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Ecological and biogeographical analyses of Mediterranean forests of northern Morocco

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ABSTRACT

Mediterranean forests in northern Morocco have been studied. Tree species composition and abundance were investigated in 84 forest sites, distributed throughout the sandstone formation of the Tangier region. The relative abundance of 15 tree and arborescent shrub species was related, by ordination analysis, to altitude, disturbance by fire, and soil fertility. High-elevation forests were dominated by *Cedrus atlantica*, *Quercus pyrenaica* and *Pinus pinaster*. Sacred forests (protected as holy burial places) had a distinct stand structure, and were considered as refuges, for maintaining biodiversity at landscape scale. The evergreen oak *Quercus suber* and the semideciduous *Quercus canariensis* co-dominated the lowland forests. The mean basal area of the studied forests was 34 m² ha⁻¹. The mean trunk size (dbh) for *Q. suber* was 24 cm and for *Q. canariensis* 36.5 cm; in both cases there were indications of declining regeneration at population level. A comparative biogeographical analysis with the equivalent region in southern Spain (separated by the Strait of Gibraltar; 14 km wide), indicated a possible biodiversity loss in the Moroccan forests.

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1. Introduction

The present-day forested landscapes in the Mediterranean Basin have been shaped by the historical management of their resources, and by the impact of human disturbances (Le Houérou, 1981; Marañón and Ojeda, 1998; Grove and Rackham, 2001). Several agents of deforestation were pointed out by Thirgood (1981): forest transformation into croplands and grasslands; timber exploitation for ship building; fuel extraction for domestic use and for mining activities; wars and invasions, fires; and overgrazing. Forests of the Rif Mountains, in northern Morocco, have historically been subjected

to intense disturbances, with a greater threat of deforestation in recent times (Mikesell, 1960; Reille, 1977; Taiqui and Cantarino, 1997; Moore et al., 1998; Benabid, 2000).

The intense human-induced disturbances are reflected in the structure and composition of Moroccan forests. Exceptionally, the areas in the immediate vicinity of tombs or shrines of holy men are considered sacred and respected by local people; they are known as *marabouts* or sacred forests (Mikesell, 1960). They have a distinct structure and species composition, with unusual abundance of long-lived trees, and have been considered remnants of the original forests of the region (Sauvage, 1961; Quézel and Barbéro, 1990; Benabid, 1991).

The region around the Strait of Gibraltar (denominated the Betic-Rifean region) has been identified as a hot-spot of plant diversity within the Mediterranean Basin (Médail and

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Quézel, 1997). Previous studies have compared the biodiversity of the forest understorey on the two sides of the Strait (northern Morocco and southern Spain), and the effects of environmental variables, disturbance, and management on forest biodiversity (Ojeda et al., 1996; Marañón et al., 1999).

Coexisting tree species have different response curves to environmental factors, determined by their genetic and physiological features, their relationships to physico-chemical variables, and their interaction with other forest organisms. However, these potential plant-environment patterns can be much altered by selective management and by natural and human-induced disturbances.

Trees are natural archives, storing past environmental events occurring in the forest. The size of the trunk, the distribution and width of growth rings, and the chemical composition of the wood can be explored as historical records.

The objectives of this study are 1) to analyse the distribution and abundance of the tree species in the forests of northern Morocco, and their relationships with environmental variables; 2) to analyse the forest structure, in particular the stem density, basal area, and trunk size distribution; 3) to evaluate the influence of the forest management on the observed structure and species composition; 4) to determine the level of tree species diversity and biogeographic patterns in the study region; and 5) to make a comparative analysis with equivalent areas in southern Spain, having similar ecological and evolutionary processes, but different management and disturbance regimes.

2. Material and methods

2.1. Study area

Forests occurring on sandstone-derived soils of the Tangier Peninsula, northern Morocco, were studied. The sandstone formation occupies about 1836 km², showing a fragmented pattern (Ojeda et al., 1996). This region is located between 35°00' and 35°55'N and between 5°00' and 6°15'W, faced by the Atlantic Ocean (west), the Mediterranean Sea (east), and the Strait of Gibraltar (north) (see Fig. 1).

The rugged mountains have maximum elevation at the peaks Khezana (1705 m), Bouhachem (1681 m), and Sounna (1603 m). The climate is Mediterranean-type with oceanic influence. The winter is wet and cool, with snow in the mountain summits, and the summer is warm and dry. Mean annual rainfall varies from 494 mm (in the lowlands; Torreta station) to 2169 mm (recorded at the highest mountain station, Bouhachem). Mean annual temperature varies from 15 °C to 19 °C (Ajbilou, 2001).

The Oligo-Miocene sandstone formation originates nutrient-poor, acid soils. These contrast with the general feature of basic soils on limestone, typical of the Mediterranean Basin. Mixed oak forests of evergreen (*Quercus suber*, *Quercus coccifera* and *Quercus rotundifolia*) and semideciduous (*Quercus canariensis* and *Quercus pyrenaica*) species dominate the landscape, occupying about 1168 km² in the four provinces—Tangier, Tetouan, Chaouen and Larache—according to the

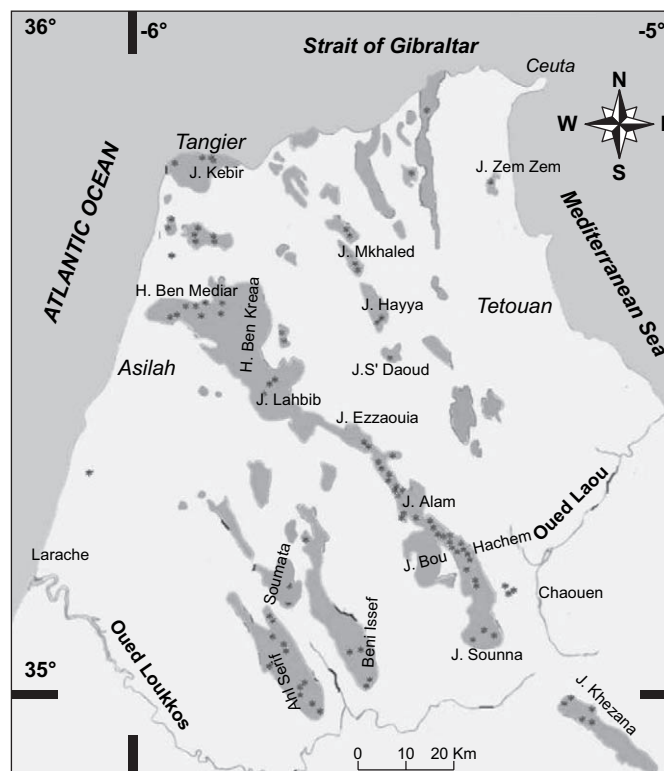


Fig. 1 – Map of the study area, with the distribution of sandstone mountains (modified from Seuter, 1980), and location of the sampled forest sites (asterisks).

inventories made by DREF (1996). Cedar forests cover more than 200 km² on the summits of the siliceous mountains of Rif and Tazekka (Benabid, 2000). The local *Pinus pinaster* forests are considered to belong to an endemic subsp. *hamiltoni* var. *maghrebiana* (according to Benabid, 2000); they form small stands at high elevation. Nomenclature follows Valdés et al. (2002).

Moroccan forests are heavily exploited for timber and fuel by a dense rural population, and are grazed by goats, cows, and sheep (Mikesell, 1960; Taiqui and Cantarino, 1997; Ajbilou, 2001). For example, the four provinces of Tangier, Tetouan, Larache and Chaouen have an area of 5316 km² and are inhabited by 331,317 people; the rural economy is based on a total of 199,544 goats, 215,881 sheep, and 105,255 cows, most of them feeding on the forest resources (Ajbilou, 2001).

For the biogeographical analysis, the whole Strait of Gibraltar region has been considered. The Strait is 14 km wide at the narrowest part, and has a maximum depth of ca. 600 m. This marine gateway connecting the Atlantic Ocean and the Mediterranean Sea was opened at the end of the Messinian salinity crisis (5.33 Myr ago) and has remained open ever since (Hsü et al., 1977; Duggen et al., 2003). During the Pleistocene glaciation, sea lowering of about 100–200 m reduced the width to about only 10 km, but did not allow a terrestrial connection between the Eurasian and African landmasses (Arroyo, 1997).

2.2. Sampling and numerical analyses

Eighty-four forest sites were selected throughout the study area, representing the main forest types in the region. A geological map (Seuter, 1980) was used to define the land patches occupied by siliceous substrate (Oligo-Miocene sandstone) as the potential study area. Within this area, representative forest stands were selected as study sites by visual inspection. Riparian forests were not included in this study.

At each forest site, a transect of 100 m was traced as representative of the patch. The overstorey cover of every tree and arborescent shrub species was measured as the line of interception along the transect, and expressed as a percentage. On the same 100 m transect, 21 sampling points were selected at intervals of 5 m. From these points, we selected the nearest tree and then the nearest neighbour; the distance between them was measured to estimate tree density using the “nearest neighbour method” (Mueller-Dombois and Ellenberg, 1974). The obtained mean distance (D) between trees was multiplied by the empirical correction factor of 1.67, and the forest density (FD) was estimated with the formula $FD = 10,000 \text{ m}^2 / (D \times 1.67)^2$, and expressed in stems ha⁻¹ (Mueller-Dombois and Ellenberg, 1974).

For each tree we measured the trunk diameter at breast height (dbh). We have considered “tree” to be those individuals with a trunk diameter greater than 7 cm, a height greater than 3 m, and a moderately developed canopy (e.g. width greater than 2 m). The individual basal area was calculated from each stem diameter, averaged, and then extrapolated (given the known density) to forest and species basal area, expressed in m² ha⁻¹ (see methods in Mueller-Dombois and Ellenberg, 1974). The distribution of trunk size classes

was analysed by intervals of 10 cm; with the exception of the first class, which was 7–15 cm.

The physical environment was characterised at each forest site. Altitude, slope, and aspect of the site were recorded. Aspect was quantified from a minimum of 1 (north) to a maximum of 9 (south and flat surfaces). A composite soil sample was obtained mixing three subsamples of 20 cm depth, taken along the transect. In the laboratory, the soil samples were oven-dried (40 °C, for at least 2 days) and crushed to pass a 2 mm sieve. Texture, acidity (in a 1:2.5 soil/water suspension) and organic matter were determined. The concentration of N (by Kjeldahl method), and the available P (by spectrophotometry), K (by flame photometry), Ca and Mg (by atomic absorption spectroscopy) was determined. The concentration of available micronutrients (Fe, Mn, Cu and Zn) and Al, after being extracted with EDTA solution, was analysed by ICP-OES (see methodological details in Page et al., 1982). Concentrations of the elements in soil are given on a dry-weight basis.

The disturbance caused by fire at the studied forest sites was estimated by visual evidence, and by the information provided by local people. Five levels of fire frequency were established, with values ranging from 1 to 3, as follows: 1) No evidence of recent fires; 1.5) some evidence of old fires; 2) notable evidence of old fires; 2.5) notable evidence of a relatively recent fire (5–10 years before); 3) very notable evidence of a recent fire (< 5 years).

The relationships between floristic trends and environmental variables were analysed by canonical correspondence analysis (CCA). In a first step, the general trend was explored for the total of 84 forest sites, 13 tree species, and 16 environmental variables. Given the heterogeneity of the data set, once the main gradient and the best-discriminated forest sites had been identified and interpreted, a second analysis was carried out, excluding the well-defined forests, to identify secondary gradients within the remnant sites. Correlations of environmental variables with the LC scores (linear combinations of environmental variables) indicated which variables were more important in structuring the floristic ordination. The significance of CCA axes was evaluated by a Monte Carlo test. We used the PC-ORD program (McCune and Mefford, 1999) for the CCA analysis.

2.3. Biogeographical analysis

The number of tree species of the study region was obtained from the Flora of North Morocco (Valdés et al., 2002). We considered all native tree species present in three nested areas: (1) the Rif area (54,700 km²), which includes the whole Rif Mountains and surrounding valleys and coasts; (2) the West Rif range (23,800 km²), including the sub-areas Tangier, W. Rif, Loukkos, Gharb, Atlantic Coast, Ouezzane, Zerhoun, Pre-Rif, and Mamora; and (3) the Tangier area (4500 km²) (Fig. 2A).

For the comparative analysis, the number of tree species was also counted in floras of equivalent areas on the northern side of the Strait of Gibraltar (southern Spain). We selected three nested areas: Andalusia (87,600 km²), western Andalusia (45,400 km²), and Algeciras (3100 km²); which are considered floristically similar to Rif, West Rif, and Tangier,

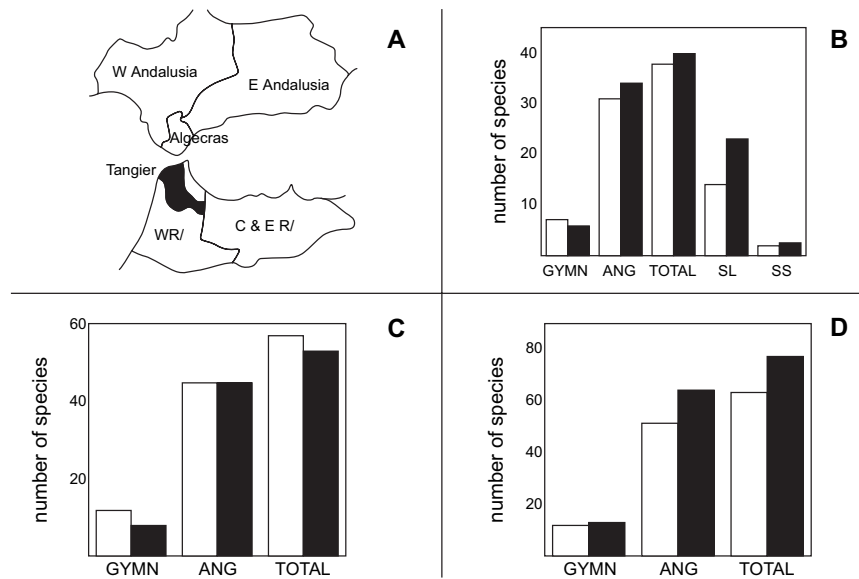


Fig. 2 – Comparative biogeographical analysis of tree species diversity in northern Morocco and equivalent regions in southern Spain. A) Map of the studied regions with the Tangier region in black; B) Number of gymnosperms, angiosperms and total tree species pool in Tangier (white bars) and Algeciras (black bars) regions; the average number of tree species per sample (SS) and the listed species (SL) in the comparative studies are also drawn; C) Number of gymnosperms, angiosperms and total tree species in West Rif (white) and western Andalusia (black); D) Number of gymnosperms, angiosperms and total tree species for the whole Rif (white) and Andalusia (black).

respectively (Valdés, 1991). We used the floras by Valdés et al. (1987); López González (2001); Castroviejo et al. (1986–2003). We also recorded the geographic range of tree species from all these sources, to ascertain if they are present on both sides of the Strait of Gibraltar, and whether they are narrow endemics.

For comparison at community level, we used two similar studies carried out in the forests on the Spanish side (Algeciras) of the Strait of Gibraltar: Ojeda (1995, with N = 20 samples) and Jurado (2002, with N = 54 samples). We counted the

number of tree species in each community sample and in the species list of each study.

3. Results

3.1. Tree species distribution and environmental gradients

A total of 15 species of trees and arborescent shrubs were identified and measured at the 84 forest sites studied (Ta-

Table 1 – Frequency, cover (within a transect of 100 m), stem density, and basal area of tree species in 84 forest sites in northern Morocco. Mean ± S.D. Nomenclature follows Valdés et al. (2002), with exception of the introduced *Myoporum* (see López González, 2001)

Tree species	Abbrev	Freq (%)	Cover (m)	Density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)
<i>Quercus suber</i> L.	Q. suber	85	38.7 ± 26.0	455 ± 477	24.7 ± 23.3
<i>Quercus canariensis</i> Willd.	Q. canariensis	35	32.6 ± 29.0	172 ± 285	90.2 ± 260.7
<i>Arbutus unedo</i> L.	Arbutus	30	23.1 ± 26.1	407 ± 670	6.1 ± 11.7
<i>Quercus pyrenaica</i> Willd.	Q. pyrenaica	13	35.2 ± 31.1	387 ± 385	18.0 ± 18.2
<i>Phillyrea latifolia</i> L.	Phillyrea	6	12.5 ± 19.4	138 ± 210	4.5 ± 9.0
<i>Cedrus atlantica</i> (Endl.) Carrière	Cedrus	4	35.8 ± 30.5	234 ± 242	9.7 ± 12.4
<i>Erica arborea</i> L.	Erica	4	1.6 ± 0.7	61 ± 41	0.5 ± 0.5
<i>Olea europaea</i> var. <i>sylvestris</i> (Mill.) Lehr	Olea	4	0.1	22 ± 21	0.3 ± 0.2
<i>Crataegus monogyna</i> Jacq.	Crataegus	2	9.6 ± 9.5	156 ± 207	3.5 ± 4.9
<i>Pinus pinaster</i> Sol. in Aiton	P. pinaster	2	87.0 ± 5.7	968 ± 714	120.8 ± 34.7
<i>Quercus coccifera</i> L.	Q. coccifera	2	49.9 ± 58.3	1510	37.7
<i>Quercus rotundifolia</i> Lam.	Q. rotundifolia	2	26.3 ± 33.4	276 ± 352	11.9 ± 15.2
<i>Pinus halepensis</i> Mill.	P. halep	2	24.9 ± 25.4	233 ± 248	7.2 ± 9.1
<i>Pistacia lentiscus</i> L.	Pistacia	1	6.6	109	1.4
<i>Myoporum tenuifolium</i>	Myoporum	1	26.5	103	1.1

ble 1). The most frequent tree species were the evergreen cork oak (*Q. suber*) the semideciduous oak (*Q. canariensis*) and the strawberry tree (*Arbutus unedo*).

The Aleppo pine (*Pinus halepensis*), which was planted in the studied forest sites, and the chinnock (*Myoporum tenuifolium*) an ornamental shrub from Australia, were excluded from the floristic ordination analysis. However, both tree species were considered in the general description of the forest structure (e.g. basal area) and diversity.

The results of the CCA analysis of the matrix of 84 samples, 13 species and 16 environmental variables, are shown in Table 2 and Fig. 3A. The first axis explained 12% of variance, and it was significantly correlated with soil fertility (K, Cu and N) and with site aspect. At the positive end of this axis 1, a sacred forest sample (at Jbel Sidi Daoud, 660 m a.s.l.), dominated by *Q. coccifera* and *Crataegus monogyna* was located. Another sacred forest (at Jbel Mkhaleh) was also separated by this axis, because of the abundance of arborescent individuals of *Phillyrea latifolia* and *Pistacia lentiscus*. Three other sacred forests studied were not different in tree composition from managed cork oak forests (see square symbols in Fig. 3A) but had trees that were larger than average (see results of stand structure and tree size, below). Thus, sacred forests were quite variable in woody species composition and environmental conditions (Fig. 3A).

The second axis explained 9.5% of variance; it had a highly significant and negative correlation ($r = -0.84$) with altitude, and positive with fire frequency (Table 2). At the negative end of axis 2 there was a cedar forest sample (at Jbel Bouhachem, 1515 m altitude), dominated by *Cedrus atlantica* and *Q. pyrenaica* (see other high-altitude forest samples with triangle symbols in Fig. 3A). At the opposite end of axis 2

were grouped most of the samples from lowland forests, dominated by *Q. suber*, and associated with a higher fire frequency and intensity (Fig. 3A). For a complementary illustration of the meaning of axis 2, the distribution of the main tree species cover along the altitudinal gradient has been graphed (Fig. 4).

Once the more singular forest types—two sacred forest and eight high-altitude forests—had been discriminated, their samples were omitted from the new, partial CCA analysis, whose results are shown in Table 2 and Fig. 3B. Together with the 10 omitted forest samples, two associated tree species—*P. lentiscus* from sacred forests and *P. pinaster* from high-altitude forests—had to be excluded, resulting in 74 samples \times 11 species \times 16 environmental variables. The first axis of this partial CCA analysis explained 17% of variance, and was negatively correlated with altitude, and slope, and soil P, N, and Mn, and positively associated with south aspect and frequency of fires (Table 2). At the negative end of axis 1 were several high elevation forests dominated by *Q. canariensis*, with *C. atlantica*, *Q. suber* and *Q. rotundifolia* in varied proportion. In general, these forests were on soils that were deep, of acidic pH and moderate fertility. While at the positive end of the same axis 1 was found a highly disturbed cork oak forest (at Haout Ben Mediar, 220 m a.s.l.). Between these two extremes of the gradient there was a wide variety of mixed oak forests with different proportions of *Q. canariensis* (towards the negative end of the axis 1) and *Q. suber* (towards the positive end of the same axis).

The second axis of this partial CCA analysis explained only 5% of variance, and was not significantly different from randomisation (Monte Carlo test $P = 0.99$). We therefore assume it had no ecological significance.

Table 2 – Results of the CCA analyses, for the total of 84 forest samples \times 13 species, and the partial CCA for 74 samples \times 11 species. Significant ($P < 0.01$) correlation coefficients between axis LC scores and environmental variables are marked in bold. Pearson correlation, with significance level of < 0.01 was used

	Total CCA (84 samples \times 13 species)			Partial CCA (74 samples \times 11 species)		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Eigenvalues	0.647	0.500	0.277	0.435	0.119	0.100
Variance explained (%)	12.3	9.5	5.2	16.6	4.5	3.8
Correlation species—environment	0.879	0.791	0.616	0.761	0.471	0.558
Significance (p) of Monte Carlo test	0.06	0.02	0.08	0.02	0.99	0.72
Correlation axis—variable						
Altitude	-0.21	-0.84	-0.13	-0.72	0.17	0.45
Slope	-0.18	-0.18	0.33	-0.35	0.04	0.09
Aspect	0.36	0.30	-0.35	0.56	0.13	0.09
Fire	-0.04	0.34	-0.26	0.36	0.03	-0.13
Soil features						
Sand	0.26	-0.03	-0.43	0.13	0.22	0.55
Aluminium	-0.10	0.12	-0.42	0.21	0.33	0.09
pH	0.26	-0.03	0.43	0.01	0.03	-0.56
Nitrogen	0.35	-0.44	0.55	-0.32	-0.44	0.11
Phosphorus	-0.07	-0.33	0.22	-0.45	-0.03	0.03
Potassium	0.54	-0.19	0.61	-0.27	-0.44	-0.15
Copper	0.53	-0.10	0.39	-0.13	-0.21	-0.20
Iron	0.25	-0.08	-0.06	-0.06	-0.35	-0.42
Manganese	-0.02	-0.27	0.22	-0.30	-0.11	-0.17
Zinc	0.15	-0.14	0.16	-0.13	-0.40	-0.13
Organic matter	0.06	-0.09	0.20	-0.04	-0.48	0.40
C/N rate	-0.04	0.12	-0.06	0.11	-0.18	0.37

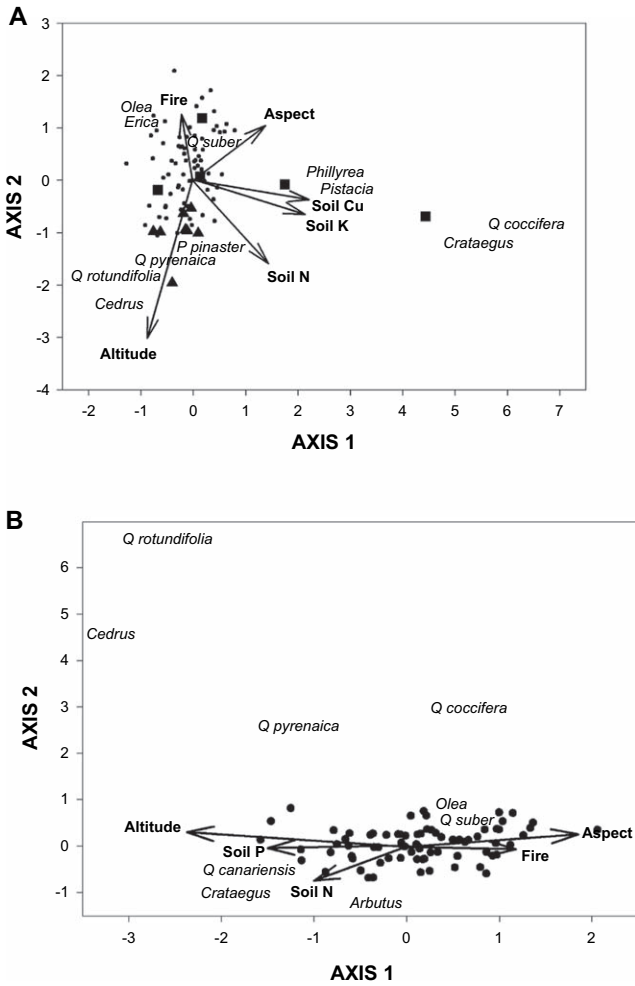


Fig. 3 – Results for the CCA analysis of the 84 forest sites (A) and the CCA partial analysis of the 75 forest sites (B). In Fig. 3A square symbols represent sacred forests and triangles high-altitude forests. For a better interpretation, environment scores were multiplied by five to build vectors.

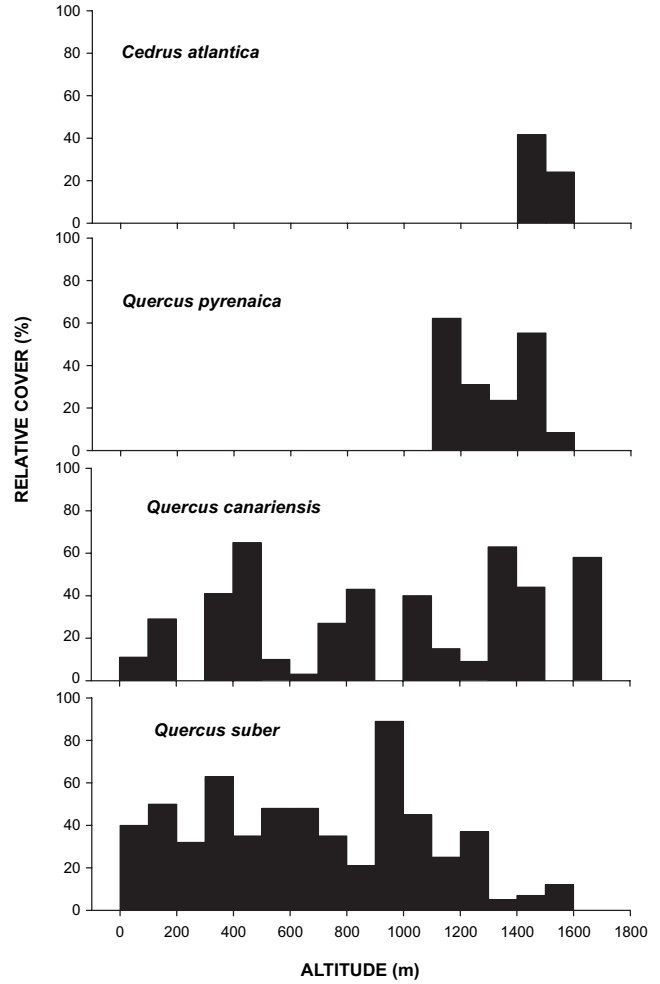


Fig. 4 – Abundance (mean cover) of tree species along the altitudinal gradient.

3.2. Forest structure and tree size

In general, the Moroccan forests studied had a mean density of 740 stems ha⁻¹ and a mean basal area of 34.1 m² ha⁻¹. The tree species richness was low: mean of 1.9 species per transect, with a range of one to five species. The total tree overstorey cover was also relatively low, with a mean of 63%. A small proportion of forest sites (14%) had very low cover (<20%), reflecting the severe exploitation of forest resources occurring in this region.

Considering the density of the different tree species (Table 1), there were dense populations of *Q. coccifera* (in one sacred forest), *P. pinaster*, *Q. suber*, and *A. unedo*. In terms of basal area, the dominant tree species of the studied Moroccan forests was *Q. canariensis*, and locally *P. pinaster* (Table 1).

The tree size distribution of *Q. suber* was right-skewed (Fig. 5). From a total of 1606 measured stems (in 73 forest samples), the mean dbh was 23.94 cm, and the largest cork

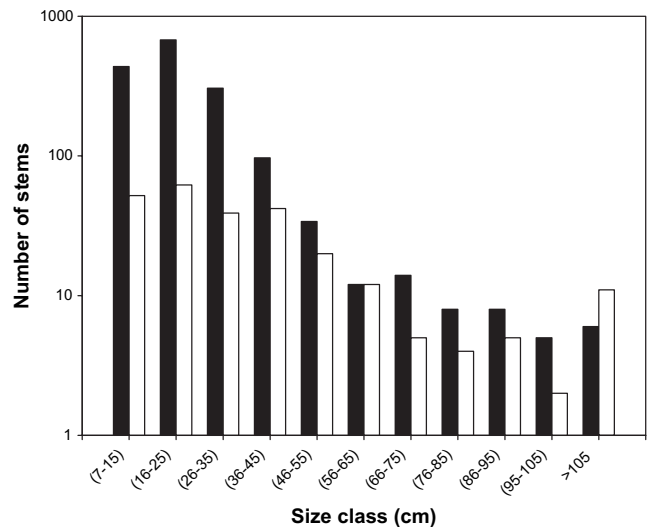


Fig. 5 – Distribution of stem diameter classes for *Q. suber* (in black; N = 1606) and *Q. canariensis* (in white; N = 254).

oak measured had 135 cm of dbh. The semideciduous oak *Q. canariensis* had a similar trend of size distribution as *Q. suber* (Fig. 5), although the mean size was larger. From a total of 254 measured stems (in 29 forest samples), the mean dbh was 36.46 cm, and the largest recorded tree had 150 cm of dbh. The number of largest trees (those exceeding 105 cm dbh) was higher for *Q. canariensis* ($N = 11$) than for *Q. suber* ($N = 6$) (see Fig. 5).

3.3. Tree species diversity and biogeography

The local species pool of 14 native taxa (including *P. halepensis*) of trees and arborescent shrubs, found at the 84 studied forest sites, represented about 37% of the tree flora in the Tangier region. The proportions of gymnosperms (21%) and angiosperms (79%) in the studied forests were similar to those for the whole Tangier tree flora (18% of gymnosperms). In comparison, forests at southern Spain (74 samples; Ojeda, 1995; Jurado, 2002) had 23 native species of trees, representing 57.5% of the Algeciras (Spanish region equivalent to Tangier) tree flora. At the community level, the average tree species richness per sample on the African side (1.9 species, see above) was lower than that for the equivalent Eurasian side (2.6 tree species per sample).

At the regional level, the pattern of tree diversity differed with the spatial scale. The total tree diversity was similar between Tangier and Algeciras, as well as between West Rif and West Andalusia (Fig. 2B, C). However, the proportion of gymnosperm was higher on the southern side of the Strait. When the largest areas (Rif and Andalusia) were compared, the northern tree flora was richer (77 vs. 64 species; Fig. 2D).

Despite the proximity between the two sides of the Strait (14 km distance at the narrowest part), there are discontinuities in the geographic range of several tree taxa. In particular, 11 out of 64 (17%) Rifean species of trees are not found in the adjacent Andalusian range, while 24 out of 77 (31%) Andalusian tree species are not found in the Rif range; therefore, the regional floristic overlap is 53 (common species) out of 88 (60%). A singular example of Moroccan tree species not present in the Spanish flora is the cedar *C. atlantica*. In other cases, there are vicariant species (e.g. *Abies marocana* in Morocco, and *A. pinsapo* in Spain) or subspecies (e.g. *Pinus nigra* subsp. *mauretana* in Morocco and *P. n.* subsp. *salzmannii* in Spain) on each side of the Strait. In two cases, the Moroccan species is not present in the Andalusian flora, but present in other places of the Iberian Peninsula; the araar tree (*Tetraclinis articulata*) forms extensive forest stands in the Rif, not far from the Strait, but it is absent from Andalusia, and there is only a small, relict population in southeast Spain; the second example, *Prunus lusitanica*, shows a singular case of niche convergence with *Rhododendron ponticum* (which is absent from Morocco)—*P. lusitanica* is abundant in the mountain streams of the Rif while *R. ponticum* dominates in virtually identical habitats in the Algeciras mountains. Many of the Andalusian tree species absent from the Rifean flora are temperate species inhabiting high mountain ranges (up to 3400 m) of Sierra Nevada, with no equivalence in the Rif Mountains.

4. Discussion

4.1. Tree species distribution and environmental gradients

Altitude, conservation (as exemplified by sacred forests), soil fertility, and fire incidence were the main factors significantly correlated with major trends of tree species composition and abundance (as shown by the CCA analysis) in North Morocco.

The changes in tree species composition with altitude is largely determined by the variation in microclimate, in particular the differential species tolerance to limiting cold. The highest peaks in the Rif are below 2500 m (that is, below the tree-line), and the summits are covered mainly by cedar (*C. atlantica*), frequently mixed with *P. pinaster* and *Q. pyrenaica* (Benabid, 2000). Altitude was a main factor in the study of forest understorey composition in southern Spain and northern Morocco (Ojeda et al., 1996), and topography partly explained woody species distribution at landscape level in south Portugal (Maltez-Mouro et al. 2005).

Cedars have long been logged for use as good-quality timber (Mikesell, 1960; Reille, 1977); however most of the cedar stems measured in this field study had a relatively small diameter (7–35 cm), thus indicating a promising regeneration stage of the population after intensive past logging (Ajbilou et al., 2003). *P. pinaster* (considered an endemic variety by Benabid, 2000) is locally abundant in some high-elevation sites of Jbel Bouhachem, forming dense and almost pure populations. Although it is currently under protection, the relative low abundance of stems in the smaller diameter classes indicates some limitations in natural regeneration (Ajbilou et al., 2003). *Q. pyrenaica* is a deciduous oak associated to acidic soils at higher elevation in the Rif Mountains (rarely below 1000 m a.s.l.). It usually forms dense forests with a closed understorey of root suckers.

The strict conservation of sacred forests has allowed the persistence of a singular tree species composition and size structure. Some species, such as *Q. coccifera* and *P. latifolia*, which are relatively frequent as shrubs in the region, show a distinct tree habit in these long-preserved forests, and co-dominate the overstorey. It is somewhat difficult to know the composition and structure of original forests in this region, partly because palaeobotanical studies in the area are scarce, and partly because of the problems in distinguishing pollen from different *Quercus* species. However, we can hypothesise that trees of Kermes oak (*Q. coccifera*) were abundant (even dominant) in the Western Mediterranean lowland forests; but they almost disappeared (as trees) after the severe deforestation. Currently, they persist in some sacred forests of northern Morocco (Charco, 1999), and in well-preserved forests of Portugal (Blanco et al., 1997). Sacred forests represent a network of refuges and sources for maintaining biodiversity at landscape scale (see review in Gadgil, 1996, with examples from Africa, Asia and Pacific islands). Independently of their religious meaning for local people, who currently protect them but whose attitude may change with time, these singular forests should be preserved by law because of their ecological value.

The evergreen cork oak (*Q. suber*) is the dominant tree species in this region, probably favoured by the acidic soils and the oceanic influence, as well as by the history of human management (Reille, 1977). The evergreen Mediterranean oaks (*Q. suber*, *Q. ilex/rotundifolia* and *Q. coccifera*) are morphologically similar to the ancestral oaks from the Tertiary inhabiting the Mediterranean Basin (Palamarev, 1989). They survived the Ice Ages and expanded during the Quaternary, associated to increasing human impact (Reille, 1977).

In contrast, semideciduous oaks (*Q. pyrenaica* and *Q. canariensis*) seem to be favoured by moister habitats, and they are more sensitive to human management. Since the end of the Boreal stage (about 7500 years B.P.), semideciduous oaks were dominant on Moroccan mountains, until a relatively recent shift to evergreen oaks, associated to human colonisation and partial deforestation for agriculture (Reille, 1977). In a gradient of annual precipitation in S. Spain, *Q. canariensis* was found in moister climate (above 900 mm) than *Q. suber*, although they form mixed forests strongly influenced by historical management (Urbieta et al., 2004). The populations of *Q. canariensis* inhabiting the most-remote areas of high mountains in the Rif are relatively well preserved. However, they are threatened in the lowland forests, where they are cut for wood and suffer frequent fires. Despite they occupy a relatively small area, their floristic interest is important because they harbour a rich understorey in endemic and taxonomically singular species (Barbéro et al., 1981; Ojeda et al., 1996; Marañón et al., 1999).

4.2. Forest structure and tree size

The distribution of tree size classes allows us to infer the demographic structure of the forest and the possible conservation problems. A reverse-J shaped distribution—that is, with a higher proportion of smaller-size individuals (assumed to be younger)—would insure the recruitment and regeneration of that tree population.

Q. suber presented a decrease of smallest trunk size (<15 cm), indicating a possible regeneration problem. Although individual trunks lower than 7 cm diameter were not censused, during the survey we found scant evidence of natural emergence and establishment of seedlings, and low density of surviving seedlings and saplings. Many of the small stems are the result of sprouting from the base (after cutting) or from roots, with potential consequences on their resistance to pests, diseases and disturbances. The main threat to *Q. suber* forests is the extensive clear-cutting to transform them into crop fields for hashish (*Cannabis indica*) cultivation. For example, in a period of only 6 years, the area of cork oak forests in Ketama region decreased from ca. 8000 ha (in 1984) to only about 500 ha (in 1990; Benabid, 2000).

The pattern of tree size distribution for *Q. canariensis* also showed a decreasing trend towards the smallest class (<15 cm). This species tends to regenerate predominantly from seeds, and has a low sprouter ability (Ceballos and Ruiz de la Torre, 1979). Its seedlings and saplings are relatively sensitive to human-induced disturbances, in particular to

burning. In southern Spain, there is a relatively high proportion of the smallest-size class (10–20 cm), while large *Q. canariensis* trees had signs of old pollarding to produce charcoal. During the last 50 years, historical changes there, notably the replacement of charcoal by gas as fuel, have profoundly affected to the management of the oak forests, and in particular *Q. canariensis* which was the main source of charcoal (Jurado, 2002). In many mixed oak stands, there is a progressive replacement of old, injured (by periodic bark extraction) cork oaks by vigorous, young, non-pollarded, semideciduous oaks. It is reasonable to predict a similar replacement trend for the Moroccan forests, if the human pressure is reduced. In Morocco, there are large *Q. canariensis* trees in the highest, remote, forest stands (at Jbel Bouhachem, Sounna and Khezana), while they are scarce in the lowlands, with the exception of some isolated sacred trees or forests. There is a current interest in preserving these veteran trees, as historical witnesses of the ecological past (for example, recorded in their growth rings), and for their ecological role in harbouring singular micro-habitats for many species of invertebrates and fungi, and thus maintaining the forest biodiversity (Marañón, 1999).

4.3. Tree species diversity and biogeography

The Tangier region of northern Morocco shows a great similarity in both edaphic (sandstone-derived soils) and climatic (mild Mediterranean) conditions with the equivalent Algeciras region in southern Spain, which determines a similar pattern of vegetation (Ojeda et al., 1996) and flora (Valdés, 1991; Arroyo, 1997). However, natural resource management and the disturbance regime are very different on each side of the Strait (Ojeda et al., 1996; Deil, 1997; Marañón et al., 1999; Ajbilou, 2001).

The tree species diversity in the set of studied forest sites in northern Morocco was lower than in equivalent sites in southern Spain. Given the similar ecological scenario of the whole Betic-Rifean region, we suggest three non-exclusive hypotheses to explain that difference. Firstly, the lower landscape heterogeneity on the southern side of the Strait. When considering larger biogeographical scales, there is a higher probability of including new ecological and historical contexts, and hence different floristic elements (see Castro Parga et al. (1997) for the Iberian Peninsula). In particular, the Rif Mountains have no high-altitude peaks (unlike Sierra Nevada in Andalusia), and in consequence lack suitable habitats for certain temperate tree species, such as *Pinus sylvestris*, which find refuge there.

Secondly, the lower tree diversity can reflect a contrasting forest management (see Marañón et al., 1999). On the Moroccan side of the Strait, the rural human population is denser, and forest resources are more heavily exploited, whereas in southern Spain, rural landscapes have been depopulated during the last 40 years (for example, only 2500 inhabitants remain within the 1700 km² of Los Alcornocales Natural Park; CMA, 1997). Historical land use, such as wood and charcoal harvesting, overgrazing, and cultivation has probably caused the local extinction of several tree species in Moroc-

can mountains, originating a biodiversity loss (e.g. Mikesell, 1960; Taiqui and Cantarino, 1997; Moore et al., 1998; Benabid, 2000). Despite that general deforestation and severe exploitation, there are still valuable forested areas to preserve there. A good example is the cedar tree (*C. atlantica*), which still covers considerable areas in N Morocco, but became extinct in S. Spain during the Holocene (Pons and Reille, 1988).

Thus, the combination of a lower spatial heterogeneity, at regional level, and a general diversity loss by human impact, could explain the lower tree species richness on the southern side of the Strait of Gibraltar, compared to the northern side (see also Marañón et al., 1999).

Thirdly, the Strait of Gibraltar functions as biogeographical barrier. Thus, striking differences in tree distribution and genetic structure in the Strait of Gibraltar region cannot be explained by spatial heterogeneity or human impact. In general, phylogeographic studies of tree populations, exhibiting a variety of pollen and seed dispersal mechanisms, indicate that the Strait has been a long-term barrier to dispersal. For example, *Q. suber* showed a high level of genetic differentiation across the Strait of Gibraltar, observed in both nuclear and cytoplasmic molecular markers. Hence the efficiency of pollen and seed flow across the Strait must be low (Tuomi and Lumaret, 1998); a similar pattern was found for *Q. ilex* (Lumaret et al., 2002). In another example, a strong differentiation in chloroplast DNA was found between the Moroccan and Spanish populations of alder buckthorn (*Frangula alnus* subsp. *baetica*; although considered as *F. a. ssp. alnus* in Valdés et al. 2002). This pattern involved a limited seed flow across the Strait (Hampe et al., 2003). The maritime pine (*P. pinaster*) also showed a limited seed flow, but the pollen flow was considerable (Burban and Petit, 2003).

The observed differentiation across the Strait can be favoured by the particular biological requirements of trees, such as long life-span and slow establishment processes, having usually a patchy distribution, and accelerated extinction rates. Tests of this hypothesis have produced contradictory evidences in herbaceous specie. For example, the annual *Bellis annua* (Fiz et al., 2002) and the perennial *Saxifraga globulifera* (Vargas et al., 1999) do show a differentiation between populations on the two sides of the Strait, while the bulbous geophyte *Androcymbium gramineum* (Caujapé-Castells and Jansen, 2003) does not.

The Rif area has a high conservation value because of its plant diversity and biogeographical relevance. At the Tangier region (western Rif), the flora is even more singular because of the uncommon acid soils. Although we have depicted here some remarkable diversity patterns, little is known yet about the historical and ecological processes behind them. The strong human pressure on Rifean forests has reduced their extent and changed their structure; nonetheless, some very specific forest types, in particular those dominated by the gymnosperms *C. atlantica* and *T. articulata*, still persist. Support is strongly recommended for studies investigating natural (e.g. historical climate changes) and human (e.g. deforestation, pollution, overgrazing) influences on the current persistence of tree species, in their southern limits within the Mediterranean forest region.

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