3): 368-378.

700 Just, T., 1947. *Geology and Plant Distribution*. *Ecological Monographs*. 17(2): 127-137.

701 Karlsson, C., 2000. Effects of release cutting and soil scarification on natural regeneration in
702 *Pinus sylvestris* shelterwoods. PhD Thesis. Department of Forest Management and Products.
703 Swedish University of Agricultural Sciences, Uppsala. ISBN 91-576-5633-9.

704 Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology.
705 *Vegetation Science*. 3: 157-164.

706 Kira, T., and Shidei, T., 1967. Primary production and turnover of organic matter in different
707 forest ecosystems of the western Pacific. *Japanese Journal of Ecology*. 17(2): 70-87.

708 Ko, W., Sparrow, D., and Weisberg, J., 2011. Land-use legacy of historical tree harvesting for
709 charcoal production in a semi-arid woodland. *Forest Ecology and Management*. 261: 1283-
710 1292.

711 Koerner, G., Bowderst, J., and Scranton, H., 1997. Instrumentation for monitoring field
712 performance of the Cincinnati GCL test plots. *Geotextiles and Geomembranes*. 15(4-6): 341-
713 365.

720 Lacoste, A., and Salanon, R., 1978. *Éléments de biogéographie et d'écologie*, Paris.

721 Linares, C., Carreira, A., and Ochoa, V., 2011. Human impacts drive forest structure and
722 diversity. Insights from Mediterranean mountain forest dominated by *Abies pinsapo* (Boiss).
723 *European Journal of Forest Research*. 130: 533-542.

724 Lookingbill, T.R., and Zavala, M.A., 2000. Spatial pattern of *Quercus ilex* and *Quercus*
725 *pubescens* recruitment in *Pinus halepensis* dominated woodlands. *J Veg Sci* 11:607-612.

726 Lososova, Z., Chytry, M., Cimalova, S., Kropac, Z., Otypcova, Z., Pysek, P., and Tichy, L.,
727 2004. Weed vegetation of arable land in central Europe: gradients of diversity and species
728 composition. *Journal of Vegetation Science*. 15: 415-422.

729 Lucas-Borja, M., Fonseca, T., Parresol, B., and Santos, P., 2011. Modelling Spanish black pine
730 seedling emergence: Establishing management strategies for endangered forest areas. *Fuel*
731 *and Energy Abstracts*. 262(2): 195-202.

732 Lucas-Borja, M., Fonseca, T., Lousada, J.L., Silva-Santos, P., Garcia, E., and Abellán, M.,
733 2012. Natural regeneration of Spanish black pine [*Pinus nigra* Arn. ssp. *salzmannii* (Dunal)]

734 Franco] at contrasting altitudes in a Mediterranean mountain area. *Ecological Research*.
735 27(5): 913-921.

736 Maestre, F.T., Cortina, J., Bautista, S., Bellot, J., and Vallejo, R., 2003. Small-scale
737 environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a
738 semiarid degraded ecosystem. *Ecosystems*. 6: 630-643.

739 Mahajan, M., and Fatima, S., 2017. Frequency, abundance and density of plant species by list
740 count quadrat method. *Epitome: International Journal of Multidisciplinary Research*. 3(7):
741 1-8.

742 Malik, Z.A., and Bhatt, B., 2016. Regeneration status of tree species and survival of their
743 seedlings in Kedarnath Wildlife Sanctuary and its adjoining areas in Western Himalaya,
744 India. *Tropical Ecology*. 57: 677-690.

745 Manso, R., Fortin, M., Calama, R., and Pardos, M. 2013. Modelling seed germination in forest
746 tree species through survival analysis. The *Pinus pinea* L. case study. *Forest Ecology and*
747 *Management*. 289: 9–21.

748 Marcuzzo, S. B., Araujo, M., M., and Longhi, S. J., 2013. Structure and environmental relations
749 of floristic groups in tropical deciduous forest fragment. *Revista Árvore*. 37(2): 275-287.

750 Mayhead, G.J., 1973. Some drag coefficients for British forest trees derived from wind tunnel
751 studies. *Agricultural and Forest Meteorology*. 12: 123-130.

752 Mekideche, S., Brakchi-Ouakour, L., and Kadik, L., 2018. Impact des perturbations
753 anthropiques sur la diversité végétale de la subéraie de Chréa, au nord de l'Algérie.

754 Mikesell, M.W., 1969. The deforestation of Mount Lebanon. *Geographical Review*. 59(1): 1-
755 28.

756 MoE, Republic of Lebanon, Ministry of Environment. 2014. The Reforestation Initiative of the
757 Ministry of Environment Lebanon.

758 Monier, E., and Wafaa, A., 2003. Soil-vegetation relationships in a coastal desert plain of
759 southern Sinai, Egypt. *Journal of Arid Environments*. 55: 607-628.

760 Mouterde, P., 1970. *Nouvelle Flore du Liban et de la Syrie*, 3 tomes Atlas, Dar El Machriq,
761 Beirut.

762 Ni, J., 2002. Plant functional types and climate along a precipitation gradient in temperate
763 grasslands, north-east China and south-east Mongolia. Laboratory of Quantitative
764 Vegetation Ecology, Institute of Botany, Chinese Academy of Sciences, Xiangshan
765 Nanxincun 20, 100093, Beijing, China.

766 Noumi, Z., 2015. Effects of exotic and endogenous shrubs on understory vegetation and soil
767 nutrients in the south of Tunisia. *J. Arid Land* 7, 481–487.

768 Padilla, F.M., and Pugnaire, F.I., 2007. Rooting depth and soil moisture control Mediterranean
769 woody seedling survival during drought. *Funct Ecol*. 2007; 21: 489–495.

770 Palmer, W., 1993. Putting Things in Even Better Order: The Advantages of Canonical
771 Correspondence Analysis. *Ecology*, Vol. 74, No. 8 (Dec., 1993), pp. 2215-2230.

772 Pandey, S.K., and Shukla, R.P., 2001. Regeneration strategy and plant diversity in degraded Sal
773 forests. *Current Science* 81:95–102.

774 Peng, W., Song, T., Zeng, F., Wang, K., Du, H., and Lu, S., 2012. Relationships between woody
775 plants and environmental factors in karst mixed evergreen-deciduous broadleaf forest,
776 southwest China. *J. Food Agric. Environ*. 10, 890–896.

777 Pons, J., and Pausas, J.G., 2006. Oak regeneration in heterogeneous landscapes: the case of
778 fragmented *Quercus suber* forests in the eastern Iberian Peninsula. *For Ecol Manag*
779 231:196–204.

780 Pons, J., and Pausas, J.G., 2007. Acorn dispersal estimated by radio-tracking. *Oecologia*
781 153:903–911.

782 Pregitzer, S., Barnes, V., and Lemme, D., 1983. Relationship of topography to soils and
783 vegetation in an upper Michigan ecosystem. *Journal of Soil Science* 47, 117-123.

- 784 Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. *Tree physiology*,
785 22 (15), 11 93- 1200.
- 786 Prévosto, B., Dambrine, E., Moares, C., and Curt, T., 2004. Effects of volcanic ash chemistry
787 and former agricultural use on the soils and vegetation of naturally regenerated woodlands
788 in the Massif Central, France. *Catena* 56(1-3):239-261.
- 789 Prévosto, B., Amandier, L., Quesney, T., de Boisgelin, G., and Ripert, C., 2012. Regenerating
790 mature Aleppo pine stands in fire-free conditions: Site preparation treatments matter. *Forest
791 Ecology and Management*, Elsevier, 2012, p. 70 - p. 77. [ff10.1016/j.foreco.2012.06.043](https://doi.org/10.1016/j.foreco.2012.06.043)
792 [ffhal-00777028](https://doi.org/10.1016/j.foreco.2012.06.043).
- 793 Prévosto, B., Gavinet, J., Ripert, C., and Fernandez, C., 2015. Identification of windows of
794 emergence and seedling establishment in a pine Mediterranean forest under controlled
795 disturbances. *Basic and Applied Ecology* 16(1).
- 796 Quézel, P. 1998. Diversité et répartition des sapins sur le pourtour méditerranéen. *Forêt
797 méditerranéenne*. 19: 93-104.
- 798 Raddi, S., Cherubini, P., Lauteri, M., and Magnani, F., 2009. The impact of sea erosion on
799 coastal *Pinus pinea* stands. A diachronic analysis combining tree-rings and ecological
800 markers. *257: 773-781*.
- 801 Rahman, I., Khan, N., and Ali, K., 2017. Classification and ordination of understory vegetation
802 using multivariate techniques in the *Pinus wallichiana* forests of Swat Valley, northern
803 Pakistan. *Sci Nat* (2017) 104:24.
- 804 Ricklefs, R.E., and Schulter, D., 1993. Species diversity in ecological communities. Historical
805 and geographical perspective. The University of Chicago Press, Chicago & London.
- 806 Ripert, C., Vennetier, M., 2002. Evaluations des potentialités forestières. Guide technique du
807 forestier méditerranéen français, chapitre 2 bis. Cemagref Antony, 61 p.
- 808 Roukoz, S. 2005. Final Report - National Consultant Mapping and Remote Sensing
809 TCP/LEB/2903. MOA, Beirut, July 2005.
- 810 Ruprecht, E., Szabó, A., Enyedi, M.Z., and Dengler, J., 2009. Stepp-like grasslands in
811 Transylvania (Romania): Characterization and influence of management on species diversity
812 and composition. *Tuexenia*, 29: 353–368.
- 813 Sánchez-Meador, A.J., Moore, M.M., Bakker, J.D., and Parysow, P.F., 2009. 108 years of
814 change in spatial pattern following selective harvest of a *Pinus ponderosa* stand in northern
815 Arizona, USA. *Journal of Vegetation Science* 20: 79-90.
- 816 Sarkissian, A.J., Brook, R.M., Talhouk, S.N., and Hockley, N., 2018. Using stakeholder
817 preferences to select native tree species for reforestation in Lebanon. *New Forests*. 49: 637-
818 647.
- 819 Scheller, R.M., and Mladenoff, D.J., 2002. Understory species patterns and diversity in old-
820 growth and managed northern hardwood forests. *Ecological Applications* 12: 1329-1343.
- 821 Searcy, K., Wilson, B., and Fownes, J., 2003. Influence of Bedrock and Aspect on Soils and
822 Plant Distribution in the Holyoke Range, Massachusetts. *The Journal of the Torrey Botanical
823 Society*, Vol. 130, No. 3. pp. 158-169.
- 824 Sfair, J., Bello, F., França, T., Baldauf, C., and Tabarelli, M., 2018. Chronic human disturbance
825 affects plant trait distribution in a seasonally dry tropical forest. *Environmental Research
826 Letters*, Volume 13, Number 2.
- 827 Sfeir, P., 2011. Stone pine and pine nuts production in Lebanon. Presented at Agropine2011:
828 International meeting on Mediterranean stone pine for agroforestry, PRAE Valladolid,
829 Spain, November. [accessed 2014 Aug 13].
- 830 Shaheen, H., Qureshi, A., and Shinwari, K., 2001. Structural diversity, vegetation dynamics
831 and anthropogenic impact on lesser Himalayan subtropical forests of Bagh district, Kashmir.
832 *Pakistan Journal of Botany*. 43: 1861–1866.

833 Tomao, A., Secondi, L., Carrus, G., Corona, P., Portoghesi, L., and Agrimi, M., 2018.
834 Restorative urban forests: Exploring the relationships between forest stand structure,
835 perceived restorativeness and benefits gained by visitors to coastal *Pinus pinea* forests.
836 Ecological Indicators. Ecological Indicators. 90: 594-605.

845 ter Braak, C.J.F., and Verdonschot, F.M., 1995. Canonical correspondence analysis and related
846 multivariate methods in aquatic ecology. Aquatic Sciences September 1995, Volume 57,
847 Issue 3, pp 255–289.

848 Tsitsoni, T. 1997. Conditions determining natural regeneration after wildfires in the *Pinus*
849 *halepensis* (Miller, 1768) forests of Kassandra Peninsula (North Greece). Forest Ecology
850 and Management, 92: 199–208.

851 Varol, Ö., and Tel, A., 2010. Ecological Features of the *Pinus pinea* Forests in the North-West
852 Region of Turkey (Yalova). Ekoloji 19(76):95-101 .

853 Wales, A., 1967. Climate, microclimate, and vegetation relationships on north and south forest
854 boundaries in New Jersey. William L. Hutcheson Mem. For. Bull. 2:1-60.

855 Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. Journal of the
856 American Statistical Association, 58: 236-244.

857 Ward, G.A., Smith, T.J., Whelan, K.R.T., and Doyle, T.W., 2006. Regional processes in
858 mangrove ecosystems: spatial scaling relationships, biomass, and turnover rates following
859 catastrophic disturbance. Hydrobiologia 569:517–527.

860 Went, W., 2003. The Effect of Temperature on Plant Growth. Ann. Rev. Plant Physiol. 4. 347-
861 362. 10.1146/annurev.pp.04.060153.002023.

862 Williams, R.J., Duff, G.A., Bowman, M.J.S., and Cook, G.D., 1996. Variation in the
863 competition and structure of tropical savannas as a function of rainfall and soil texture along
864 a large-scale climatic gradient in the Northern Territory, Australia Journal of Biogeography,
865 23. pp. 747-756.

866 Yu, M., and Sun, O.J., 2013. Effects of forest patch type and site on herb-layer vegetation in a
867 temperate forest ecosystem. Forest ecology and management, 300, 14-20.

868 Zhao, N., Yang, Y., and Zhou, X., 2010. Application of geographically weighted regression in
869 estimating the effect of climate and site conditions on vegetation distribution in Haihe
870 Catchment, China. *Plant Ecology*, 209, 349-359.

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878 **Supplementary material**

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881 **Table S1:** Description of the variables and abbreviations used in the study

Variable description	Abbreviation used
Mean temperature of the site (°C)	Temp
Mean precipitation of the site (mm)	Rain
Plot exposure (degree)	Aspect
Soil pH	pH
Site altitude (m)	Altitude
Plot slope (degree)	Slope
Soil water holding capacity	Soil moisture
Carbon-Nitrogen ratio of soil	C/N
Geology of the bedrock	Marl, Limestone, Sandstone
General topography of plot	Downhill, Top
Anthropic factor in plot (terraces with human intervention, human intervention only)	Anthro.Terr.Hint, Anthro.Hint
Reaction with Chloric Acid of the upper soil layer	HClA.Yes

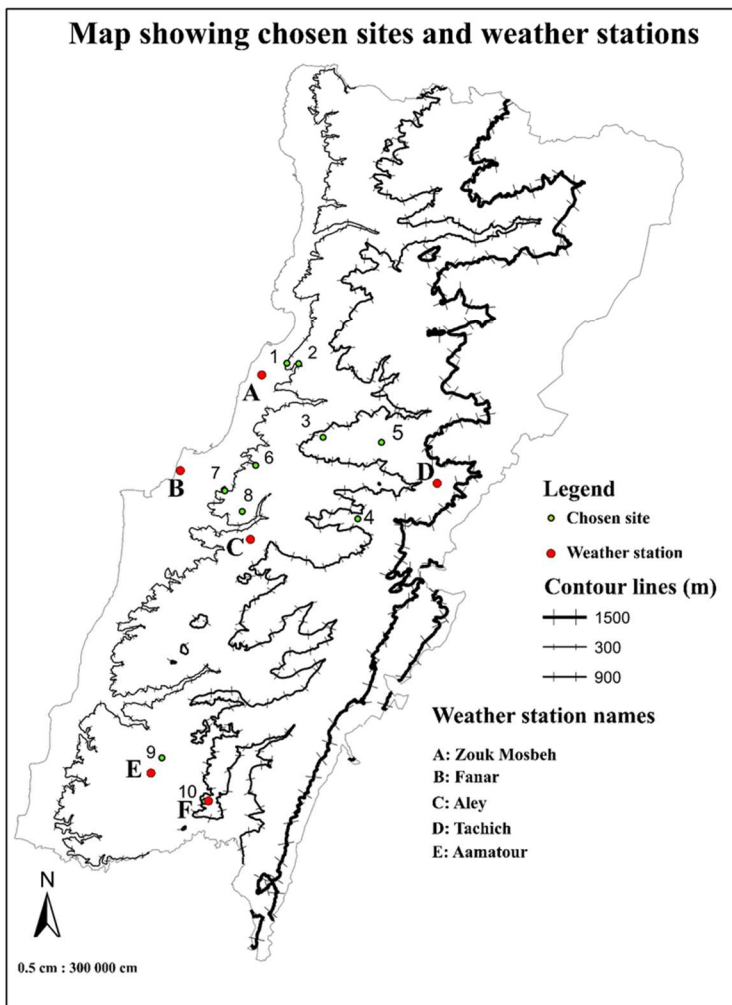
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884 **Table S2.** Location of the weather stations and methods used to determine climatic data
 885
 886 Computations of mean annual temperature and mean annual precipitation were achieved by the
 887 Lebanese Agricultural Research Institute (LARI) using 6 different weather stations (see map).
 888 Computations were done with ArcGis, kriging was preferentially used for temperature and
 889 IDW (Inverse Distance Weighting) for precipitation.

890 Distances between sampled sites and weathers stations are reported below.

- 891
- 892 distance from site 1 to station A: 3.1 km
- 893 distance from site 2 to station A: 3.7 km
- 894 distance from site 3 to station A: 10.4 km
- 895 distance from site 4 to station D: 10.1 km
- 896 distance from site 5 to station D: 7.8 km
- 897 distance from site 6 to station B: 9 km
- 898 distance from site 7 to station B: 5.2 km
- 899 distance from site 8 to station B: 8.3 km
- 900 distance from site 9 to station E: 1.9 km
- 901 distance from site 10 to station F: 0.6 km



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