Syntaxonomy and Synecology of Quercus coccifera Mediterranean Shrublands in Greece

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ORIGINAL RESEARCH

Syntaxonomy and Synecology of *Quercus coccifera* Mediterranean Shrublands in Greece

Georgios Tsiourlis · Pavlos Konstantinidis · Pantelis Xofis

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Abstract *Quercus coccifera* (kermes oak) is the most common species of the Mediterranean maquis with a wide distribution across the Mediterranean Basin. This paper presents a syntaxonomic overview of the *Q. coccifera* plant communities in the Mediterranean zone of Greece (Quercetea ilicis*)* based on the classification of 221 relevés from 34 (17 continental and 17 insular) mountainous areas throughout Greece. Two associations and eight sub-associations are described and presented in a synoptic constancy table. Querco cocciferae–Pistacietum lentisci is the most widespread, is found in the entire continental Greece and most islands, and is further subdivided into five sub-associations reflecting primarily local peculiarities in the disturbance regime and the influence of local floristic elements. Rhamno lycioidis–Cocciferetum (Rivas Goday & Rivas-Martínez 1954), on the other hand, is geographically confined on the island of Crete and is further subdivided into three sub-associations, reflecting differences in the annual precipitation, and they are characterized by the presence of many phryganic and grazing-resistant species. Climate and the anthropogenic pressure have been identified to be the most important factors determining the structure and the floristic composition of *Q. coccifera* Mediterranean shrublands of Greece.

Keywords Kermes oak · Mediterranean shrublands · Phytosociology · Quercetea ilicis · *Quercus coccifera* · Vegetation classification

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Introduction

Quercus coccifera (kermes oak) is the most common species of the Mediterranean maquis, thriving in a wide variety of often contrasting environments (Balaguer et al. 2004). Characteristics, such as frugality, resprouting ability, and resilience to coppicing allow it to grow in unfavorable soil conditions and under severe human pressure (Liakos and Moulopoulos 1967). Overgrazing, overexploitation by humans and wildfires which have altered the physiognomy and composition of natural vegetation in the Mediterranean Basin, is thought to be one of the main factors responsible for the predominance of the species across the region (Mavrommatis 1980; Raus 1980; Trabaud 1987). Its prodigious regenerative capacity is supported by stored energy reserves in the roots (Konstantinidis et al. 2005) and by supplies of water and nutrients made available by an extensive and deeply penetrating rooting system (Tsiourlis 1992) that allows it to extract water reserves which are inaccessible to other species during the summer draught (Rambal 1984). It can, thus, maintain a high transpiration level for this period necessary to develop its young leaves. This gives it a competitive advantage over grasses and may explain the difficulties of establishing and maintaining perennial grasses after a brush-to-grass conversion (Poissonet et al. 1981).

Although *Q. coccifera* shrub formations do not usually exceed a height of 2 m, in the absence of grazing and fire, it

can form maquis formations up to 4–5 m high (Konstantinidis and Tsiourlis 2003) or even forests with a height of about 15 m, such as the ones observed mostly in Crete (Barbéro and Quézel 1980; Kypriotakis et al. 1996).

Q. coccifera is found across the entire Mediterranean region apart from Egypt (Ozenda 1964). In the Middle East, *Q. coccifera* is traditionally named *Quercus calliprinos*, which is a plain synonym of *Q. coccifera* (Greuter et al. 1986). It is distributed from 45°30′ N in the Peninsula of Istria to 31°00′ N in Negev (Israel) and from 9°30′ E in Cascais (Portugal) to 37°00′ E on the Mountains of Alaouites in Syria (Cañelas 1993). It dominates low and high shrub formations, such as the garrigue in Southern France (Lossaint and Rapp 1971; Poissonet et al. 1978), "coscojares" in Spain (Terradas 1999; Loidi et al. 1994), and "prinones" in continental Greece (Mavrommatis 1982; Papachristou 1998).

In Greece, *Q. coccifera* dominated vegetation formations occupy an area of more than 1.5 million hectares (Platis and Papanastasis 2003). It can be found within all life zones influenced by the Mediterranean climatic conditions (Konstantinidis 1990; Dimopoulos 1993), and its altitudinal distribution in Southern and Western Greece reaches 1,200 m asl, in Central Greece 1,000 m asl, and in Northern Greece 700 m asl (Mavrommatis 1980), while in some areas, such as in Crete, it can be found even higher (1,600 m) as recorded by Tsiourlis et al. (2001). It is most abundant in the continental part of Greece, apart from the northwest and northeastern parts, but it is also widespread in most islands apart from Cyclades. In the Thermo-Mediterranean life zone in particular, it codominates alongside with *Pistacia lentiscus* and in its drier parts with *Ceratonica siliqua* which are both character species of this life zone (Debazac 1969).

Several regional classifications were conduced across the Mediterranean region regarding the shrublands communities dominated by *Q. coccifera*. Many different associations and nomenclatures have been adopted while they often describe in fact the same plant communities, even at the level of sub-association. The most characteristic of those are Cocciferetum Braun-Blanquet (1924, 1936), Quercetum cocciferae Braun-Blanquet and Bolòs 1957, and Rhamneto–Cocciferetum Braun-Blanquet and Bolòs 1957 in western Mediterranean, as well as, Quercetum calliprini Boyko 1954 (Boyko 1954; Zohary 1973) in Eastern Mediterranean.

Only few studies, however, refer to the synecology and syntaxonomy of *Q. coccifera* shrublands in Greece (Adamovič 1906, 1909 cited by Bergmeier 1990 and Theodoropoulos 1991; Horvat et al. 1974; Barbero and Quézel 1976; Mavrommatis 1980; Raus 1980, 1982; Karagiannakidou-Iatropoulou 1983; Konstantinidis 1990; Bergmeier 1990; Dimopoulos 1993; Chasapis et al. 2004).

The aim of the current study is to present a systematic classification of the *Q. coccifera* dominated Mediterranean shrubland formations of the Quercetea ilicis vegetation zone, which is its natural distribution area, throughout Greece, and to attempt to identify the ecological parameters affecting their distribution.

The prevalence of *Q. coccifera*-dominated plant communities in the Eastern Mediterranean landscape is reciprocal to the scarce syntaxonomic knowledge about this vegetation type. In this respect, the vegetation data provided by this study are generally worth being communicated to the scientific community.

Materials and Methods

Study Area

Phytosociological data across continental and insular Greece were collected on areas that were considered representative of the main Mediterranean shrubland types of *Q. coccifera*. The areas represent a variety of environmental conditions since they are distributed from north to south and east to west of Greece, covering almost the entire country (Fig. 1).

The study area includes 34 areas. Seventeen across continental Greece: Vertiscos and Cholomon (Northern Greece), Mavrovouni, Telethrio, and Ochi (Eastern Greece), Erimanthos, Mani, Chelmos, and Taigetos (Southern Greece), Acherontas, Akarnanika, Arakinthos, Arta, and Parga (Western Greece), Oiti, Sounio, and Parnitha (Central Greece). Three areas across Ionian Sea, namely: Ainos and Kalo Oros (Kefalonia island) and Lefkada. Five areas across Aegean Sea: Lesvos, Ampelos, and Kerkis (Samos Island) and Andros and Kithira. And nine areas across Crete: SE Crete, Moni Kapsa, and Thryptis (Eastern Crete), Dikti-Omalos, Dikti-Lasithi, Giouchtas, and Idi Oros (Central Crete) and Rodopos and Lefka Ori (Western Crete).

Table 1 shows the geological and climatic conditions and the number of relevés of the various study areas. The selected study areas cover most of the southeastern part of the Balkan Peninsula, located between the 34th and 40th parallel, with a meridional extent from 19° to 28° E, including Aegean Sea, Ionian Sea, and the East Mediterranean Sea.

The climate of the Quercetea ilicis vegetation zone is typical Mediterranean with mild and rainy winters, warm and dry summers, and an extended period of sunshine throughout the year. However, the climatic conditions vary from the semidry conditions of Attica, Crete, and Eastern Greece to the relatively subhumid to humid conditions of Northern and Western Greece.

Fig. 1 Map of Greece with the mountainous study areas

A common characteristic of all the above areas is their mountainous character and their sharp relief, independently of their size. The geologic structure is quite similar in most areas, where a calcareous substratum is dominant with parts of recently formed (Miocene and Pliocene) sea sediments (mostly in islands), while other geological formations are only occasionally met. The dominant soil type in the islands is terra rossa followed by rendzina and alluvial soils (Kagiabaki 2003). The calcareous substratum consists mainly of limestone, dolomite, and marls, while parts of flysch are found in between limestone (Vardinogianni 1994; Trichas 1996), resulting in soils with an alkaline reaction. The steep relief as well as the overgrazing and often occurrence of wildfires result in increased soil erosion and subsequent degradation of the soil chemical and physical properties (Vardinogianni 1994) leading often to desertification (Tsiourlis et al. 2001).

Data Collection and Analysis

From 1996 to 2006, 221 relevés were collected during May and June using the Braun-Blanquet (1964) approach. The plots were located at various altitudes, expositions, inclinations, and relief. Plot size was set at 300 m^2, and an effort was made to achieve high ecological and physiognomic homogeneity within each plot (Dafis 1970; Athanasiadis 1986). The following parameters were recorded for each relevés: elevation, inclination, exposition, and species abundance for each vegetation layer. Vascular plants were identified using "Flora Europaea" (Tutin et al. 1964–1980; Diapoulis 1939–1949; Kavvadas 1956–1964). The nomenclature of taxa follows "Flora Europaea" (Tutin et al. 1964–1980).

The identification of vegetation units was done using the polythetic-divisive method TWINSPAN (Hill et al. 1975; Hill 1979). The original Braun-Blanquet scale of abundance was converted into an ordinal scale (Bergmeier and Dimopoulos 2001), with values ranging from 1 to 7 corresponding to the original seven classes of abundance. The pseudospecies cut levels used were 0.1, 3.1, 4.1, 5.1, and 6.1 ordinal scale units. Classification in five levels was performed, and the minimum number of samples to justify further division was set at 5. The maximum number of indicator pseudospecies was set at 7, and all pseudospecies

Table 1 Study areas of *Quercus coccifera* shrublands in Greece: location, main climatic parameters, and number of relevés

Areas	Geographic coordinates	Altitude (m)	Exposition (degree)	Slope (%)	Substrate	Climate	Number of relevés
Vertiskos	41°00′, 23°20′	50–200	0–360	10–50	Limestone	Subhumid Mediter.	5
Cholomon	40°32′, 23°15′	70–250	0–360	15–45	Limestone	Subhumid Mediter.	5
Mavrovouni	22°20′, 36°55′	400–750	0–180	10–50	Limestone, schists	Subhumid Mediter.	7
Telethrio	23°09′, 38°54′	50–450	0–360	20–70	Limestone	Subhumid Mediter.	5
Ochi	24°28′, 38°07′	350–600	90–270	15–40	Limestone	Subhumid Mediter.	5
Erimanthos	22°00′, 38°00′	400–700	270–360	35–55	Limestone, flysch	Subhumid Mediter.	5
Mani	22°26′, 36°40′	180–360	180–270	10–40	Limestone	Subhumid Mediter.	9
Chelmos	22°15′, 38°00′	400–850	360–45	20–35	Limestone	Subhumid Mediter.	5
Taigetos	22°20′, 36°55′	400–900	135–315	20–40	Limestone	Subhumid Mediter.	9
Acherontas	20°30′, 39°15′	30–450	90–270	20–40	Limestone	Humid Mediterranean	9
Akarnanika	21°26′, 38°28′	160–370	45–220	5–50	Limestone	Subhumid Mediter.	5
Arakinthos	21°25′, 38°30′	400–600	50–200	15–40	Limestone, flysch	Subhumid Mediter.	6
Arta	20°57′, 39°13′	290–500	0–180	20–45	Limestone	Subhumid Mediter.	8
Parga	20°23′, 39°18′	150–350	90–180	20–30	Limestone	Subhumid Mediter.	8
Oiti	22°19′, 38°30′	400–600	150–360	10–60	Limestone	Subhumid Mediter.	5
Sounio	24°02′, 37°41′	20–250	189–360	10–30	Limestone	Semiarid Mediter.	10
Parnitha	23°43′, 38°10′	600–800	90–360	20–50	Limestone, schists	Humid Mediterranean	5
Ainos	20°43′, 38°12′	90–350	45–220	5–40	Limestone	Humid Mediterranean	5
Kalo Oros	20°35′, 38°20′	350–500	0–360	5–45	Limestone	Humid Mediterranean	10
Lefkada	20°36′, 38°43′	90–270	0–360	5–25	Limestone	Humid Mediterranean	5
Lesvos	26°45′, 39°20′	650–850	0–360	10–25	Limestone, schists	Subhumid Mediter.	6
Ampelos	26°50′, 37°07′	250–550	0–360	10–40	Limestone	Subhumid Mediter.	5
Kerkis	26°40′, 37°40′	400–750	150–270	20–60	Limestone	Subhumid Mediter.	5
Andros	24°50′, 37°55′	200–550	90–270	15–50	Limestone	Subhumid Mediter.	5
Kithira	23°00′, 36°20′	120–450	25–340	5–50	Limestone	Subhumid Mediter.	7
SE Crete	26°14′, 35°04′	200–800	0–360	20–80	Limestone	Semiarid Mediter.	5
Moni Kapsa	26°03′, 35°02′	400–550	0–360	50–90	Limestone	Semiarid Mediter.	5
Thryptis	25°52′, 35°05′	200–1350	0–360	30–90	Limestone	Semiarid Mediter.	6
Dikti-Omalos	25°26′, 35°03′	600–1400	0–360	0–80	Limestone	Semiarid Mediter.	7
Dikti-Lasithi	25°30′, 35°08′	450–1600	0–360	0–90	Limestone	Semiarid Mediter.	11
Giouchtas	25°08′, 35°14′	400–700	0–360	30–90	Limestone	Semiarid Mediter.	6
Idi Oros	24°50′, 35°15′	450–1600	0–360	10–90	Limestone	Semiarid Mediter.	12
Rodopos	23°45′, 35°36′	200–400	0–360	20–60	Limestone	Subhumid Mediter.	5
Lefka Ori	24°02′, 35°17′	600–1300	45–220	20–60	Limestone	Subhumid Mediter.	5

were available as indicator species. The initial classification resulted in a large number of groups, but not all of them represented distinctive vegetation units, so some of the groups were merged at higher division levels. This process was aided by the results of a Detrended Correspondence Analysis (DCA; Hill 1973, 1974). TWINSPAN classification is based on a single-axis ordination for the differentiation of the groups and provides relatively little information on the floristic relationships between the groups and the degree of floristic overlapping between them (Gauch 1982). Ordination analysis using DCA, on the other hand, uses all the information contained in the samples by species data matrix, and in two-dimensional samples, ordination diagram is more informative and allows the identification of both the floristic consistency of the identified groups and the floristic relationships between groups.

After construction of a synoptic table, the table was reordered into a diagnostic table clearly showing the differences between the plant communities. This table was used for the identification of diagnostic species and for denomination of the different plant communities.

The nomenclature of the plant communities was typified with the International Code of Phytosociological Nomenclature (ICPN; Weber et al. 2000). However, referred syntaxa names before 2002 are literally cited and not obligatory in accordance with ICPN. The definition of

"vegetation zones" and "subzones" follows Dafis (1973) and Athanasiadis (1986) for Greece.

Results

Based on TWINSPAN and DCA results, eight distinctive vegetation units were identified (Fig. 2) and, following the Braun-Blanquet approach, were classified under two associations and eight sub-associations. Table 2 shows the frequencies of the diagnostic species for the corresponding vegetation units. According to these results, the syntaxonomic synopsis of the *Q. coccifera* shrublands in the mountains of Greece is:

Quercetea ilicis Braun-Blanquet 1947

Quercetalia ilicis Braun-Blanquet 1947

Quercion ilicis Braun-Blanquet 1934 em. Rivas-Martínez 1975

1. Querco cocciferae–Lentiscetum Braun-Blanquet et al. 1936

Or typified with ICPN (Weber et al. 2000) as Querco cocciferae–Pistacietum lentisci

- 1.1 Querco cocciferae–Pistacietum lentisci typicum
- 1.2 Querco cocciferae–Pistacietum lentisci euphorbietosum rigidae
- 1.3 Querco cocciferae–Pistacietum lentisci arbutetosum andrachni
- 1.4 Querco cocciferae–Pistacietum lentisci fraxinetosum orni
- 1.5 Querco cocciferae–Pistacietum lentisci anthemidetosum tinctoriae

2. Rhamno lycioidis–Quercetum cocciferae Braun-Blanquet and Bolòs 1954

- 2.1 Rhamno lycioidis–Quercetum cocciferae phagnaletosum graeci
- 2.2 Rhamno lycioidis–Quercetum cocciferae berberidetosum creticae
- 2.3 Rhamno lycioidis–Quercetum cocciferae cerastietosum brachypetali

1. Querco cocciferae–Pistacietum lentisci (Table 2, Group 1; Fig. 2)

Character species: *P. lentiscus*, *Phillyrea media*, *Asparagus acutifolius*, *Geranium lucidum*, *Ruscus aculeatus*, *Medicago minima*, *Clematis vitalba*, *Teucrium capitatum*, *Pyrus spinosa*, *Teucrium chamaedrys*, *Smilax aspera*, *Quercus pubescens*, *Medicago lupulina*, *Anthyllis hermanniae*, *Rosa canina*, *Melica ciliate*, *Paliurus spina–christi*.

Ecology: The climate on the areas where this association is found is characterized by warm winters (mean temperature 0–5°C) with precipitations that can reach 600–1,000 mm. Altitudinal range is between 20 and 900 m. All the expositions are encountered while the slopes vary from relatively gentle to very steep. Substrates are mainly limestone with several areas on flysch and schist, while the

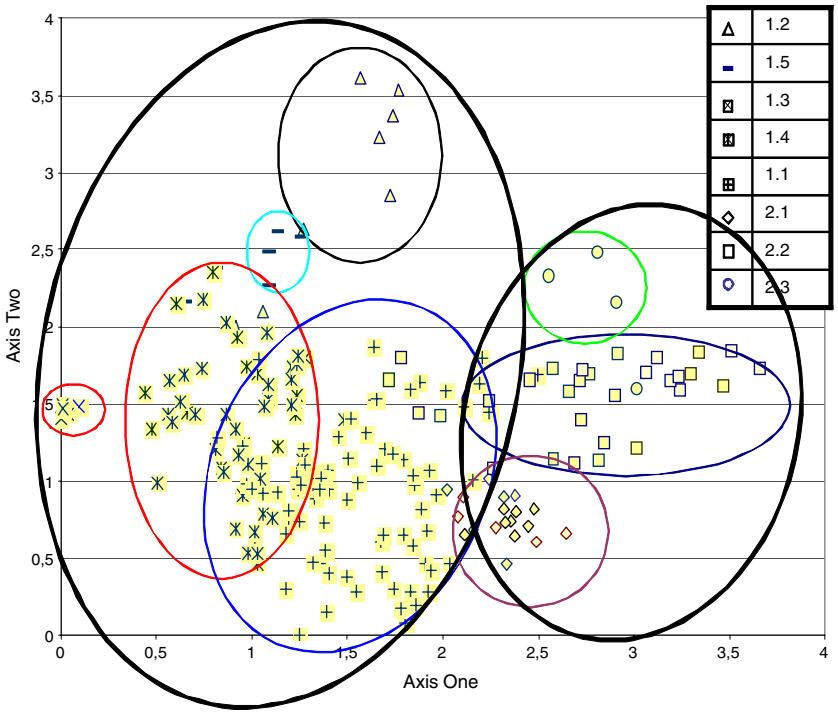

Fig. 2 DCA samples ordination diagram. The codes in the legend correspond to the group numbers assigned to the sub-associations as following: *1.1* Querco cocciferae–Pistacietum lentisci typicum, *1.2* Querco cocciferae–Pistacietum lentisci euphorbietosum rigidae, *1.3* Querco cocciferae–Pistacietum lentisci arbutetosum andrachni, *1.4* Querco cocciferae–Pistacietum lentisci fraxinetosum orni, *1.5*Querco cocciferae–Pistacietum lentisci anthemidetosum tinctoriae, *2.1* Rhamno lycioidis–Quercetum cocciferae phagnaletosum graeci, *2.2* Rhamno lycioidis–Quercetum cocciferae berberidetosum creticae, *2.3* Rhamno lycioidis–Quercetum cocciferae cerastietosum brachypetali

Table 2 Synoptic table of the *Quercus coccifera* Mediterranean shrublands showing the frequencies of species in each of the identified associations and sub-associations

Group number	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3
Number of relevés	86	6	41	28	6	27	23	4
Character species of Quercetea, Quercetalia, Quercion ilicis								
Quercus coccifera	V	V	V	V	V	V	V	V
Pistacia terebinthus	II	II	IV	III	III	I	I	III
Lonicera implexa	II	III	I	II	III		I	
Rubia peregrina	II		IV	III	II	II	IV	
Calicotome villosa	III	I	III	IV	IV	III	I	
Quercus ilex	I		V	I	I			
Phlomis fruticosa	I	II	IV	IV	II	I	I	
Cistus creticus	IV	I	IV	IV	IV	III	I	II
Cistus salviifolius	II			III	II	II	II	
Euphorbia acanthothamnu	I			II	I	III	II	
Erica manipuliflora	I		IV	III	I			
Juniperus oxycedrus	II		III	I	I			
Myrtus communis	III		IV	II	I		I	
Olea europaea	III	V	IV	III	II	III		II
Urginea maritima	I		II	IV		IV	III	
Spartium junceum	I		I	III	II	I		
Genista acanthoclada	I			III		III		III
Cercis siliquastrum	I	I	IV	I	II			
Micromeria juliana	I	IV	V	III	I	I		
Arbutus unedo	II		V	III	II			
Erica arborea	II		IV	II	II		I	
Clematis flammula	I		IV	III	I			
1. Character species of Querco cocciferae-Pistacietum lentisci								
Pistacia lentiscus	IV	II	IV	IV	IV			
Phillyrea media	IV	V	V	IV	IV	II		
Asparagus acutifolius	V	V	IV	V	IV			
Geranium lucidum	II	V	IV		I			
Ruscus aculeatus	I		III	IV	I			
Medicago minima	I	V	IV	I	I			
Clematis vitalba	II		IV	III				
Teucrium capitatum	III		III	III	I		I	
Pyrus spinosa	II	III	III	I	I	I		
Teucrium chamaedrys	I	III	I	I	I		II	
Smilax aspera	II		III	III	II		I	
Quercus pubescens		II	IV	I				
Medicago lupulina		II	II	I	I			
Anthyllis hermanniae	I		IV	IV	I	I		
Rosa canina	I	II	III	I	I			
Melica ciliata	I		IV	II		I		
Paliurus spina-christi		III	I	III	II			
1.1 Character species of Querco cocciferae-Pistacietum lentisci typicum								
Juniperus phoenicea	IV						I	II
Thymus sibtthorpii	V							
Vicia parviflora	V							
Fumana arabica	III	I				I		
Arisarum vulgare	III					I	I	
Prasium majus	III			I		I		

Group number	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3
Number of relevés	86	6	41	28	6	27	23	4
Fumana thymifolia	III		I	I		I		
Carex distachya	III							
Cistus monspeliensis	III							
Vicia cretica	III							
Brachypodium sylvaticum	III			II		I		
Tamus communis	III							
Lagurus ovatus	III	I						
Campanula glomerata	III							
Helictotrichon convolutum	II			I				
Lonicera etrusca	II						I	
Piptatherum miliaceum	II			I		II		II
Lonicera xylosteum	II							
Centaurium tenuiflorum	II							
Psoralea bituminosa	II			I				
Melica minuta	II							
Micromeria graeca	II							
Muscari comosum	II							
Scorzonera crocifolia	II							
Petrorhagia dubia	II	I					I	
Lavandula stoechas	II							
Valantia muralis	II							
Asterolinon linum-stellatum	II							
Crupina crupinastrum	II	I						
Asperula rigida	II							
Silene sieberi	I							
Bromus fasciculatus	I	I						
Teucrium alpestre	I							
Papaver rhoeas	I							
Bupleurum fruticosum	I							
Anemone coronaria	II					II		II
Melittis melissophyllus	I							
Silene gigantea	II							
Astragalus monspessulanum	II							
Euphorbia cyparissias	II			I				
Scutellaria rupestris	II							
Trifolium hirtum	I							
Potentilla micrantha	IV		I			I		
Helichrysum microphyllum	III				I			
Thlaspi perfoliatum	II			I		I	I	
Piptatherum coerulescens	IV					II		
Gastridium ventricosum	III						II	
Crepis cretica	III					I	I	
Muscari spreitzenhoferi	III					I		
1.2 Character and diagnostic species of Querco cocciferae-Pistacietum lentisci euphorbietosum rigidae								
Euphorbia rigida	IV							
Prunus cocomilia	IV	I						
Ornithogalum nutans	IV							
Lagoecia cuminoides	IV	I	I			I	I	
Rhagadiolus stellatus	IV	I	I					
Ranunculus rumelicus	III					I		

Table 2 (continued)

Group number	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3
Number of relevés	86	6	41	28	6	27	23	4
Anemone pavonina		III		I				
Silene cretica		III		I	I		I	
Trifolium grandiflorum		III						
Veronica arvensis	I	III		I				
Arabis verna		III					I	II
Cardamine hirsuta		III		I				II
Torilis nodosa		II	I	I				
Vicia cuspidata		II			I			
Sherardia arvensis		II		I				
Aubrieta deltoidea		II	I		I			
Cerastium comatum	I	II						
Minuartia hybrida		I		I				

1.3 Character and diagnostic species of Quercococciferae-Pistacietum lentisci arbutetosum andrachni

Arbutus andrachne			V	III				
Melica rectiflora			V	III		II		
Colutea arborescens			IV					
Stipa capensis			IV			I		
Trifolium squamosum	I		IV					
Fumana procumbens			IV	III				
Origanum vulgare			IV	I				
Hippocrepis emerus			IV	III				II
Dittrichia viscosa			IV					
Trifolium scabrum			IV	I				II
Agrostis capillaris			IV					
Laurus nobilis			IV		I			
Convolvulus elegantissima			III	I				
Vicia tenuifolia			IV					
Silene atropurpurea			III	II			I	
Bromus arvensis			III	I	I			
Carpinus orientalis	l		III					
Crepis neglecta			II	II				
Rhus coriaria			II	V				
Bromus intermedius			III	I		I	I	

1.4 Character and diagnostic species of Querco cocciferae-Pistacietum lentisci fraxinetosum orni

Fraxinus ornus	I			IV				
Crataegus monogyna	I	III		IV				
Crepis hellenica				III	I			
Hedera helix	I			III			I	
Abies cephalonica	I		I	III				
Hypochaeris achyrophorus	I			III		I	I	
Campanula ramosissima				II				
Clinopodium vulgare				II		I		
Lathyrus laxiflorus			I	II	I			
Adiantum capillus-veneris				I				
Centaurea cyanus				I				

1.5 Character and diagnostic sp. of Querco cocciferae-Pistacietum lentisci anthemidetosum tinctoriae

Anthemis tinctoria				II	IV			
Aegilops triuncialis				I	IV			

Group number	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3
Number of relevés	86	6	41	28	6	27	23	4
Orlaya daucoides					IV			
Avena sterilis	I	I			III			
Ballota acetabulosa			I	I	III			
Bromus squarrosus					III			
Sonchus oleraceus			I	I	III			
Carex halleriana	I			I	II			
Convolvulus althaeoides				I	II	I		
Dorycnium pentaphyllum		I		I	II			
Galium laconicum				I	II			
Milium vernale				I	I			

2. Character species Rhamno lycioidis-Quercetum cocciferae Braun-Blanquet & Bolòs 1954

Rhamnus lycioides			I	I		IV	II	IV
Asparagus aphyllus				I		V	IV	
Daphne sericea	I			II		III	III	V
Centaurea raphanina				II		II	IV	II
Sarcopoterium spinosum			II	II		III	I	
Lamyropsis cynaroides					I	II	III	II
Reichardia picroides				II		II	I	II
Origanum onites	I			I		II	I	
Orchis quadripunctata				I		II	I	II
Cyclamen graecum				I		I	III	
Biscutella didyma						I	I	II
Satureja thymbra				I	I	I	II	
Phlomis lanata				I		IV	II	
Acer sempervirens				II		II	V	II
Asteriscus spinosus	I			II		III	I	
Euphorbia characias				I		I	III	II
Lathyrus aphaca				I			I	III

2.1 Character and diagnostic species of Rhamno lycioidis - Quercetum cocciferae phagnaletosum graeci

Phagnalon graecum				II		IV	I	
Linum strictum				I		II		II
Gagea graeca				I		II		
Cyclamen creticum				I		II	I	
Rumex tuberosus				I		II	I	
Anemone hortensis					I	III	I	
Anthyllis vulneraria			II	I		III		
Ricotia cretica	I					II		
Asphodeline lutea						III	I	
Sedum litoreum	I					I		

2.2 Character and diagnostic sp. of Rhamno lycioidis - Quercetum cocciferae berberidetosum creticae

Berberis cretica							IV	II
Daucus guttatus				I			II	
Arum idaeum	I						III	
Erophila verna						I	III	
Cardamine graeca							III	II
Anthemis rigida					I		III	II

Table 2 (continued)

Group number	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3
Number of relevés	86	6	41	28	6	27	23	4
2.3 Charact. and diff. species of Rhamno lycioidis - Quercetum cocciferae cerastietosum brachypetali								
Cerastium brachypetalum			II				I	V
Polygala venulosa			I		I			III
Arenaria leptoclados								II
Alyssum minutum	I							II
Rhamnus alaternus				I				II
Companion species								
Bromus sterilis	II	V	III	I	III	II		
Salvia fruticosa	I			II	I	III	I	II
Sanguisorba minor	I	I	I	I	II		II	
Anthoxanthum odoratum	I	IV	IV	I	I		II	II
Scaligeria napiformis	I	I	I	III	I	II	I	II
Lamium amplexicaule		IV		I			III	II
Stellaria media		II		III	I		I	
Stipa bromoides		I	IV	III		II	I	
Pteridium aquilinum		III	I	I	III			
Carlina corymbosa	II	II	I	III		II	III	II
Cynosurus effusus		II	I	I			II	
Poa bulbosa			II	II		II	I	
Dactylis glomerata	II	IV	IV	IV		IV		
Galium aparine		V	I	III	III		I	
Galium murale		V		I	I	I	III	II
Leontodon tuberosus		IV		II		III	I	
Trifolium angustifolius	I		IV	II			I	
Trifolium campestre		II	IV	III	II	II	I	
Trifolium fragiferum			IV	II		II		
Trifolium physodes	V		III	I			II	III
Trifolium stellatum		II	II	III	II	II		
Trifolium tomentosum				I		II	I	II
Trifolium uniflorum		II		I		II	I	IV
Aira elegantissima	II		I	II			I	II
Allium subhirsutum				III		II		
Cynosurus echinatus	I		IV	I		I	III	
Geranium robertianum			II	I		III	I	
Eryngium campestre	II		II	I		II	III	II
Geranium rotundifolium			II	I	I		II	
Osyris alba			I	I		III		
Asplenium ceterach		I	II	I			I	
Avena barbata			IV	III		III		
Brachypodium distachyon			I	II	I			
Briza maxima			I	II			I	
Coridothymus capitatus	IV		IV	III		III		
Carex flacca	I		III	II		II		
Hypericum empetrifolium	II		III	III	II	III		
Crepis fraasii			III	II		II	III	
Brachypodium retusum			IV		II	II	II	II
Asphodelus ramosus			III			IV	III	II
Bromus madritensis			I	I		I	II	
Catapodium rigidum			I	I		I	I	II
Crucianella latifolia	I		I	II			I	II

Group number	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3
Number of relevés	86	6	41	28	6	27	23	4
Geranium molle			II	I		I	I	
Campanula spatulata			III	I		II	III	II
Blackstonia perfoliata			I	I				
Cyclamen hederifolium	I	II		II	I			
Teucrium divaricatum				I		I		
Teucrium microphyllum						I		
Bupleurum glumaceum			I	I				
Cerastium glomeratum			I	I	I			
Ceratonia siliqua				I	I			
Daucus carota			I	I				
Dorycnium hirsutum			II	II				
Echinops ritro			I		I			II
Erodium cicutarium			I	I			I	
Galactites tomentosa	I			I			I	
Galium monachinii						I	I	
Helichrysum conglobatum			I				I	
Hordeum bulbosum				I	I	I	I	
Hordeum murinum			I			I	I	
Hypericum perfoliatum				II	I			
Iris unguicularis			I	II		II	I	
Knautia integrifolia			I	I				
Legousia hybrida							I	
Leontodon cichoriaceus	I		I					II
Lolium rigidum			I	I		I		
Micromeria nervosa				I		I		
Myosotis ramosissima	I			I			I	
Ononis spinosa				I		I		II
Picnomon acarna		I	I		I	I		
Scorzonera cretica				I		I		
Silene vulgaris			I	I		I		II
Stellaria pallida				I		I		
Tordylium apulum				II				
Urospermum picroides				I	I			
Vicia grandiflora			I					II
Anthemis chia	I			I		I	I	

Species with a single appearance have been omitted. Character and diagnostic species for each vegetation unit are shown in rectangles. Frequency classes are: I=species recorded in 1–20% of all relevés of each vegetation unit, II=21–40%, III=41–60%, IV=61–80%, V=81–100%

soil properties vary from relatively deep and productive to shallow and infertile. The shrub layer cover varies from 20% to 90%, and the understory is rather dense reaching up to 70%.

Distribution records: Cholomon, Lesvos, Mavrovouni, Akarnanika, Oiti, Telethrio, Ainos, Taigetos, Acherontas, Arakinthos, Erimanthos, Chelmos, Arta, Parga, Andros, Kithira, Sounio, Mani, Ochi, Dikti-Lasithi, Parnitha, Lefkada, Kalo Oros, Rodopos, Ampelos, Kerkis, and Lefka Ori.

Nomenclatural and syntaxonomic notes: This association is widespread in the Mediterranean Basin and it is one of the first associations described by Braun-Blanquet et al. (1936), in Southern France and Western Mediterranean. As a result of its wide distribution the same association has been described by many researchers, while in some cases, the same formations are classified under different associations. We adopted the same typification as Rivas-Martínez et al. (2001, 2002), which renamed it as Querco cocciferae–Pistacietum lentisci Br.-Bl., Font Quer, G. Br.-Bl., Frey, Jansen, & Moor 1936 nom. mut. propos (art. 45; addenda) in the checklist of plant communities of Spain. Despite its wide distribution and the subsequent variation in the local ecological conditions, there is a constant presence of diagnostic Mediterranean shrubs of higher taxa (e.g., *Quercus ilex*, *Olea europaea* var. *sylvestris*, *Pistacia terebinthus*, *Calicotome villosa*, *Erica manipuliflora*, *Spartium junceum*, *Arbutus unedo*, *Erica arborea*).

As expected, an association with such a wide distribution is further distinguished in sub-associations reflecting variation in its composition as a result of local floristic influences and variations in the ecological conditions.

1.1 Querco cocciferae–Pistacietum lentisci typicum (Table 2, Group 1.1; Fig. 2)

Character species: *Juniperus phoenicea*, *Thymus sibthorpii*, *Vicia parviflora*, *Fumana arabica*, *Arisarum vulgare*, *Prasium majus*, *Fumana thymifolia*, *Carex distachya*, *Cistus monspeliensis*, *Vicia cretica*, *Brachypodium sylvaticum*, *Tamus communis*, *Lagurus ovatus*, *Campanula glomerata*, *Potentilla micrantha*, *Helichrysum microphyllum*, *Piptatherum coerulescens*, *Gastridium ventricosum*, *Crepis cretica*, *Muscari spreitzenhoferi.*

Ecology: Mean ecological parameters of the association: subhumid Mediterranean climate, limestone (flysch and schist) substrates; mean slopes 30%, shrub cover of 60%, and herbs 40%; moderate grazing.

Distribution records: Andros, Kithira, Taigetos, Aherontas, Arakinthos, Arta, Telethrio, Mavrovouni, Sounio, Mani, Ochi, Dikti-Lasithi, Parnitha, Lefkada, Ainos, Kalo Oros, Rodopos, Vertiscos, Holomon, Ampelos, Kerkis, Lefka Ori.

Nomenclatural and syntaxonomic notes: The sub-association shares most of the floristic characteristics described above for the association, including the majority of the typical Mediterranean evergreen shrubs. *J. phoenicea* is a character species of the sub-association especially on areas with a strong maritime influence. On the other hand, Mavrommatis (1980) distinguished similar communities with the abundance of *J. phoenicea* as Oleo-lentiscetum juniperetosum. There are also similarities with plant communities outside Greece including Pistacio lentisci–Juniperetum phoeniceae Trinajstić 1987 identified by Pandża (2004) in Croatia (island of Murter) and Quercetum cocciferae brachypodietosum or Cocciferetum brachypodietosum in the Quercetum cocciferae association identified by Wraber (1952) in Southern France.

1.2 Querco cocciferae–Pistacietum lentisci euphorbietosum rigidae (Table 2, Group 1.2; Fig. 2)

Character and diagnostic species: *Euphorbia rigida*, *Prunus cocomilia*, *Ornithogalum nutans*, *Lagoecia cuminoides*, *Ranunculus rumelicus*, *Anemone pavonina*, *Silene cretica*, *Trifolium grandiflorum*, *Veronica arvensis*, *Arabis verna*, *Cardamine hirsuta*.

Ecology: Altitudinal range of 650–850 m, subhumid Mediterranean climate, limestone (schist) substrates, gentle slopes (10–25%), mean shrub cover 30% and herbs 40%; severe grazing and frequent wild fires.

Distribution records: Lesvos.

Nomenclatural and syntaxonomic notes: This sub-association is floristically the most dissimilar in comparison with Querco cocciferae–Pistacietum lentisci typicum. Due to its proximity to Turkey, it is enriched with floristic elements from Minor Asia (Rechinger 1943; Davis 1965–1985; Edmondson 1982; Hansen and Nielsen 1993). Further, its distribution in relatively higher altitudes leads to the absence of character shrubs and climbing species of Quercion ilicis, such as *Q. ilex*, *C. villosa*, *O. europaea* var. *sylvestris*, *Myrtus communis*, *Cercis siliquastrum*, *Cistus salviifolius*, *Urginea maritima* (*Drimia maritima*). The sub-association has a floristic relationship to the Siderito dichotomae–Quercetum cocciferae identified by Karaer et al. (1999) in Keltik Valley of Minor Asia.

1.3 Querco cocciferae–Pistacietum lentisci arbutetosum andrachni (Table 2, Group 1.3; Fig. 2)

Character and diagnostic species: *Arbutus andrachne*, *Melica rectiflora*, *Colutea arborescens*, *Stipa capensis*, *Trifolium squamosum*, *Fumana procumbens*, *Origanum vulgare*, *Hippocrepis emerus*, *Dittrichia viscosa*, *Trifolium scabrum*, *Agrostis capillaries*, *Laurus nobilis*, *Convolvulus elegantissima*, *Vicia tenuifolia*, *Silene atropurpurea*, *Bromus arvensis*, *Carpinus orientalis*, *Bromus intermedius.*

Ecology: Mean altitude of 400 m (90–900 m), subhumid to humid (more than 1,000 mm of precipitations) Mediterranean climate, limestone (flysch) substrates, mean slopes

30%, mean shrub cover 60% (30–80%), and herbs cover 40%; moderate grazing.

Distribution records: Western Greece and along the central axis of peninsular Greece: Akarnanika, Oiti, Telethrio, Ainos, Taigetos, Acherontas, Arakinthos, Erimanthos, Chelmos, Arta, Parga.

Nomenclatural and syntaxonomic notes: The character species are more hygrophilous including *A. andrachne*, *C. arborescens*, *L. nobilis*, *C. orientalis*, *and Rhus coriaria*.

This sub-association has similarities with plant communities beyond the Quercetea ilicis in Northern Greece including *Q. coccifera–C. orientalis* described by Chasapis et al. (2004) in Chortiatis and Coccifero–Carpinetum described by Oberdorfer (1948). We noted also some similarities with plant communities outside Greece such as Melico–Quercetum cocciferae Br. Bl., Silva and Rozeira 1964 identified in Southern France.

1.4 Querco cocciferae–Pistacietum lentisci fraxinetosum orni (Table 2, Group 1.4; Fig. 2)

Character and diagnostic species: *Fraxinus ornus*, *Crataegus monogyna*, *Crepis hellenica*, *Hedera helix*, *Abies cephalonica*, *Hypochaeris achyrophorus.*

Ecology: Mean altitude of 550 m (150–900 m), subhumid to humid Mediterranean climate, limestone (flysch) substrates, mean slopes 30%, mean shrub cover 60% (20–80%), and herbs cover 50%; moderate to severe grazing.

Distribution records: Western Greece and Peloponnese: Acherontas, Arakinthos, Arta, Parga, Oiti, Erimanthos, Chelmos, Taigetos.

Nomenclatural and syntaxonomic notes: The floristic composition of the sub-association includes a large number of relatively hygrophilous species (e.g., *F. ornus*, *H. helix*, *Clinopodium vulgare*, *Lathyrus laxiflorus*, and *Adiantum capillus–veneris*) while the endemic *A. cephalonica* is present in higher altitudes. Querco cocciferae–Pistacietum lentisci fraxinetosum ornus appears to have similarities with plant communities outside Greece and especially with Crataego monogynae–Quercetum cocciferae described by Martínez-Parras et al. (1985), in the medium Mediterranean subhumid bioclimatic zone, in Spain. Further, this sub-association is reported by Ladero et al. (2002) in the surroundings of Alhama de Granada Baths and Costa et al. (1998) in Portugal.

1.5 Querco cocciferae–Pistacietum lentisci anthemidetosum tinctoriae (Table 2, Group 1.5; Fig. 2)

Character and diagnostic species: *Anthemis tinctoria*, *Aegilops triuncialis*, *Orlaya daucoides*, *Avena sterilis*, *Ballota acetabulosa*, *Bromus squarrosus*, *Sonchus oleraceus*.

Ecology: Altitudinal range of 450–750 m, subhumid Mediterranean climate, schist (limestone) substrates, mean slopes 25%, northeast–south orientations, mean shrub cover 50% (30–70), and herb cover 60%; moderate to severe grazing.

Distribution records: Mavrovouni.

Nomenclatural and syntaxonomic notes: Despite the subhumid climate, we noted the presence of xerophilic species probably as a result of severe grazing. Raus (1980) has distinguished within the shrublands of Mavrovouni, a degraded low forest of the Ostryo–Carpinion orientalis (Quercetalia pubescentis, Querco–Fagetea), rich in *C. orientalis*, on areas that have sufficient water supply (*Q. coccifera–C. orientalis* community).

2. Rhamno lycioidis–Quercetum cocciferae Braun-Blanquet and Bolòs 1954 (Table 2, Group 2; Fig. 2)

Character species: *Rhamnus lycioides*, *Asparagus aphyllus*, *Daphne sericea*, *Centaurea raphanina*, *Sarcopoterium spinosum*, *Lamyropsis cynaroides*, *Reichardia picroides*, *Origanum onites*, *Orchis quadripunctata*, *Cyclamen graecum*, *Biscutella didyma*, *Satureja thymbra*, *Phlomis lanata*, *Acer sempervirens*, *Asteriscus spinosus*, *Euphorbia characias*, *Lathyrus aphaca.*

Ecology: Mean ecological parameters of the association: semiarid Mediterranean climate, limestone substrates, terra rossa, rendzina, and alluvial soils; all the orientations, mean slopes 40%, shrub cover 40%, and herb cover 10%; moderate to severe grazing. Especially for Crete, there is a precipitation gradient from west (subhumid) to east (semidry) and from the sea level to the top of the three main mountainous massives (Lefka Ori, Idi, and Dikti).

Distribution records: Mainly in Crete and some other islands of the Aegean: Dikti-Lasithi, Dikti-Omalos, Thryptis, Moni Kapsa, SE Crete, Giouchtas, Idi, Lefka Ori, Sounio, Ochi, Andros.

Nomenclatural and syntaxonomic notes: The character species is *R. lycioides* (*R. graecus*), which thrives in sunny and dry environments. The abundance of *S. spinosum*, *P. lanata*, *Ononis onites*, *E. characias*, *Phagnalon graecum*, and *S. thymbra* demonstrates the important phryganic influence of the association. This association which is mainly restricted to Crete includes many local endemic species, such as *Ph. lanata*, *Ebenus cretica*, *C. raphanina* subsp. *raphanina*, *Scorzonera cretica*, *Teucrium microphyllum*, *Teucrium alpestre*, *C. cretica*, and some protected species such as *Ophrys* spp. or *Orchis* spp. There is a wide variety of shrublands, from well conserved and dense to more degraded accompanied by species like *U. maritima* (*D. maritima*), *Asphodelus aestivus*, and *Asphodeline lutea*. This association has been identified by many phytosociologists working in the western Mediterranean and particularly in the Iberian Peninsula in regions of similar bioclimatic type. The association presents similarities with Asparago–Rhamnetum oleoidis cocciferetum Rivas Goday 1959 and

Rhamno velutini–Quercetum cocciferae (Rivas-Martinez et al. 2001). Moreover, Rivas-Martinez et al. (2001) identified in the Iberian Peninsula a superior taxonomic unit the Rhamno lycioidis–Quercion cocciferae Rivas Goday ex. Rivas Martinez 1975.

2.1 Rhamno lycioidis–Quercetum cocciferae phagnaletosum graeci (Table 2, Group 2.1; Fig. 2)

Character and diagnostic species: *P. graecum*, *Linum strictum*, *Gagea graeca*, *Cyclamen creticum*, *Rumex tuberosus*, *Anemone hortensis*, *Anthyllis vulneraria*, *Ricotia cretica*, *A. lutea*, *Sedum litoreum*.

Ecology: Wide altitudinal range from 20 to 1,600 m with a mean of 700 m; mean slopes 40%, shrub cover of 30–90% (mean 40%), and herb cover 20%. The areas where the sub-association is found have the driest climate in the country and grazing is severe.

Distribution records: Dikti-Lasithi, Dikti-Omalos, Thryptis, Moni Kapsa, SE Crete, Giouchtas, Idi, Sounio, Ochi.

Nomenclatural and syntaxonomic notes: This sub-association is considered as the more xerothermic expression of the association and is mainly distributed in the eastern and central parts of Crete comprising many phryganic species, such as *P. graecum*, *A. vulneraria*, *A. lutea*.

2.2 Rhamno lycioidis–Quercetum cocciferae berberidetosum creticae (Table 2, Group 2.2; Fig. 2)

Character and diagnostic species: *Berberis cretica*, *Daucus guttatus*, *Arum idaeum*, *Erophila verna*, *Cardamine graeca*, *Anthemis rigida*.

Ecology: Altitudinal range from 200 to 1,600 m with a mean of 800 m; mean slopes 40%, shrub cover between 40–90% (mean 50%) and herb cover 10%; Severe grazing.

Distribution records: Dikti-Lasithi, Dikti-Omalos, Thryptis, Idi, Andros.

Nomenclatural and syntaxonomic notes: The sub-association was identified in the higher altitudes and degraded areas of Eastern and Central Crete, where grazing activities are important. The character species is the well adapted to grazing spiny shrub of Cretan mountains *B. cretica,* which originates from the neighboring orophrygana. Orophrygana is the endemic habitat of the upper altitudinal zone of Cretan mountains (>1,100 m), characterized by *B. cretica*, *Astragalus angustifolius*, and *Euphorbia acanthothamnos*, which results from the broad contact between phrygana (in lower altitudes) and hedgehog heaths in supra- and oro-Mediterranean zones of Crete (Tsiourlis et al. 2001). The sub-association includes many Cretan endemic species, such as *Centaurea idaea*, which is typical in high altitudes.

2.3 Rhamno lycioidis–Quercetum cocciferae cerastietosum brachypetali (Table 2, Group 2.3; Fig. 2)

Character and diagnostic species: *Cerastium brachypetalum*, *Polygala venulosa*, *Arenaria leptoclados*, *Alyssum minutum*, *Rhamnus alaternus.*

Ecology: Altitudinal range from 600 to 1,300 m; mean slopes 40%, shrub cover of 50–90% (mean 60%) and herbs 15%; Severe grazing. The main character of the areas where the sub-association is found is the high level of precipitations which exceeds 1,500 mm (Grove et al. 1993). Shallow calcareous lithosols and rendzina soils dominate throughout much of the massif. They often represent degraded soil profiles with limited water supply (Vogiatzakis et al. 2003); Severe grazing.

Distribution records: Lefka Ori.

Nomenclatural and syntaxonomic notes: *P. venulosa* is a species with distribution in Southern Greece, the Aegean, Anatolia, and Cyprus. Lefka Ori has a high number of endemic plants (Strid 1996).

Discussion

Q. coccifera Greek shrublands have suffered dramatic changes under anthropogenic activities (coppice, overgrazing, and deforestation) that have affected both their physiognomy as well as their floristic composition. Human pressure has also affected the distribution of these formations which often extend beyond their natural distribution limits, occupying areas abandoned by species less resistant to human activities (Dafis and Jahn 1975; Barbero and Quézel 1976; Raus 1980; Pavlides 1982; Vardakis et al. 1987; Bergmeier 1990; Konstantinidis 1990; Theodoropoulos 1991; Dimopoulos 1993; Chasapis et al. 2004). Moreover, this highly anthropogenic distribution and composition of *Q. coccifera* shrublands led some ecologists to suggest that these ecosystems should not be classified below the level of the association (Raus 1980; Bergmeier 1990). The unwillingness, however, to classify *Q. coccifera* shrublands below the association level has resulted in the "blanket" classification of all *Q. coccifera* dominated shrublands under Quercetum cocciferae, based only on physiognomic criteria and avoiding further classification, which in reality shows important floristic variation.

Shrublands with *Q. coccifera* in continental and insular Greece, apart from Crete, are mainly distributed within the growth zone of *P. lentiscus* that characterizes the Thermo-Mediterranean bioclimate (Debazac 1969; Mavrommatis 1980). These shrubland formations consist mainly of sclerophyllous species such as *Q. coccifera*, *P. latifolia*, and *J. phoenicea*, while some thermophillous deciduous broadleaved species often participate at lower percentages.

The results of the current study suggest that the *Q. coccifera* shrublands in Greece within the Quercetea ilicis vegetation zone, the natural growing zone of *Q. coccifera*, can be divided into two broad groups defined primarily by their geographic distribution. The first group comprises the *Q. coccifera* shrublands of continental as well as insular Greece apart from Crete, while the second group comprises those of Crete.

The first group was classified under the Querco cocciferae–Pistacietum lentisci while the second group under the Rhamno lycioidis–Quercetum cocciferae. The two associations are clearly separated along the first ordination axis of the DCA analysis (Fig. 2), where the former occupies the left part and the latter the right part of the axis. The ordination diagram suggests that the relevés collected from Akarnanika, which is the region with the highest amount of annual rainfall among the study areas, are plotted on the far left part of the axes, while those collected from Crete, and especially central and eastern Crete, which are the driest areas, are plotted on the far right part of the axis. This indicates that the main variation in species composition of the *Q. coccifera* shrublands of Greece, as expressed by the identification of two different associations, is related primarily to differences in rainfall and consequently to soil moisture availability.

Querco cocciferae–Pistacietum lentisci was recorded almost in the entire continental Greece and on most islands, with a considerably lower occurrence on Crete. The association has a distribution mainly in the subhumid Mediterranean climatic zone characterized by a mean altitude of 500 m. Occasionally, it is found beyond these limits exploiting gaps created in local communities by anthropogenic activities. In those cases, the association is enriched with species of the upper vegetation of thermophillous deciduous oaks Quercetea pubescentis. The percentage cover in the shrub layer is mainly a function of the local environmental conditions and especially of the local anthropogenic pressures: dense in depressions and scarce around settlements and areas where grazing is intense.

According to our results throughout Greece, *P. lentiscus* and *Ph. latifolia* coexist within the Quercetea ilicis, apart from Crete, and are among the most common accompanying species in the *Q. coccifera* shrublands. Thus, the association Querco cocciferae–Phillyreetum mediae (latifoliae) described, among others, by Barbero and Quézel (1976); Bergmeier (1990) and Dimopoulos (1993) for different regions of Greece is in fact similar to the Querco cocciferae–Pistacietum lentisci association described here. Mavrommatis (1980) classifies the same formations in Greece under the Oleo–Lentiscetum, while Horvat et al. (1974) identified Coccifereto–Lentiscetum in the warmer areas of Eastern, Central, and Southern Greece, as well as in Southern Chalkidiki and in the island of Thassos in Northern Greece.

The wide distribution of the association results in a number of sub-association reflecting local peculiarities. The five identified sub-associations are clearly separated along the second ordination axis of the DCA analysis (Fig. 2). The lower part of the axis is occupied by Querco cocciferae–Pistacietum lentisci typicum which, as already noted, occurs on areas which are relatively less degraded by intense human presence. On the upper part of the axis, on the other hand, the relevés from the island of Lesvos are plotted, which are the most degraded among the studied areas, forming the Querco cocciferae–Pistacietum lentisci euphorbietosum rigidae. The relevés collected from the rest of the areas are plotted in between the above two forming three additional sub-associations occurring on areas with intermediate level of human pressure. Thus, the second axis appears to be representing a gradient of human induced degradation.

The significant effect of human pressure led many researchers to suggest that *Q. coccifera* shrublands are of secondary nature, mainly due to grazing and coppicing for firewood production that has led to the degradation of *Pinus halepensis* or *Pinus brutia* forests (e.g., Horvat et al. 1974; Barbero and Quezel 1976; Mavrommatis 1980; Konstantinidis 1990; Bergmeier 1990). According to our results, human-induced degradation can cause differentiations in *Q. coccifera* shrublands allowing some elements of the neighboring flora to participate and often alter both the physiognomy and the floristic composition of the shrublands.

Rhamno lycioidis–Quercetum cocciferae association is found mainly on Crete as a result of the drier conditions prevailing on most part of the island compared to the rest of the country. The association is floristically enriched by a significant number of species characteristic of semidry and dry environments and also grazing resistant species, such as species characteristic of the abundant phryganic ecosystems in the island (Tsiourlis et al. 2007). An important differentiation from the widespread previous association is its altitudinal distribution: almost from the sea level to almost the timber line (1,600 m asl; Tsiourlis et al. 2001). The Cretan forests are differentiated from the neighboring areas such as Peloponnese and Middle East, by belonging exclusively to the Quercetea ilicis in all the altitudinal range (Barbero et Quézel 1980), while communities from Quercetea pubescentis common in the others parts of the country, like *Q. pubescens* and *Q. frainetto* forests (e.g., Horvat et al. 1974; Raus 1980; Konstantinidis et al. 2002) or even *Castanea sativa* forests (e.g., Raus 1980; Bergmeier 1990; Konstantinidis et al. 2008) are absent in Crete (Zaffran 1990). It appears the primary forest of Crete used to be a dense sclerophyllous Mediterranean forest (Greuter 1966). So the *Q. coccifera* shrublands of Crete are degradation forms of these primary forests with *Q. coccifera* accompanied by *Q. ilex*, which currently has only limited local

distribution (Greuter 1966; Zaffran 1990; Kypriotakis et al. 1996). Quézel (1981), also believes that climax plant communities in the Mediterranean zone were not always forests, so well as Kypriotakis et al. (1996) and Tsiourlis et al. (2001) and that applies especially in Crete.

The identification of three sub-associations of the Rhamno lycioidis–Quercetum cocciferae is primarily the result of the west–east gradient of precipitation and, to a lesser extent, the result of the varying degree of degradation, which is severe almost everywhere in Crete.

As already mentioned, the current study is confined within the Quercetea ilicis vegetation zone. However, *Q. coccifera* formations often extend beyond this vegetation zone. Bergmeier (1990) stated that the classification of *Q. coccifera*-dominated vegetation units, from meso-Mediterranean levels up to montane levels, comprise at least two classes being syntaxonomically involved, i.e., Quercetea ilicis and Quercetea pubescentis, or even three, if Rhamno–Prunetea is adopted as a class of its own. Karagiannakidou-Iatropoulou (1983) and Chasapis et al. (2004) adopted syntax mentioned by Raus (1980) for E. Thessaly for the pseudomaquis of Mt. Chortiatis (N Greece) and assigned them also to Quercetea pubescentis (Ostryo–Carpinion orientalis and Quercion confertae). Thus, it appears that there is a need to conduct an even wider sampling and use of bibliographical relevés beyond Quercetea ilicis in order to achieve a complete classification for the entire *Q. coccifera* shrublands of Greece.

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