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Title:

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

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Highlights

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

Abstract

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

1-Introduction

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

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

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

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

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

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

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

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

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

2-Material and Methods

2.1. Study area: Mount-Lebanon

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

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

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

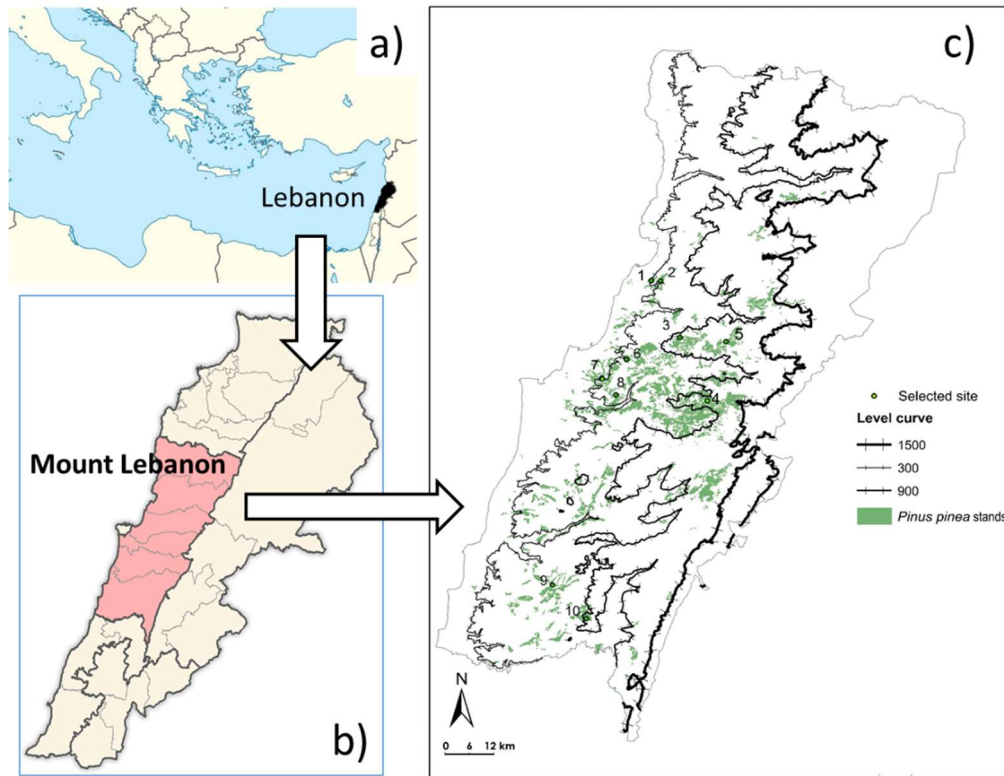


Fig. 1. a) The location of Lebanon in the eastern part of the Mediterranean basin. b) The location of Mount Lebanon in the country. c) The distribution of *Pinus pinea* stands in Mount Lebanon, the selected sites are indicated (1 to 10).

2.2. Sampling design

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

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

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

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

Table 1: Surface of stone pine stands in km² according to soil, altitude and slope classes. 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 (km ²)	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

2-3 Measurements

2.3.1. Floristic composition.

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

2.3.2. Environmental factors

The altitude, slope and aspect were measured in each plot and the local topography was described according to general observations of the plot (see Table S1 for description of the factors). We also used the climatic data for each site provided by the Lebanese Agricultural Research Institute (LARI) such as annual mean temperature and rainfall by referring to recorded values in the last 10 years at the nearest stations to selected sites (see Table S2 for more details). The nature of the bedrock was noted in the field, the types observed were sandstone (a soft, grey or ochre rock, barely cemented by some limonite), siliceous sandstone (with presence of quartz grains), marl (fossiliferous green marl) and limestone (Dubertret, 1955). To detect the presence of lime in the upper layer, a field test of fine earth reaction to HCl (diluted at 10%) was carried out (presence or absence of reaction) in each plot. Two pits were randomly dug, and two soil samples of 400 g were collected for each pit, corresponding to the first two soil horizons, these were used to measure pH, the ratio C/N and to estimate the soil texture. Soil texture in each plot was estimated by sedimentation tests in addition to the feel method on the collected samples (Jaja, 2016; FAO, 2006). Soil texture was coded by giving a coefficient of 0 (absent), 1 (present) or 2 (dominant) for the proportion of sand, silt and clay (Ripert and Vennetier, 2002). The water content (mm water/cm of soil) associated to each texture was then determined using the soil textural triangle and the data given

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

2.3.3. Dendrometric and regeneration measurements

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

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

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

2-4 Data analysis

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

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

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

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

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

3-Results

3-1- Floristic composition

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

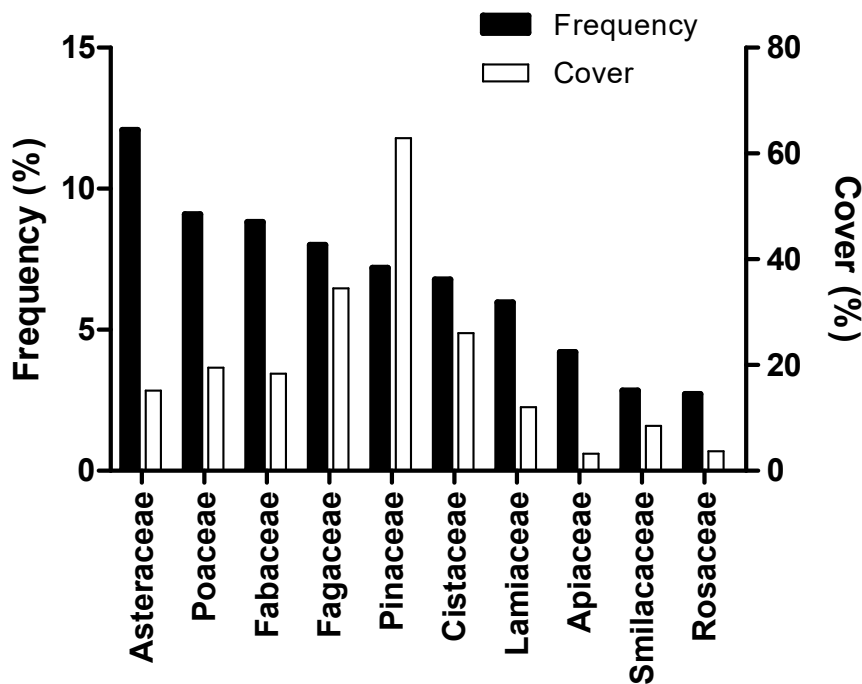


Fig. 2. Percentage frequency (based on species occurrence) and percentage cover (based on species cover) of the main plant families.

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

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

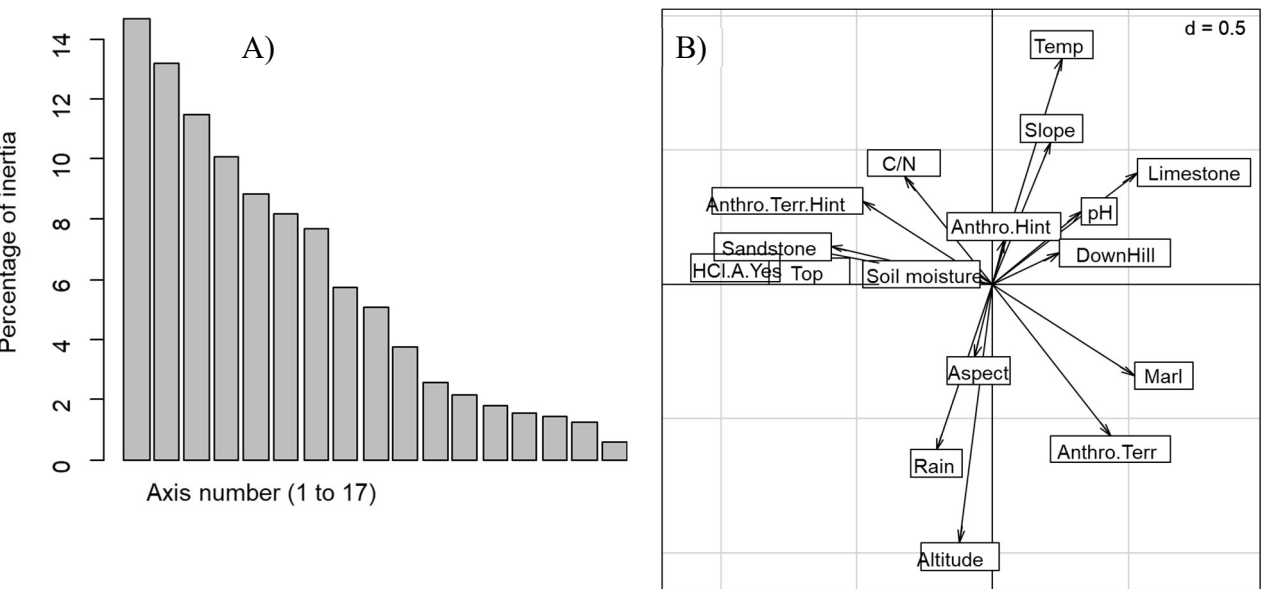


Fig.3. Results of the CCA. A) Percentage of inertia for each axis, B) projection of the measured factors, the scale of the graph is given by a grid, the size of which is indicated in the upper right corner ($d=0.5$). Abbreviations (see also Table S1): Anthro.Terr (presence of terraces); Anthro.Terr.Hint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

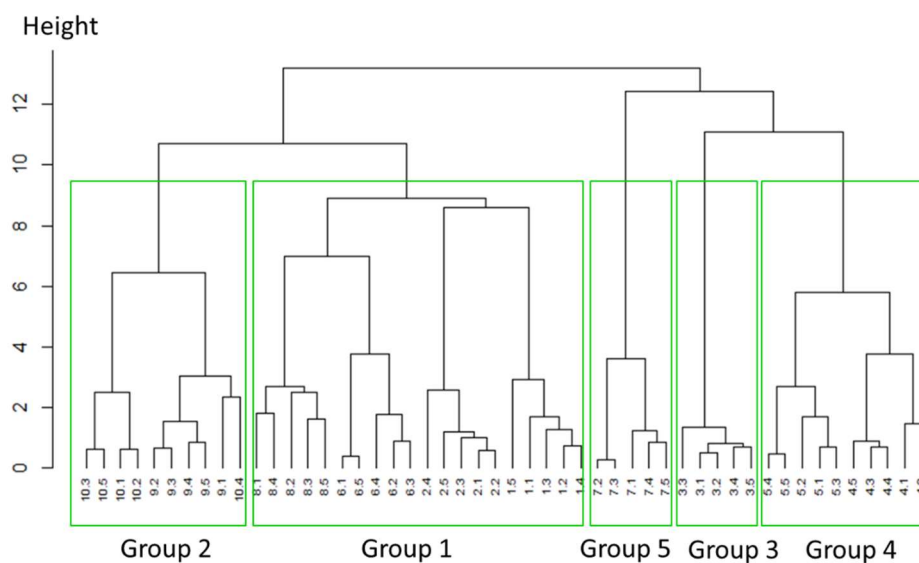
The clustering analysis applied on the CCA results revealed 5 groups (Fig. 4A). The projection on the factorial map of plots classified within these 5 groups as well as major plant species are indicated Fig. 4B.

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

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

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

A)



B)

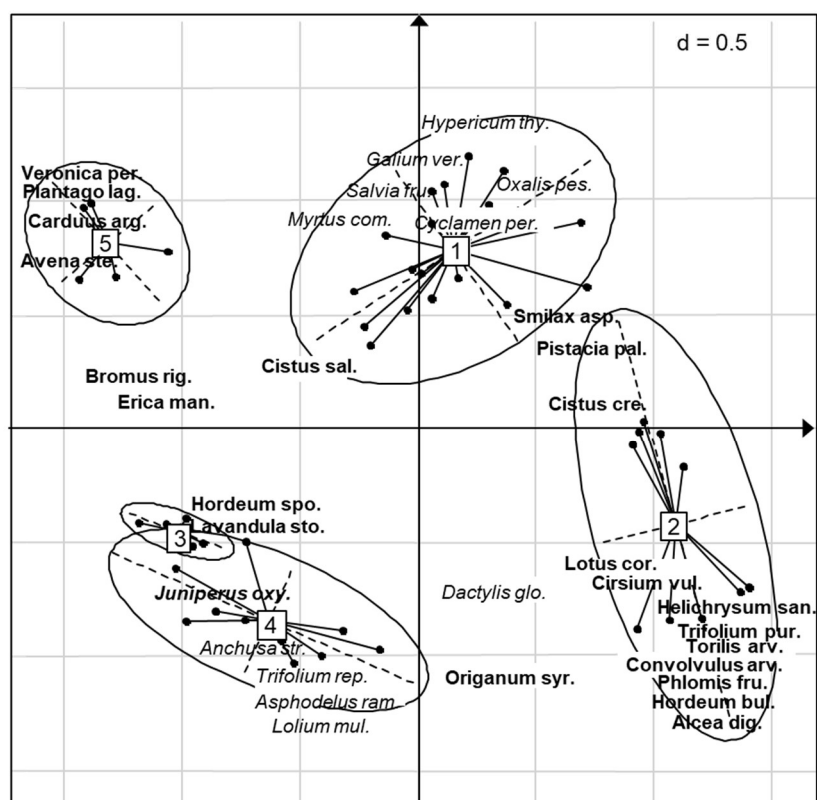


Fig. 4. A) Results of the clustering analysis based on CCA results. B) The projection of species and plots on the factorial map of the CCA. The five groups resulting from the clustering analysis are indicated by the ellipses (1 to 5). Only plants with a contribution superior to 1.5 of the mean

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

3-3- Stand characteristics

The main dendrometric characteristics of the pine stands in the study area indicated that stands 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 relatively low mean height ($11.1 \text{ m} \pm 0.02$) (Fig. 5). The stands were also dense ($849 \text{ stems.ha}^{-1}$) with a high basal area ($49 \text{ m}^2.\text{ha}^{-1} \pm 0.21$).

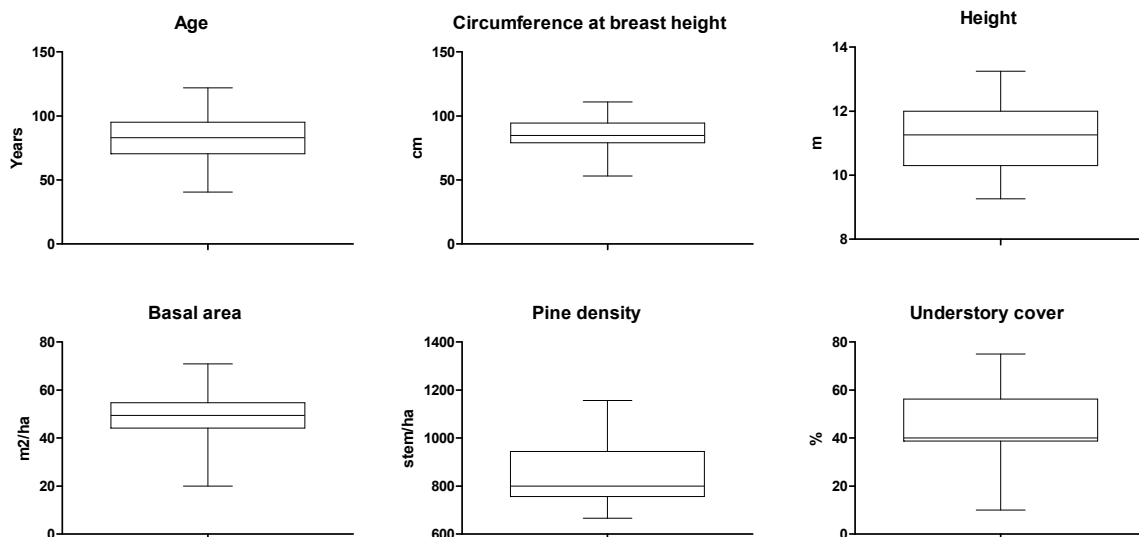


Fig.5. Box and Whiskers plots of main dendrometric characteristics of the pine stands (all data) indicating min, max, median and fourth quartiles.

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

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

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

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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)

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3-4- Regeneration of pine seedlings and tree saplings

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

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Table 3. Results of the GLMM (fixed factors only) giving the number of pine seedlings 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

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

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

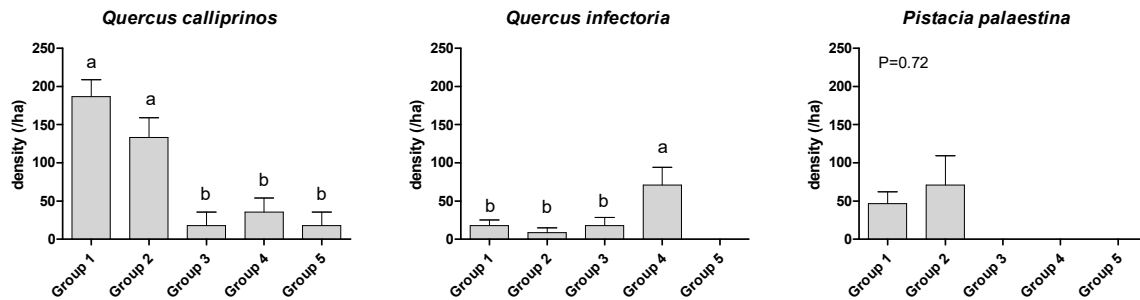


Fig. 6. The density of the three main tree species in each group. Different letters indicate statistical differences ($P < 0.05$) among groups (no letters = not significant).

4- Discussion

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

4.1. Classification of pine stands

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

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

Topographic variability such as elevation and slope are considered as key factors influencing vegetation cover due to their effect on specific microclimates (Coblentz and Riitters, 2004; Coblentz and Keating, 2008; Zhao *et al.*, 2010). Altitude has been noted for its role in influencing the distribution of plant communities (Alessandro and Marcello, 2003; Lososova *et*

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

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

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

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

4.2. Stand characteristics and regeneration

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

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

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

4.3. Lessons and main implications for management

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

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Supplementary material

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	HCl.A.Yes

Table S2. Location of the weather stations and methods used to determine climatic data

Computations of mean annual temperature and mean annual precipitation were achieved by the Lebanese Agricultural Research Institute (LARI) using 6 different weather stations (see map). Computations were done with ArcGis, kriging was preferentially used for temperature and IDW (Inverse Distance Weighting) for precipitation.

Distances between sampled sites and weathers stations are reported below.

distance from site 1 to station A: 3.1 km
distance from site 2 to station A: 3.7 km
distance from site 3 to station A: 10.4 km
distance from site 4 to station D: 10.1 km
distance from site 5 to station D: 7.8 km
distance from site 6 to station B: 9 km
distance from site 7 to station B: 5.2 km
distance from site 8 to station B: 8.3 km
distance from site 9 to station E: 1.9 km
distance from site 10 to station F: 0.6 km

