Turkish Journal of Botany

http://journals.tubitak.gov.tr/botany/

Research Article

Turk J Bot
(2016) 40: 595-609
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doi:10.3906/bot-1601-24

Abiotic factors affecting the distribution of oaks in Lebanon

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Received: 15.01.2016 • **Accepted/Published Online:** 12.05.2016 • **Final Version:** 06.12.2016

Abstract: This study is a first tentative attempt to understand the driving abiotic factors affecting the distribution of 7 oak taxa and 3 hybrids in Lebanon and to elucidate differences amongst the ecological niche. A field survey was conducted all over Lebanon, where taxa at 91 points were georeferenced and inventoried. GIS tools were used to overlay attributed data for the studied parameters including biogeographic, bioclimatic, and orographic parameters. Discriminant factor analysis (DFA) was performed to evaluate the variables maximizing the variance among oak species and to point out the most discriminatory factors shaping their actual distribution. The results showed that altitude, minimal temperature of the coldest month, maximal temperature of the hottest month, precipitation, and volcanic and deep soils are the major driving factors. *Quercus ithaburensis* Decne. grows solely on deep volcanic soils. *Quercus cerris* L. and *Quercus cedrorum* Kotschy thrive in areas with high precipitation ranges. An altitudinal gradient was generated, showing that *Quercus pubescens* Willd., *Quercus cedrorum* Kotschy, and *Quercus look* Kotschy are particularly located at higher altitudes, whereas *Quercus ithaburensis* Decne. is found at the lowest ones. *Quercus calliprinos* Webb and *Quercus infectoria* Olivier show a large plasticity in their biogeographical range, explaining their large area of occupancy in Lebanon.

Key words: *Quercus*, biogeographical range, abiotic factors, ecological niche, Lebanon

1. Introduction

Oaks constitute a major group of trees and shrubs of highly important biodiversity value that are regrouped under the genus *Quercus* L. (*Fagaceae*), out of which 30 are found in the Euro-Mediterranean region (Govaerts and Frodin, 1998; Denk and Grimm, 2010). Lebanon is considered a biodiversity hotspot of the East Mediterranean Basin and a habitat for 7 oak taxa (Abi Saleh et al., 1976; Tohmé and Tohmé, 2014). The high polymorphism and the occurrence of hybrids amongst oak species resulted in a series of taxonomy and nomenclature revisions, with an undetermined number of synonyms, subspecies, and varieties that often changed since the first elaborated oak list of Lebanon (Mouterde, 1966; Bussoti and Grosoni, 1998). To avoid any confusion, the 7 taxa identified by previous works conducted in Lebanon (Mouterde, 1966; Tohmé and Tohmé, 2014) are detailed and referred to by their accepted names in the World Checklist of Selected Plant families (WCSP), based on Govaret and Frodin (1998), and the International Plant Names Index (http://www.ipni.org/index.html). Note that the WCSP and Roskov et al. (2015) mention the presence of additional oak taxa; however, these were not described by previous Lebanese authors, nor found during our field survey. The following species were therefore considered in this study: *Quercus calliprinos* Webb syn. *Quercus coccifera* L., *Q. cedrorum* Kotschy syn. *Q. petraea* subsp. *pinnatiloba* (K.Koch), *Q. cerris* L., *Q. infectoria* Olivier, *Q. ithaburensis* Decne., *Q. look* Kotschy, and *Q. pubescens* Willd. subsp. *Pubescens*, which is the accepted name of *Q. pinnatifida* Gmel. referred to by Mouterde (1966) as a synonym of *Q. lanuginosa* Lam. (Govaerts and Frodin, 1998).

In addition, we identified 3 hybrids similar to those in Turkey cited by Menitsky (2005): *Q. cerris* L. × *Q. infectoria* Olivier, *Q. infectoria* Olivier × *Q. petraea* (Matt.) Lieb., and *Q. brantii* Lindley × *Q. infectoria* Olivier, herein after noted respectively as *Q. cerris* × *infectoria*, *Q. infectoria* × *cedrorum*, and *Q. brantii* × *infectoria*.

Many of these taxa occur in edge conditions, or in disjoined azonal areas of distribution, when compared to the species area of distribution, sensu Gaston (1991) in latitudinal, longitudinal, or altitudinal ranges. In most cases, these fragmented populations are remnants of forests resulting from anthropogenic activities shaping the landscape (Talhouk et al., 2005; Jomaa et al., 2009).

Few investigations have been done to date to determine the ecological or bioclimatic characterization of tree species, namely oaks, in Lebanon and the Levant

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and the major abiotic factors driving their distribution. Moreover, these works focused mainly on syntaxonomic studies and the attribution of species to vegetation levels and bioclimatic zones (Zohary, 1961; Abi Saleh et al., 1976; 1996; Akman et al., 1978; Al Eisawi, 1996; Danin, 2001; Ketenoglu et al., 2010).

Abi Saleh et al. (1976) defined the major forest vegetation series in Lebanon, based on climate and mother rock type. Further, the same author (Abi Saleh, 1982) described the altitudinal zonation of vegetation in Lebanon and divided it into 5 stages from sea level: Thermo, Meso, Supra, Montane, and Oro Mediterranean for the Mediterranean bioclimatic zones on the western slopes of Mount Lebanon, and 4 equivalent stages (Meso to Oro) in the Mediterranean steppe further inland. Each stage has roughly an altitudinal range of 500 m, with the Oro Mediterranean above 2000 m altitude. Abi Saleh and Safi (1988) produced a vegetation map for Lebanon, adapted from previous works (Quezel, 1976; Barbéro et al., 1985).

Several authors carried out in-depth investigations on the bioclimatic tolerance for different oaks species in the Near East, including *Q. cedrorum* Kotschy, *Q. cerris* L., *Q. coccifera* L., *Q. ithaburensis* Decne., and *Q. pubescens* Willd. using Emberger Quotient (Q), winter variant (m), the length of the dry period (LDP), and the dry season water deficit (DSWD) (Quezel, 1976, 1980; Quezel and Barbéro, 1985; Dufour-Dror and Ertas, 2004; Kargioglu et al., 2009; Serteser et al., 2009; Kargioglu et al., 2011; Ugurlu et al., 2012; Ugurlu and Oreland, 2012). Nonetheless, exploration of the distribution of oak species according to bioclimatic, orographic, and geographic characteristics in Lebanon has never been carried out except through a regional study targeting *Q. calliprinos* Webb (Ozturk et al., 2010).

This paper aims at revealing the potential niche of the 7 taxa and eventual hybrids identified in Lebanon, starting from the realized niche of each, filling the gaps related to the environmental and physical characterization of oak species in Lebanon and the Near East. The result would allow us to:

- Understand what the abiotic environmental factors are affecting the distribution of oak species in Lebanon. In practice, conclusions related to potential area for future reforestation activities aiming at ecosystem restoration and biodiversity conservation will be pointed out.

- Identify the most appropriate abiotic environmental parameter to study the potential niche of oak species in Lebanon and at regional level, where in most cases meteorological data collection and information are not always available or homogeneous. In a second step, this work will be a baseline for upscaling investigations directing the bioclimatic niche at regional level for many oak species that are rarely studied, especially those on their edge conditions.

- Delineate the geographical range or extent of occurrence of oak species at national level, and determining whether the biogeographic range of these species could be similar, overlapping, or separated. Conclusions would contribute to IUCN red listing of rare oak species at national and regional levels, which are deficient for Lebanon (Oldfield and Eastwood, 2007).

2. Materials and methods

We selected 91 sampling plots in which we sampled 5 trees of each species. The number of sampling plots per species were representative of the respective area of occupancy of the species and distributed as follows: 23 for *Q. calliprinos*, 23 for *Q. infectoria*, 15 for *Q. cerris*, 10 for *Q. pubescens*, 7 for *Q. look*, 4 for *Q. ithaburensis*, 4 for *Q. cedrorum*, 2 for *Q. infectoria* × *cedrorum*, 2 for *Q. cerris* × *infectoria*, and 1 for *Q. brantii* × *infectoria* (Figure 1). For widely distributed species such as *Q. calliprinos* Webb and *Q. infectoria* Olivier, we selected representative populations that express the diversity in the range of bioclimatic conditions, and vegetation stages and series, sensu Abi Saleh et al. (1996), and their area of occupancy as illustrated in the forest map of Lebanon (FAO/MOA, 2005). As for the remaining taxa, almost all populations were georeferenced, due to their limited subpopulations and restricted area of occupancy.

In each site, geographic, orographic, and bioclimatic parameters were recorded on site or generated through ArcMap by georeferencing the sites and overlaying them on the required maps (Table 1).

A set of parameters were used to determine the bioclimatic niche of oak species. Since Lebanon is under the Mediterranean climate zone sensu Köppen where a Csa/Csb climate rules (Peel et al., 2007), the differentiation amongst plant species' requirements of humidity and temperature is mostly expressed through Emberger's quotient (Emberger, 1955; Abi Saleh et al., 1976). This quotient (Q) is calculated as follows:

$$Q = \frac{200 \times P}{M^2 - m^2}$$

where P is the mean annual precipitation (mm), M is the maximal temperature average of the hottest month, and m is the minimal temperature average of the coldest month (K). In this study we converted Q into °C by adding 546.24.

Climatic data were retrieved from the *Atlas Climatique du Liban* (MoPW, 1966), with 20 years' data for temperature (M and m), and precipitation (P) from the closest meteorological stations in terms of geographical distance and bioclimatic zone/altitude.

We used another method for estimating annual rainfall in each site, by georeferencing each site on the precipitation map of Lebanon. As a result, sites were located between 2

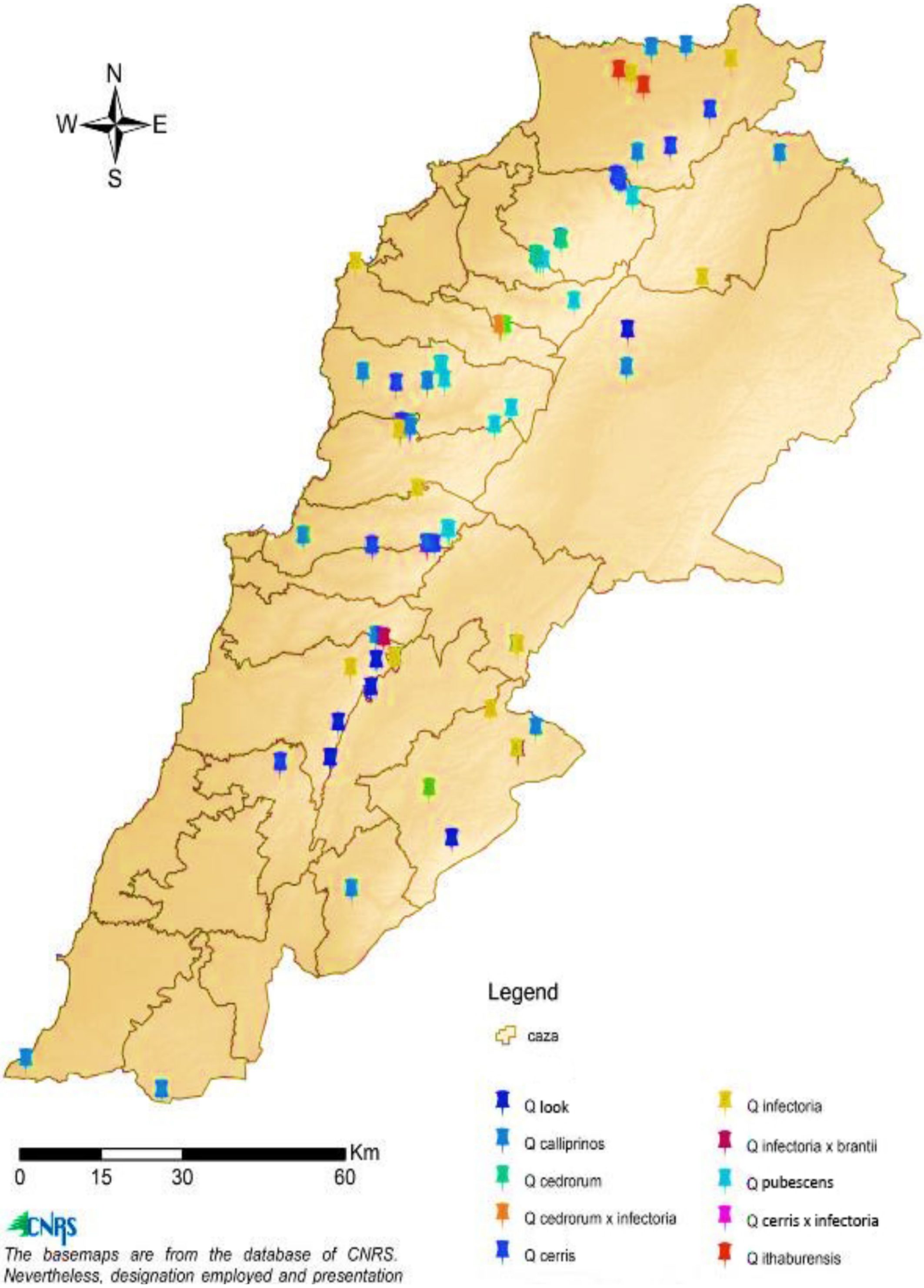

Figure 1. Distribution of the sampled sites with oak species in Lebanon (major points are only shown for visibility).

isohyets, and therefore 2 values covering the precipitation range within a site were obtained: *P1* and *P2* for the lowest and highest values, respectively. Consequently, 2 values for Q were calculated for each site: *Q1* and *Q2.*

In addition, we used the climagram of Emberger that allows one to distribute oak species according to bioclimatic zones by combining on a chart the values of Emberger's quotient (*Q*) and the winter variant (*m*) (Quezel and

Table 1. List of parameters used with their description and source of data.

Parameter	*Description*	*Source*
A	Aspect (degrees)	Field measurement
DtS	Distance to sea (m)	GIS
M	Maximal temperature average of the warmest month (°C)	GIS/weather station
m	Minimal temperature average of the coldest month (°C)	GIS/weather station
MR	Mother rock type	GIS/geological map
MY	Maximal temperature average of 3 years	Weather station
my	Minimal temperature average of 3 years	Weather station
P	Precipitation value (mm)	closest weather station
P1	Precipitation value of the lowest isohyet (mm)	GIS/precipitation map
P2	Precipitation value of the highest isohyet (mm)	GIS/precipitation map
Q	Emberger's quotient value	closest weather station
Q1	Emberger's quotient value	based on *P1 (Q min)*
Q2	Emberger's quotient value	based on *P2 (Q max)*
S	Slope (%)	Field measurement
SD	Soil depth (in classes of 10 cm)	Field measurement
Tar	Temperature annual range	This work
X	Longitude (decimal degrees)	Field measurement
Y	Latitude (decimal degrees)	Field measurement
Z	Altitude (m)	Field measurement

Barbéro, 1985; Barbéro et al., 1992; Abi Saleh et al., 1996; Dufour-Dror and Ertas, 2004) based on the data retrieved from the represented meteorological stations (Figure 2).

In order to understand the major factors affecting the distribution of oak species in Lebanon, discriminant factor analysis (DFA) was conducted to extract those environmental variables that maximize the variance among the studied species. Seven acknowledged taxa plus 3 hybrids were analyzed. *Q. brantii* × *infectoria* was excluded from the analysis because a single station was found for this hybrid. The present analysis will use a multivariant approach for multiple species rather than single species analysis, due to the limited area of occupancy of some species, which does not allow robust statistical analysis.

A correlation matrix was computed from the original dataset, which included continuous and categorical variables. Intraclass covariance matrixes were additionally done to determine the relative amounts of differences retrievable among the sites belonging to a single species, to estimate variance for multiple dimensions datasets. The robustness of the assessed distances among species was further tested by the Fisher coefficients and their relative P-values. Finally, the coefficients of the canonical discriminant functions, the eigenvalues of each environmental variable, the barycenters scores, and the a priori/a posteriori classification with the probability of affinity were calculated, using SPSS 17.0 and XLSTAT 5.03 add-in for Microsoft Excel.

3. Results

The variance within the sampled species, thus within their niches, was retrieved from DFA by using a dimensional reduction of the original dataset; the first 2 linear uncorrelated variables (namely F1 and F2) explain 63.9% of the cumulative difference among species (Figure 3). On the other hand, the DFA detected a reduced number of original variables that maximize the variance among species (Table 2; Figure 4). In fact, our findings gave high eigenvalues scores to some variables that are positively or negatively correlated with the groups defined by DFA (Table 2; Figure 4). This was mostly reflected in Table 2, which shows that the major factors (F1 axis) affecting species distributions are climatic parameters related to minimal winter temperature or winter variant (*m*, *my*), maximal temperature of the hottest month (*M*), minimal and maximal precipitation isohyets (*P1*, *P2*) as well as elevation (which strongly affects both temperature and precipitation). The influence of environmental factors on the local scale contributes to a lesser extent (F2 axis), with factors such as the amount of rainfall retrieved from local stations (*P*), and volcanic and deep soils.

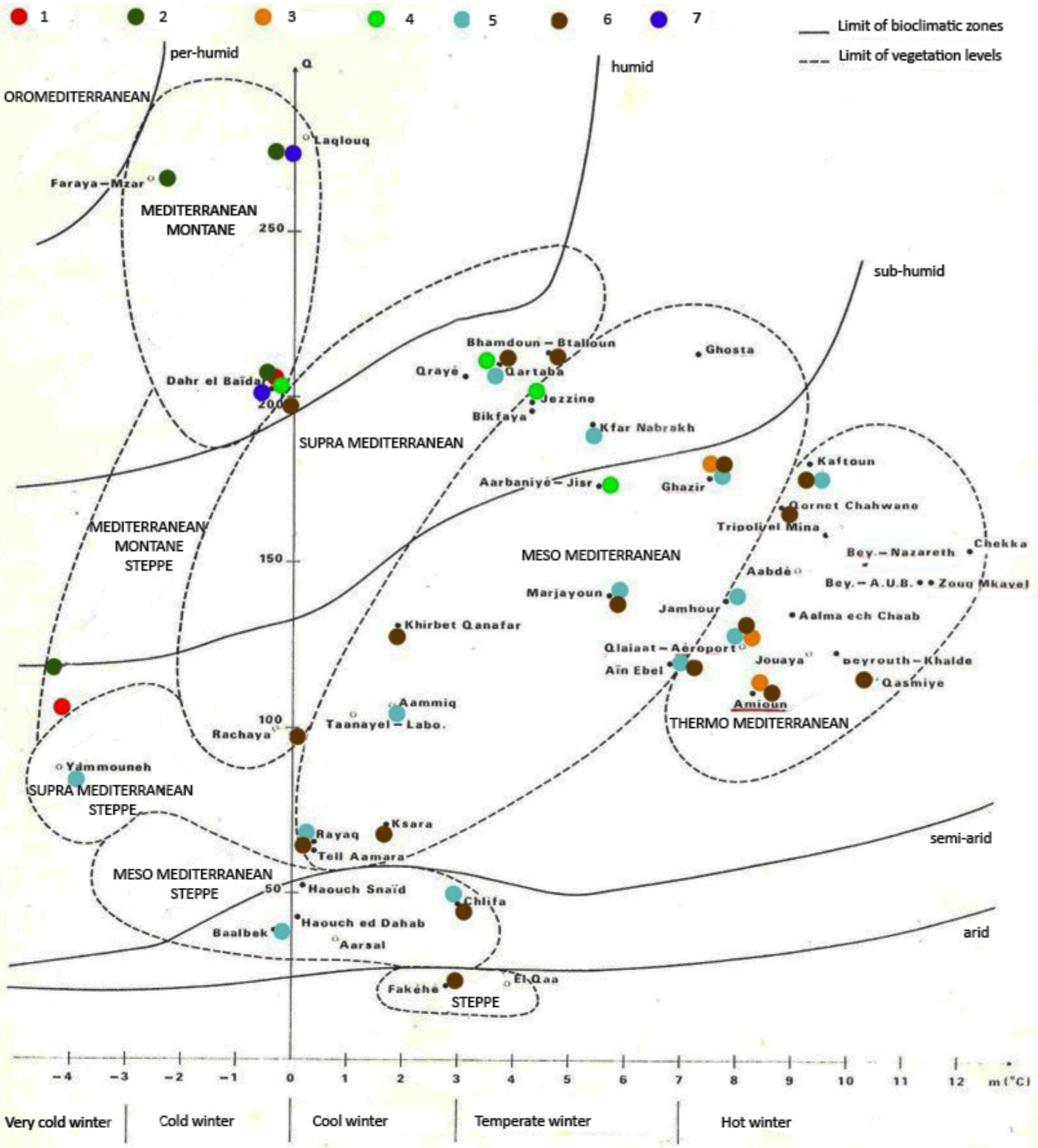

Figure 2. Distribution of oak sampling points according to the climagram of Emberger *(Quercus look:* 1; *Quercus pubescens:* 2; *Quercus ithaburensis: 3; Quercus cerris: 4; Quercus infectoria: 5; Quercus calliprinos: 6; Quercus cedorum:* 7).

It is evident that even data of minimal temperature of the coldest month (e.g., *my*) for a 3-year period are still valid for such analysis, even if temperatures are slightly higher than those of the long period averages (*m*). Conversely, for temperature averages of the hottest month, *My* values influence species distribution less when compared to *M*. This could be related to the methodology of extrapolating temperature data in the short term from different meteorological stations, and to the high variability between *My* and *M* values.

By comparing Figure 3 with Figure 4, species can be distributed according to the winter variant (*m, my*), being a major climatic parameter contributing to species distribution. *Q. pubescens* Willd., *Q. infectoria* × *cedrorum*, *Q. cedrorum* Kotschy, and to a lesser extent *Q. look* Kotschy are negatively related to these parameters.

Maximal temperature averages of the hottest month are also a major contributor to the variance in species distribution. *Q. calliprinos* Webb and *Q. ithaburensis* Decne. are the most positively affected by high temperatures,

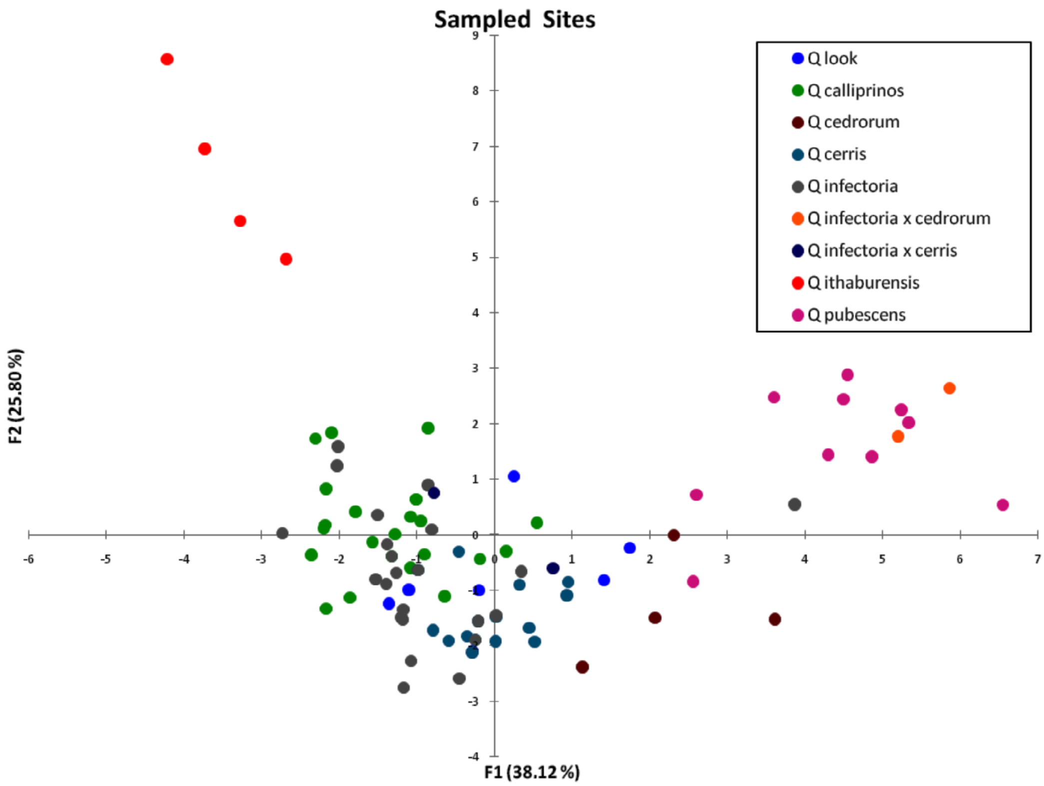

Figure 3. Factor scores of the sample sites plotted on the 2 main functions of DFA.

whereas *Q. pubescens* Willd. and *Q. cedrorum* Kotschy are negatively affected by this parameter.

Precipitation parameters (*P1*, *P2*) constitute the third major climatic factor affecting species distribution according to a bioclimatic range.

Elevation is the major parameter affecting oaks species' distribution in Lebanon. An altitudinal gradient could be drawn with *Q. ithaburensis* Decne. at the lowest altitudes, followed by *Q. calliprinos* Webb, *Q. infectoria* Olivier, *Q. cerris* L., *Q. look* Kotschy, *Q. cedrorum* Kotschy, and *Q. pubescens* Willd. (Figures 3 and 5). All other orographic and geographic parameters are minor contributors to the distribution of species.

Deep soils (SD 30–40) and soils developed on volcanic mother rocks (MR volcanic and mixed calcareous with volcanic) are secondary contributors (F2 axis) to oak species distribution in Lebanon (Table 2; Figure 3). In view of this, *Q. ithaburensis* Decne. is strongly related to mature volcanic soil types (depth between 30 and 40 cm) and it strongly differs from the other species (Figures 3 and 4).

However, descriptive statistics allowed us to characterize the species' biogeographic amplitude for the sampled populations (Table 3). Species located at lower and higher elevations (respectively *Q. ithaburensis* Decne., *Q. look* Kotschy, *Q. cedrorum* Kotschy, and *Q. pubescens* Willd.) have the most restricted altitudinal range, and those on middle altitudes a wider range (*Q. calliprinos* Webb, *Q. cerris* L., and *Q. infectoria* Olivier).

A similar observation is worth mentioning regarding distance to the sea (*DtS*), where *Q. cedrorum* Kotschy, *Q. cerris* L., *Q. ithaburensis* Decne., and *Q. pubescens* Willd. have restricted ranges and are closer to the sea when compared to *Q. calliprinos* Webb, *Q. infectoria* Olivier, and *Q. look* Kotschy, which have wider ranges and can reach distant locations inland (Table 3).

Figure 5 shows the relative amounts of differences within each species (black circles) centered on the barycenters, meaning a dispersion index of sites belonging to the same species around its theoretical center. These values are also partially affected by the sample size, so that the magnitude of circles such as for *Q. cerris* × *infectoria* and *Q. infectoria* × *cedrorum* should be taken carefully.

Table 4 explains whether the realized niches of the different oak species are significantly distant from each other. In other words, we study the degree of similarity in the abiotic environmental factors affecting species distribution. The more significant distance (P-values) in environmental factors affecting species distribution, the higher the probability that their niche is separated. Fisher's linear discriminant rule pointed out that the linear combination of predictors was not able to statistically

Table 2. Eigenvalues of the correlation matrix for the original set of variables on the 2 main components, F1 and F2, of the determinant factor analysis. Classes of categorical and nominal variables are shown separately in this table. Symbols for the parameters are described in Table 1. Bold values indicate the parameters that mostly maximize the variance explained by F1 or F2.

Parameter	F1	F2
Z	**0.6683**	–0.2617
S	0.1344	0.0495
DtS	0.0320	–0.0416
X	0.0307	0.2891
Y	0.0770	0.3197
my	**–0.4502**	–0.0194
My	–0.3240	0.0477
P1	**0.4472**	–0.1056
Q min	0.2499	–0.1308
P2	**0.4596**	–0.1026
Q max	0.2320	–0.1264
P	0.0289	**–0.4023**
M	**–0.6999**	–0.0699
m	**–0.7319**	0.0674
Tar	0.1071	–0.1209
Q	–0.0255	–0.3143
SD (0–10)	–0.1423	–0.0895
SD (10–20)	–0.0943	–0.1274
SD (20–30)	0.3091	–0.1470
SD (25–35)	0.3147	0.0433
SD (30–40)	–0.2640	**0.4270**
A (North)	0.0653	0.0023
A (Northeast)	–0.1033	–0.0077
A (East)	–0.1034	–0.1019
A (Southeast)	–0.0199	–0.0105
A (South)	–0.0408	0.3588
A (Southwest)	0.1250	0.0843
A (West)	0.1588	–0.1006
A (Northwest)	–0.0575	–0.2116
MR (calcareous red)	0.0429	–0.1892
MR (calcareous red-dolomite)	0.1219	–0.0917
MR (volcanic)	–0.3442	**0.4673**
MR (mixed calcareous red and sandy)	–0.0880	–0.0298
MR (calcareous white)	–0.0545	–0.0676
MR (mixed calcareous red and white)	0.0452	–0.1471
MR (sandy)	0.1266	–0.0904
MR (mixed calcareous and volcanic)	–0.1964	**0.4677**
MR (moraine)	0.2499	0.1096

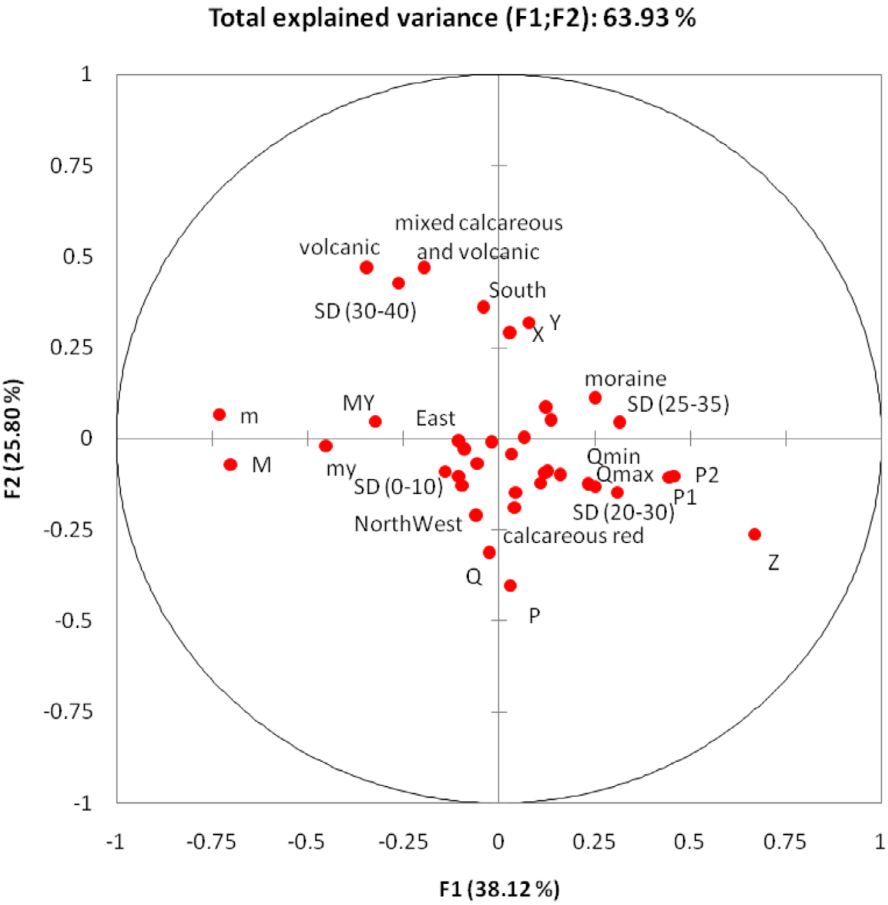

Figure 4. Eigenvalues of the biogeographic parameters plotted on the DFA graph. For clarity of the plot, not all the parameters are labeled.

separate some taxa, for example the hybrids *Q. cerris* × *infectoria* and *Q. infectoria* × *cedrorum* (Table 4).

The realized niches of *Q. ithaburensis* Decne. and *Q. pubescens* Willd. are strongly distinguished from other taxa. The realized niche of *Q. calliprinos* Webb is also significantly distant from all species, except for *Q. look* Kotschy, *Q. cerris* × *infectoria*, and *Q. infectoria* Olivier. The realized niche of *Q. infectoria* Olivier is overlapping and close to those of most species, except *Q. look* Kotschy, *Q. ithaburensis* Decne., and *Q. pubescens* Willd.

It is also evident that *Q. cerris* L., *Q. cedrorum* Kotschy, and *Q. look* Kotschy have no significant difference between their respective realized niches.

4. Discussion

4.1. Major abiotic environmental factors affecting oak distribution in Lebanon

This investigation showed that climate is the major driving factor affecting oak species' distribution in Lebanon, where temperature (minimal and maximal) and precipitation range are the major drivers shaping the distribution pattern of most oak species. Elevation is an important biogeographical factor, yet it is highly affecting both temperature and precipitation, and contributes in amplifying the differences in the realized niche of oak species, leading to a possible altitudinal zonation of the vegetation (Abi Saleh, 1982; Quezel and Barbéro, 1985).

Climate is known as the major factor affecting the geographical distribution of plant species in general (Cox and Moore, 1999; Lugo et al., 2015), while climate extreme events such as drought combined with the high demographic pressure in the Mediterranean region have contributed to increased pressure on natural ecosystems through forest fire, grazing, cutting, and habitat fragmentation by a long history of human activities (Quezel and Bonin, 1980; Khury et al., 2000; Hajar et al., 2009; Jomaa et al., 2009; Touchan et al., 2014). As a result, orographic factors (slope, aspect) and soil characteristics are affecting species distribution only at local level, and do not constitute a major driving force in the distribution of species (Dufour-Dror and Ertas, 2004).

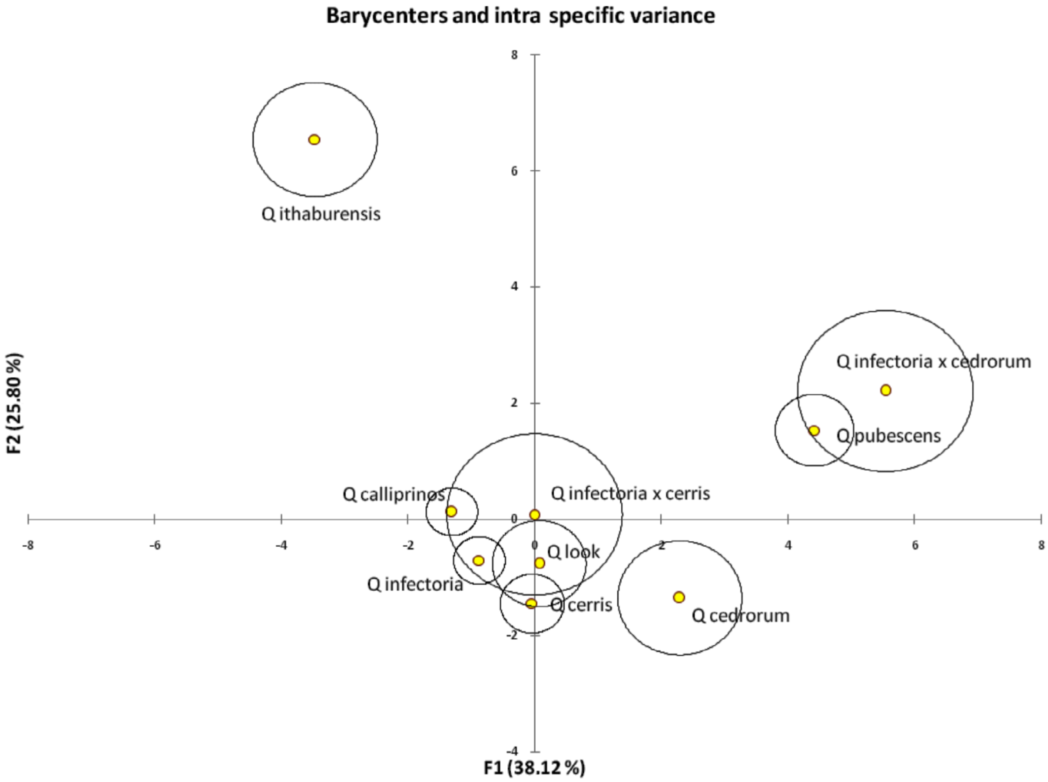

Figure 5. Coordinates of the barycenters of the study oaks (yellow dots) and relative dispersion of the populations around each barycenter (black circles).

4.2. Bioclimatic analysis

Winter variant (*m*) and maximal temperature of the hottest month (*M*) are major factors affecting the distribution of oaks in Lebanon. Species normally found further north in latitude or at higher altitude such as *Q. pubescens* Willd., *Q. cedrorum* Kotschy, and *Q. infectoria* × *cedrorum* are negatively affected by temperature.

An increase in precipitation affects positively the distribution of *Q. cedrorum* Kotschy and to a lesser extent *Q. cerris* L. as these relic species are normally found in northern Mediterranean countries and require humid conditions with average annual rainfall above 1100 mm, and a range between 800 and 1400 mm (Abi Saleh et al., 1976; Quezel and Barbéro, 1985; Hedge and Yaltirik, 1994; Kargioglu, 2011). Conversely, *Q. ithaburensis* Decne. and *Q. calliprinos* Webb are not significantly affected by rainfall amount, as the former species is known to withstand long periods of drought (Dufour-Dror and Ertas, 2004; Ortiz et al., 2010). Yet, the higher the precipitation, the higher is the diversity of observed oak taxa in Lebanon.

The minimal average temperature of the coldest month over a 3-year period (*my*) seems to be significant and allows us to calculate the winter variant for a shorter period in order to discriminate between species, and overcome the lack of continuous meteorological data.

Although Emberger's quotient is not found to be a major climatic parameter shaping the distribution of oak taxa, it remains a necessary parameter along with the winter variant to display on a climagram of the bioclimatic range of plants according to bioclimatic zones and vegetation levels. By pointing out Q and winter variant (*m*) values of each point of distribution of oak species on the climagram of Emberger as adapted to Lebanon by Abi Saleh et al. (1976) as illustrated in Figure 2, we confirm our results in relation to precipitation and temperature parameters:

– *Q. calliprinos* Webb has a large plasticity allowing this species to grow everywhere except in bioclimatic zones with cold and very cold winter variants. Its exclusive presence in the steppe (arid) zone is additional information that was not described by previous authors in Lebanon (Abi Saleh et al., 1976, 1996).

– *Q. cedrorum* Kotschy is distributed in the perhumid bioclimatic zone with cold and very cold winter variants (Mediterranean montane vegetation level), confirming the findings of previous works (Quezel and Bonin, 1980; Abi Saleh et al., 1996; Kargioglu et al., 2011).

– *Q. cerris* L. is essentially distributed in the Supra Mediterranean vegetation level, and also in the Mediterranean Mountain and Meso Mediterranean levels, within the humid bioclimatic zone with cold,

Table 3. Descriptive statistics of the biogeographic range of oak species investigated. For continuous variables, minimum and maximum values are given in brackets, excepted for those species represented by only 2 sites. For categorical and nominal variables, the frequency number per class (in percentage) is reported.

Parameter	*Q. look*	*Q. calliprinos*	*Q. cedrorum*	*Q. cerris*	*Q. infectoria*	*Q. infectoria × cedrorum*	*Q. cerris× infectoria*	*Q. ithaburensis*	*Q. pubescens*
Z	1654 (1516–1808)	943 (74–1745)	1654 (1450–1766)	1280 (664–1634)	1099 (177–1811)	1756	1452	325 (182–592)	1755 (1591–1902)
S	36.6 (20–60)	27.3 (5–60)	30.5 (10–60)	33.2 (0–90)	20.7 (5–45)	31.0	12.5	31.2 (5–65)	32.8 (20–60)
DtS (km)	32.8 (23.0–50.0)	21.4 (1–51)	20.4 (17–23.5)	17.2 (9.2–27)	24.0 (1–49.5)	23.5	16.0	18.3 (12–29)	22.5 (17.2–28.3)
X	35.8103 (35.64–36.13)	35.8391 (25.14–36.4)	35.9421 (35.8–36.1)	35.9259 (35.6–36.3)	35.8686 (35.3–36.3)	35.9267	35.7861	36.1932 (36.1–36.3)	35.9481 (35.82–36.1)
Y	33.6829 (33.44–34.20)	33.9662 (33.06–34.6)	34.2513 (34.1–34.3)	34.1788 (33.5–34.5)	33.9576 (33.1–34.6)	34.2083	33.9662	34.5956 (34.5–34.6)	34.1564 (33.9–34.38)
my	7.2 (5.1–10.1)	9.2 (4.2–15.8)	6.9 (4.6–10)	7.7 (4.6–10.5)	8.8 (4.2–15.9)	5.4	6.5	9.6 (8–10.4)	5.1 (1.9–11.5)
MY	26.9 (25.6–28.6)	26.4 (23.6–29.4)	24.8 (23.6–26)	25.5 (23.5–27.7)	26.3 (23.6–29.5)	25.2	26.4	26.6 (25.7–27.2)	25.3 (23.4–28.1)
P1	1028 (600–1200)	943 (300–1400)	1200 (1100–1400)	1107 (800–1400)	961 (300–1400)	1200	1300	800 (800–800)	1240 (900–1400)
Q min	179.9 (111–215)	192.8 (50–287)	235.2 (202–301)	216.5 (168–286)	190.7 (60–287)	210.1	231.9	161.9 (155–170)	220.9 (144–342)
P2	1128 (700–1300)	1030 (400–1400)	1275 (1200–1400)	1207 (900–1400)	1022 (400–1400)	1300	1350	900 (900–900)	1310 (1000–1400)
Q max	197.4 (129–233)	210.8 (67–315)	249.3 (221–301)	236.0 (186–301)	203.3 (80–315)	227.6	239.7	182.1 (175–191)	233.4 (160–368)
P	1203 (979–1371)	1032 (191–1491)	1396 (1371–1471)	1438 (1295–1471)	1058 (412–1471)	899	1421	877 (782–1099)	993 (899–1371)
M	28.2 (23.4–34.6)	29.3 (23.4–34.2)	24.5 (23.4–28)	27.6 (23.4–31.1)	29.8 (22.8–36.1)	22.8	25.7	30.5 (29–32.3)	22.9 (22.8–23.4)
m	−2.0 (−0.4–4.20)	4.6 (−0.4–10.5)	0.6 (−0.4–3.7)	3.3 (−0.4–5.5)	3.3 (−4.2–10.3)	−4.0	1.6	8.0 (7.7–8.3)	−3.3 (−4.0–−0.4)
Tar	30.2 (23.8–38.8)	24.8 (19.5–32.5)	23.9 (23.8–24.3)	24.3 (23.5–25.6)	26.4 (20.2–38.8)	26.8	24.0	22.5 (21.3–24)	26.2 (23.8–26.8)
Q	153.2 (88–202)	149.3 (22–214)	204.3 (202–210)	205.5 (174–209)	147.1 (39–214)	118.8	206.1	134.6 (111–177)	135.5 (119–202)
SD 0–10	43%	30%	25%	0%	9%	0%	0%	0%	0%
SD 10–20	43%	57%	25%	27%	30%	0%	50%	0%	30%
SD 20–30	14%	9%	25%	60%	35%	50%	50%	0%	60%
SD 25–35	0%	4%	0%	13%	26%	0%	0%	100%	10%
SD 30–40	0%	0%	25%	0%	0%	50%	0%	0%	0%
A-NE	14%	9%	0%	20%	22%	0%	0%	25%	10%
A-E	14%	9%	0%	7%	9%	0%	0%	0%	0%

Table 3. (Continued).

A-NW	14%	9%	0%	33%	26%	0%	0%	0%	10%
A-W	43%	17%	75%	7%	9%	50%	0%	0%	10%
A-S	14%	30%	0%	0%	4%	50%	50%	50%	20%
A-SE	0%	9%	0%	0%	13%	0%	0%	0%	10%
A-N	0%	13%	25%	33%	17%	0%	50%	25%	30%
A-SW	0%	4%	0%	0%	0%	0%	0%	0%	10%
MR-calcareous red	71%	53%	50%	40%	48%	100%	0%	0%	30%
MR-calcareous red dolomite	29%	22%	25%	26%	22%	0%	100%	0%	40%
MR-volcanic	0%	17%	0%	0%	9%	0%	0%	75%	0%
MR-mixed calcareous red and sandy	0%	4%	0%	0%	4%	0%	0%	0%	0%
MR-calcareous white	0%	4%	0%	7%	0%	0%	0%	0%	0%
MR-mixed calcareous red and white	0%	0%	25%	7%	4%	0%	0%	0%	0%
MR-sandy	0%	0%	0%	20%	13%	0%	0%	0%	20%
MR-mixed calcareous and volcanic	0%	0%	0%	0%	0%	0%	0%	25%	0%
MR-moraine	0%	0%	0%	0%	0%	0%	0%	0%	10%

cool, and temperate winter variants. Previous works never mentioned the presence of this species in the Meso Mediterranean level in Lebanon (Abi Saleh et al., 1976, 1996) although Quezel and Bonin (1980) mentioned this possibility in the east Mediterranean basin. *Q. cerris* is comparable to *Q. cedrorum* Kotschy by its humidity requirement (Ugurlu et al., 2012).

– *Q. infectoria* Olivier is another species showing high plasticity that could be differentiated from *Q. calliprinos* Webb by its limitation to thrive in arid zones and the possibility to tolerate bioclimatic zones with cold and very cold winters. Consequently, it is the exclusive oak species thriving in Supra Mediterranean presteppe vegetation level in Lebanon.

– *Q. ithaburensis* Decne. is exclusively found in the Thermo Mediterranean and Meso Mediterranean vegetation levels (subhumid zone with hot winter variant). This work is considered the first description of this species in Lebanon, while our results are consistent with the findings of previous investigations (Al Eisawi, 1996; Danin, 2001; Dufour-Dror and Ertas, 2004).

– *Q. look* Kotschy is distributed in both Mediterranean montane and Mediterranean montane presteppe vegetation levels (in humid and subhumid bioclimatic zones with cold and very cold winter variant). Our results show that the species can thrive not only in presteppe conditions but also in more humid conditions on the western slopes of southern Mount Lebanon, in association with *Cedrus libani* (Abi Saleh et al., 1996).

– *Q. pubescens* Willd. is distributed in Mediterranean montane and Mediterranean montane presteppe vegetation levels (in perhumid, humid, and subhumid bioclimatic zones with cold and very cold winter variants). Although it might be similar to *Q. look* Kotschy, this species shows higher Q values and a wider range, allowing it to thrive in more humid conditions. This could also be explained by the different origins of both species, where *Q. look* Kotschy is confined to the Near East while *Q pubescens* Willd. has a much broader area of distribution and is capable of thriving in cold but more humid conditions (Quezel and Bonin, 1980; Hedge and Yaltirik, 1994; Menitsky, 2005; Blondel et al., 2010). Based on humidity requirements,

Table 4. Fisher's distance matrix (lower triangle) with associated P-values (upper triangle) for the oaks species investigated in this study. Bold values in the upper triangle show significant distances among species at $\alpha < 0.05$ level.

	Q. look	*Q. calliprinos*	*Q. cedrorum*	*Q. cerris*	*Q. infectoria*	*Q. infectoria* × *cedrorum*	*Q. infectoria* × *cerris*	*Q. ithaburensis*	*Q. pubescens*
Q. look	--	0.2643	0.1038	0.1728	**0.0451**	**0.0427**	0.9850	**<0.0001**	**0.0005**
Q. calliprinos	1.2144	--	**0.0113**	**0.0139**	0.3718	**0.0073**	0.9849	**<0.0001**	**<0.0001**
Q. cedrorum	1.4814	2.0421	--	0.0789	**0.0131**	0.5870	0.5303	**<0.0001**	**0.0059**
Q. cerris	1.3406	1.9923	1.5542	--	0.4561	**0.0111**	0.9890	**<0.0001**	**<0.0001**
Q. infectoria	1.6983	1.1033	2.0071	1.0298	--	**0.0056**	0.9838	**<0.0001**	**<0.0001**
Q. infectoria × *cedrorum*	1.7121	2.1508	0.9267	2.0463	2.2177	--	0.3176	**0.0007**	0.6182
Q. infectoria × *cerris*	0.4872	0.4875	0.9704	0.4678	0.4923	1.1561	--	0.0709	0.5044
Q. ithaburensis	3.5394	3.2604	3.8212	4.2466	3.8635	2.7448	1.5822	--	**<0.0001**
Q. pubescens	2.7989	4.7442	2.2033	3.5895	4.3043	0.9030	0.9908	4.7691	--

our results enable us to separate *Q. pubescens* Willd. from *Q. cedrorum* Kotschy in terms of bioclimatic conditions, which was not possible through phytosociologic studies (Abi Saleh et al., 1976, 1996).

4.3. Biogeographic analysis

The altitudinal gradient of species is consistent with the bioclimatic drivers, namely the winter variant and Q as shown in the Emberger climagram (Figure 2). In view of this, our results confirm the ecological descriptions already available in the literature (Zohary, 1961; Quezel and Bonin, 1980; Abi Saleh, 1982; Abi Saleh et al., 1996; Al Eisawi, 1996; Danin, 2001; Blondel et al., 2010).

It is worth mentioning that despite the fact longitude (X), latitude (Y), and distance to the sea (DtS) are not significant contributors to species distribution at national scale (Table 2), Lebanon is considered the western and northern limit of *Q. look* Kotschy, and the southern limit of *Q. cedrorum* Kotschy, *Q. cerris* L., and *Q. pubescens* Willd., which are represented through endemic subspecies or varieties adapted to the local environment in isolated stands. Consequently, this isolation of oak species at edge conditions explains the restricted range of species growing at higher altitudes, and relatively at a short distance to the sea where both cool temperatures and relative humidity are ensured.

4.4. Soil analysis

Soil type and depth are important parameters to add, in order to enable higher accuracy in species distribution pattern as well as vegetation series (Quezel and Barbéro, 1985). In Lebanon *Q. ithaburensis* Decne. is strictly developed on volcanic mature soils, whereas it may grow on both chalky mother rock and basaltic soils, and in alluvial deep soils in the Jordan Valley, Golan, and in Sharon plain, however (Zohary, 1961; Quezel and Barbéro, 1985; Al Eisawi, 1996; Danin, 2001; Dufour-Dror and Ertas, 2004).

The confinement of *Q. ithaburensis* Decne. to volcanic mature soils in Lebanon in a separate niche from other oak species incites further syntaxonomic investigation in order to assess a new potential plant association in Lebanon.

4.5. Realized niche of oak species and their overlapping

The realized niches retrieved from the investigated sites pointed out that most of them are overlapped (cf. min/max range in Table 3 and Supplementary Materials 6-19), due to the plasticity of each species regarding bioclimatic factors and to the marked adaptive traits, a common response to their low dispersal capacity (Petit and Hampe, 2006; Delzon et al., 2013; Gerber et al., 2014; Vessella et al., 2015). Although the area of occupancy of *Q. calliprinos* Webb is overlapping with that of *Q. cerris* L. for example, the significant distance between the realized niches of both species is due to the difference in the factors affecting their distribution (temperature, precipitation, soil characteristics, etc.). Conversely, *Q. look* Kotschy does not intersect in its area of occupancy with *Q. calliprinos* Webb, yet the major environmental factors affecting the distribution of both species are similar. *Q. cedrorum* Kotschy is geographically distant from *Q. look* Kotschy, as the former is confined to the western slopes of northern Mount Lebanon while the area of occupancy of the latter is located further south and inland. In fact, if the major environmental factors contributing to species distribution are similar in both species (elevation and minimal winter temperatures), other factors of lesser eigenvalues scores contribute to their biogeographical separation (*DtS*, *Q*, and *Tar*).

However, *Q. ithaburensis* Decne. and *Q. pubescens* Willd. can be discriminated from the rest as these species require specific environmental conditions (i.e. volcanic mature soils for the former and high elevation for the latter).

This study enables us to set priorities for the conservation of species with restricted range and limited area of occupancy and realized niche (i.e. *Q. look* Kotschy, *Q. cedrorum* Kotschy, *Q. pubescens* Willd., and *Q. ithaburensis* Decne.) and further update the IUCN red list of oaks (Oldfield and Eastwood, 2007).

Prospective investigations should aim at better understanding the effect of bioclimatic gradient on the morphological variability of different oak species and hybrids, in an attempt to better understand their capacity to adapt to climate conditions, and understand why hybrids would be stabilized in a closer or distant niche from their parents.

Finally, this work can be considered a solid baseline to build upon in order to assess the impact of climate change on the bioclimatic niche of oak species, under different scenarios, at both national and regional scale.

Acknowledgments

This work conducted under the Master of Biodiversity-Management and Conservation of Natural Resources at the Lebanese University, and sponsored by Tannourine Cedar Reserve committee and the Association for the Protection of Jabal Moussa.

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Supplementary Materials

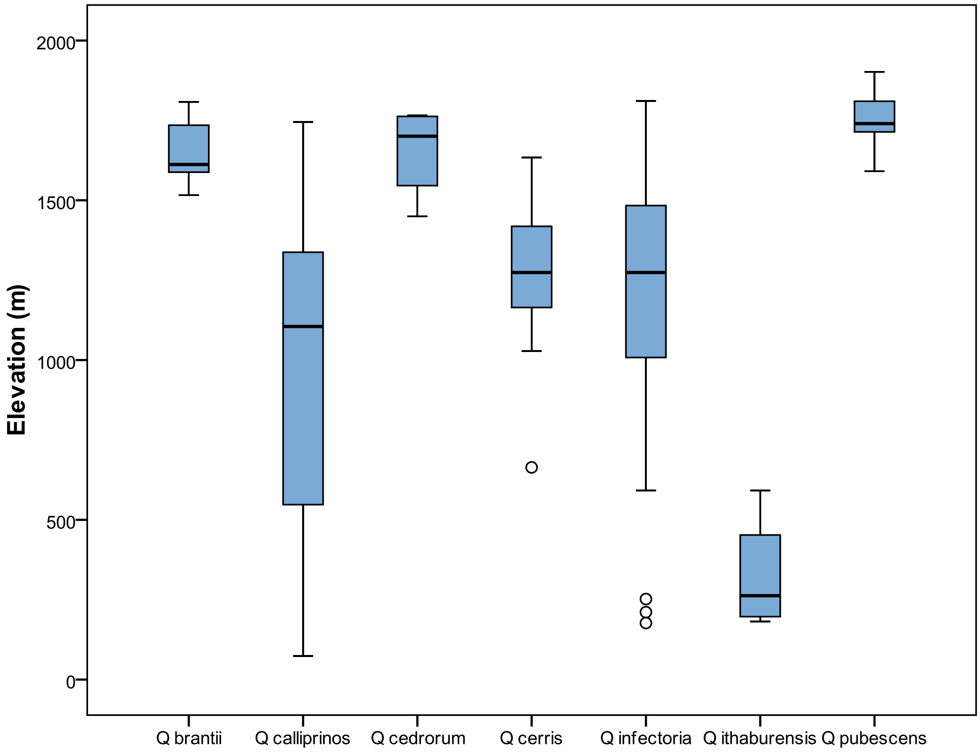

Figure 6. Distribution range of oaks according to elevation. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles are outliers.

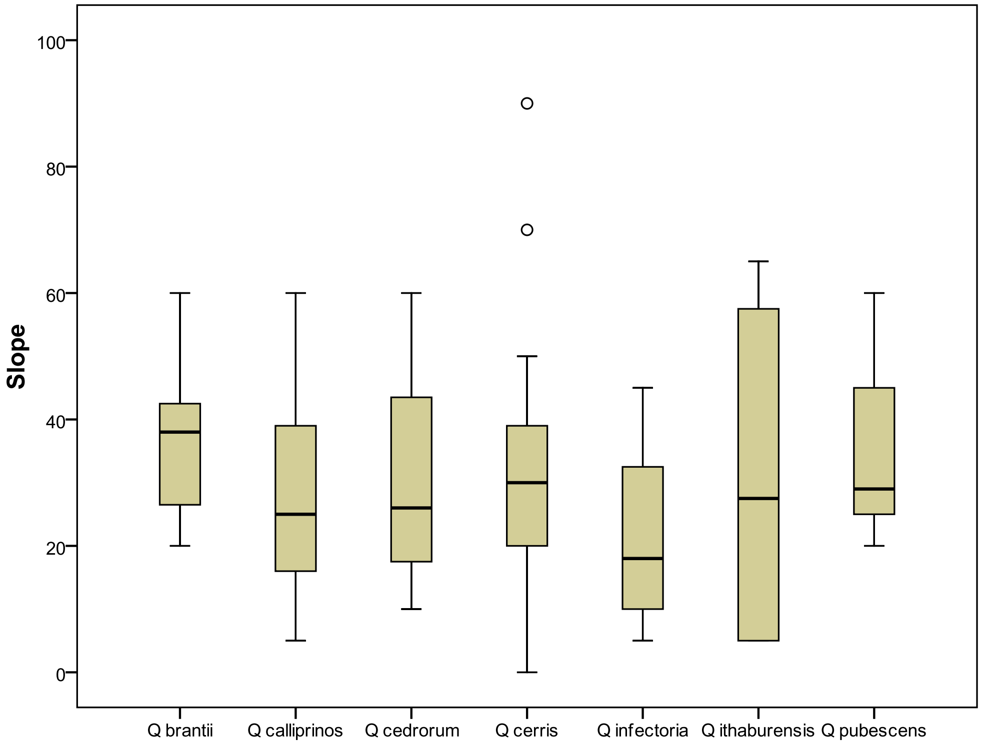

Figure 7. Distribution range of oaks according to slope. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles are outliers.

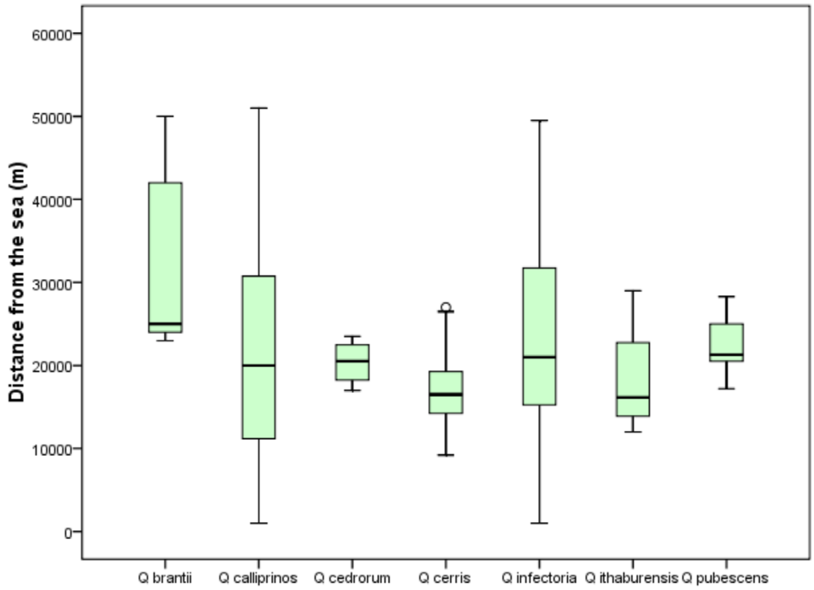

Figure 8. Distribution range of oaks according to distance from the sea. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles are outliers.

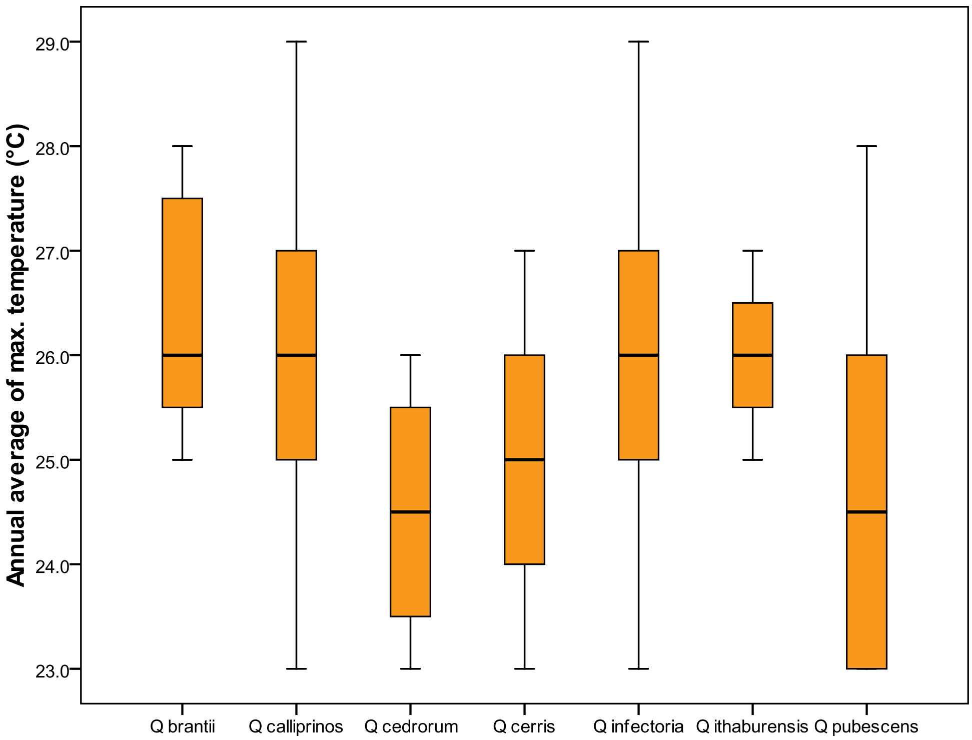

Figure 9. Distribution range of oaks according to the annual average of minimal temperature. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles are outliers.

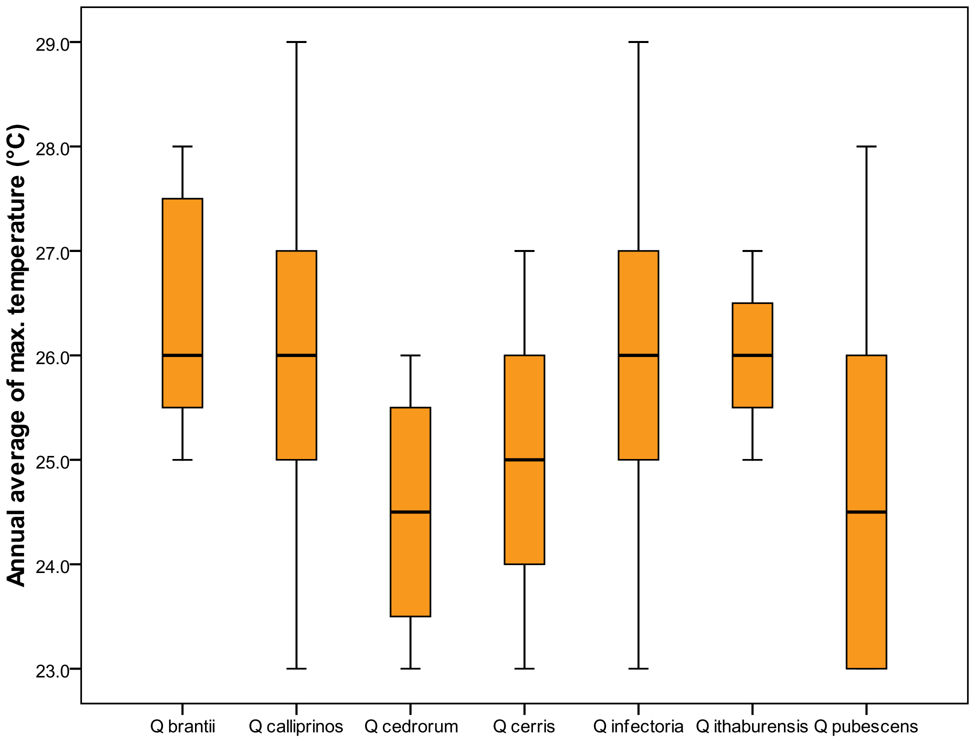

Figure 10. Distribution range of oaks according to annual average of maximal temperature. Boxes show the standard deviation, while bars show the range. The line in the box is the average value.

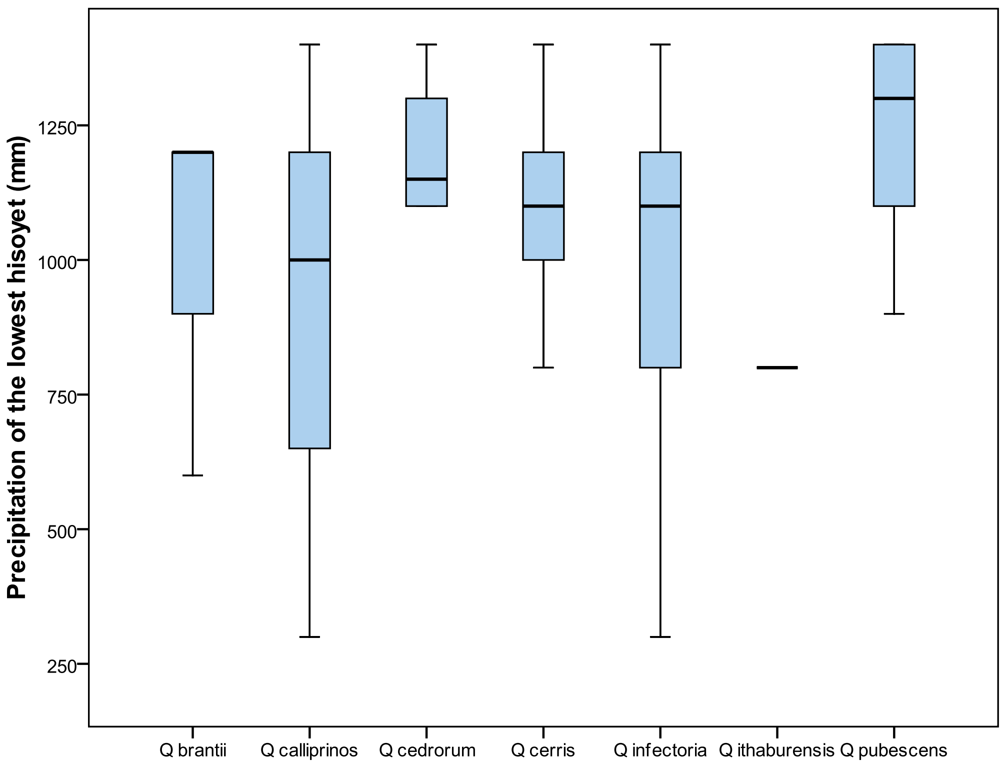

Figure 11. Distribution range of oaks according to precipitation of the lowest isohyet. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. In the case of *Quercus ithaburensis*, all values are similar (within same isohyet range).

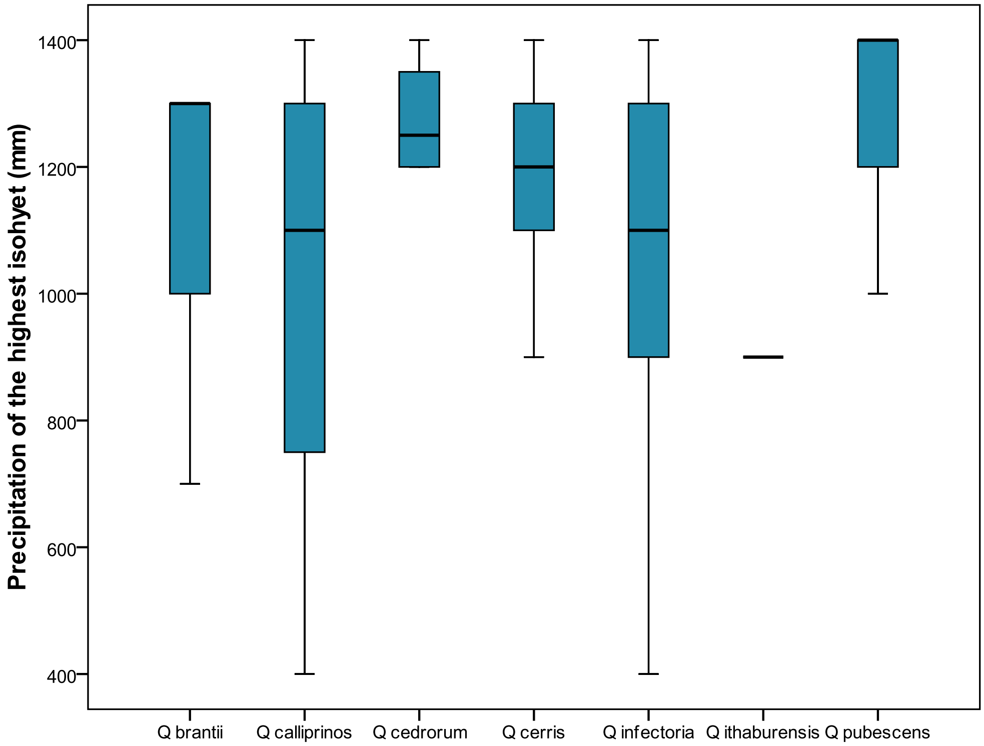

Figure 12. Distribution range of oaks according to precipitation of the highest isohyet. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. In case of *Quercus ithaburensis*, all values are similar (within same isohyet range).

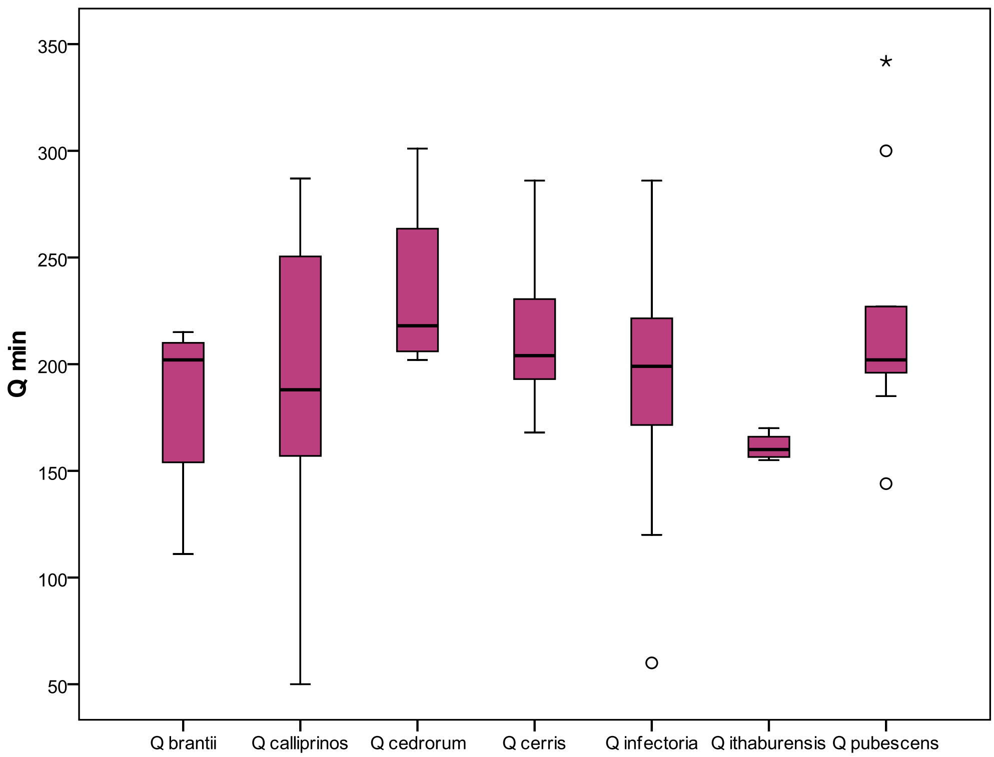

Figure 13. Distribution range of oaks according to Q minimal values. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles are outliers.

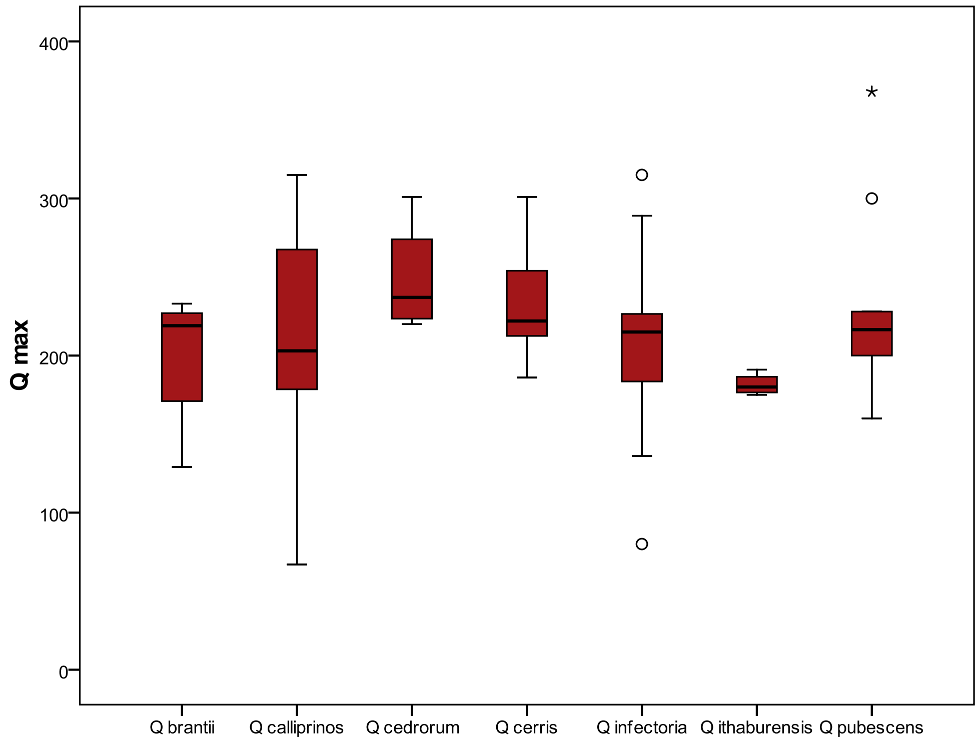

Figure 14. Distribution range of oaks according to Q maximal values. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles are outliers.

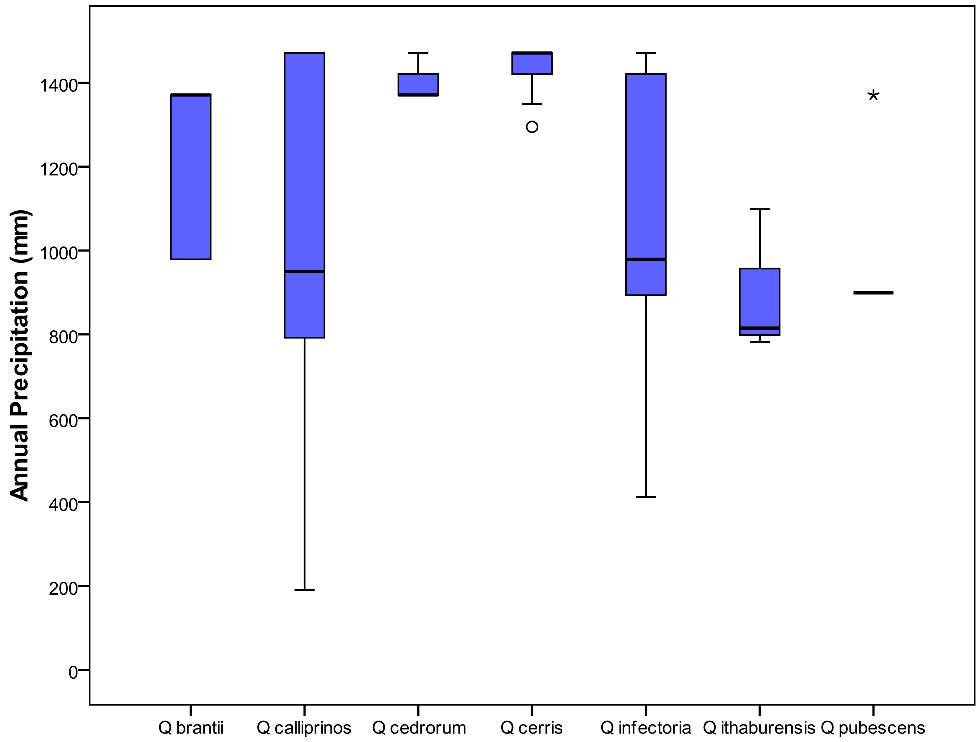

Figure 15. Distribution range of oaks according to the annual average precipitation. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles and star are outliers.

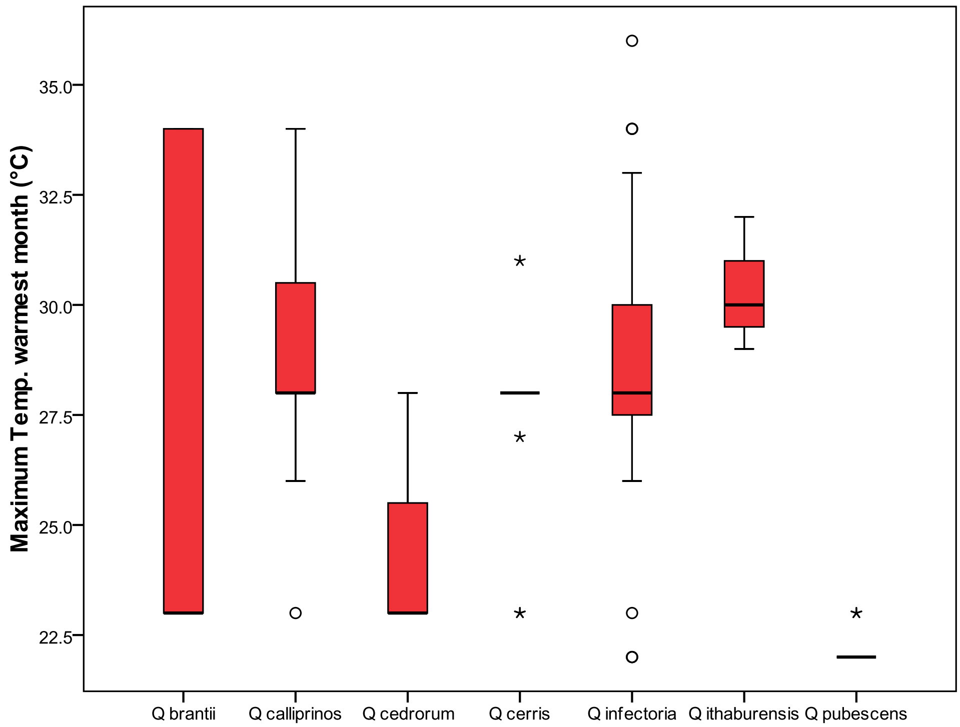

Figure 16. Distribution range of oaks according to the maximum temperature of the warmest month. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles and stars are outliers.

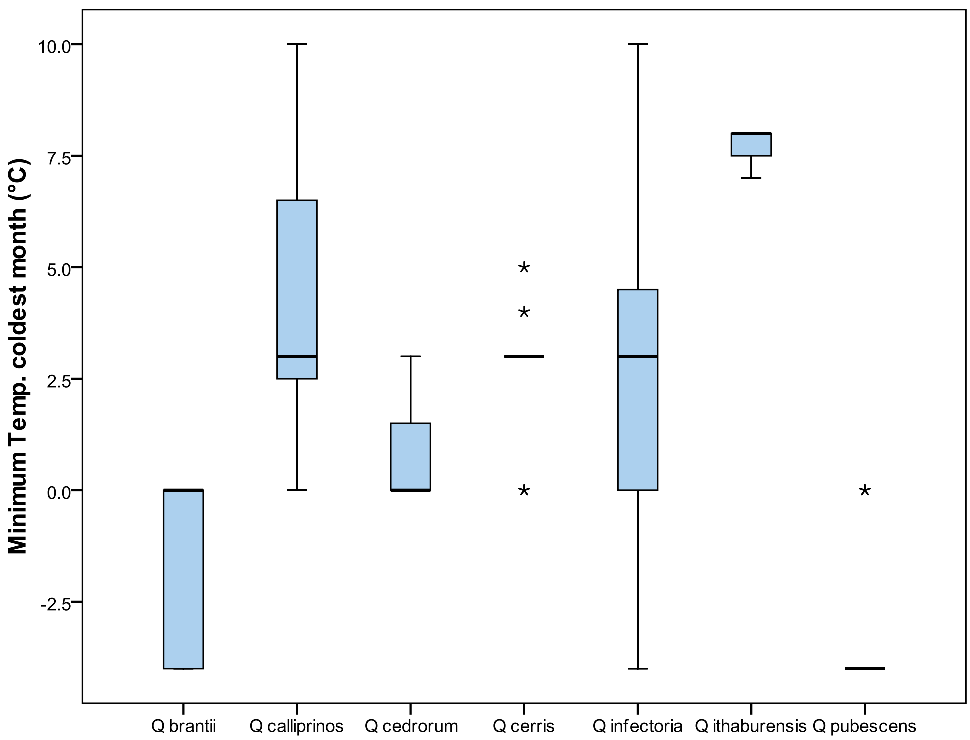

Figure 17. Distribution range of oaks according to the minimum temperature of the coldest month. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Stars are outliers.

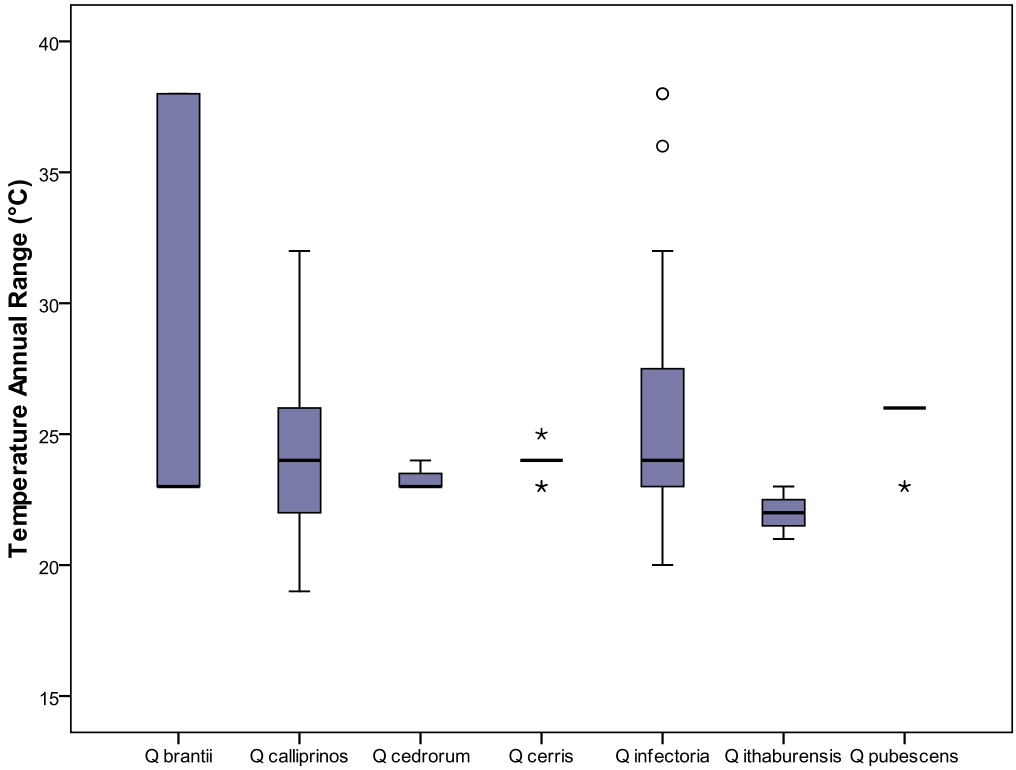

Figure 18. Distribution range of oaks according to the temperature annual range. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles and stars are outliers.

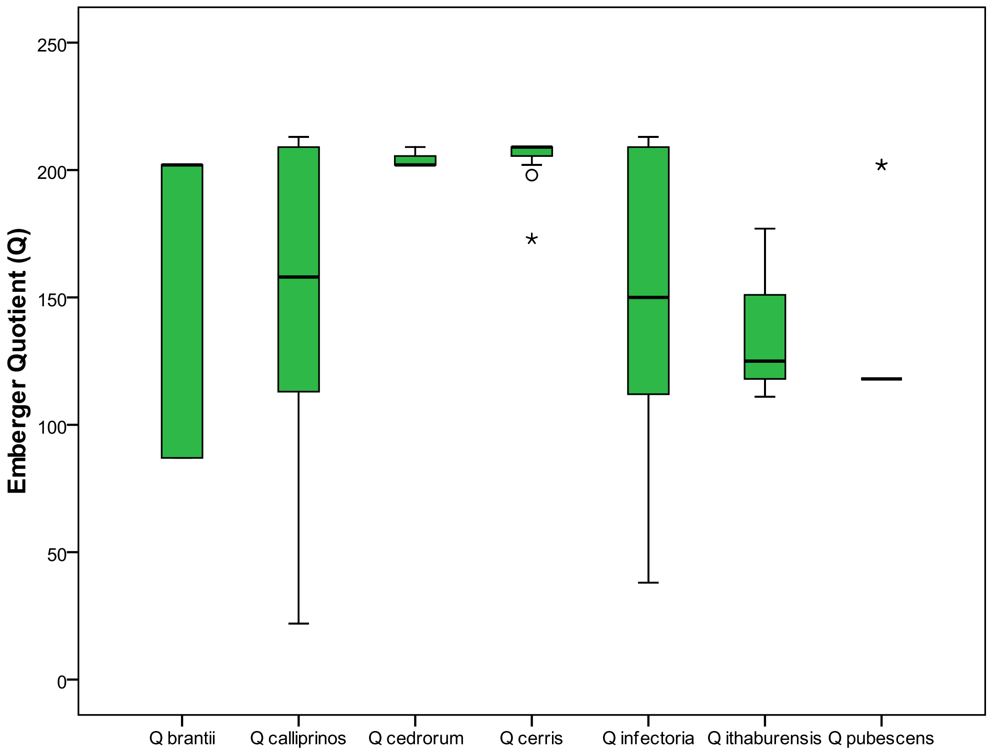

Figure 19. Distribution range of oaks according to Emberger's quotient (Q) values. Boxes show the standard deviation, while bars show the range. The line in the box is the average value. Circles are outliers.