Phytosociological and ecological discrimination of Mediterranean cypress ('Cupressus sempervirens') communities in Crete (Greece) by means of pollen analysis

José Antonio López-Sáez, Arthur Glais, Ioannis Tsiripidis, Spyros Tsiftsis, Daniel Sánchez-Mata, Laurent Lespez

ARTICLES

Mediterranean Botany
ISSNe 2603-9109

EDICIONES COMPLUTENSE

https://dx.doi.org/10.5209/mbot.59789

Phytosociological and ecological discrimination of Mediterranean cypress (*Cupressus sempervirens*) communities in Crete (Greece) by means of pollen analysis

José Antonio López-Sáez[1], Arthur Glais[2], Ioannis Tsiripidis[3], Spyros Tsiftsis[4], Daniel Sánchez-Mata[5] & Laurent Lespez[6]

Received: 5 April 2018 / Accepted: 29 April 2019 / Published online: 7 November 2019

Abstract. Sixty modern surface samples collected from mosses in different cypress forest communities (*Cupressus sempervirens* L.) on the island of Crete (Greece) were analysed for their pollen content. The samples were taken from six different cypress phytosociological associations between 23 and 1600 m asl, and fall within distinct rainfall and temperature regimes. The aims of this paper are to provide new data on the modern pollen rain from the Aegean islands, and to perform these data using multivariate statistics (hierarchical cluster analysis and canonical correspondence analysis) and pollen percentages. The discrimination of pollen assemblages corresponds to a large extent to the floristic differentiation of *Cupressus sempervirens* forest vegetation and indicates the existence of three new associations.
Keywords: *Cupressus sempervirens*; Crete; Greece; Palynology; Phytosociology; Multivariate Analyses.

Discriminación fitosociológica y ecológica de las comunidades de ciprés (*Cupressus sempervirens*) en Creta (Grecia) mediante análisis polínico

Resumen. Sesenta muestras de lluvia polínica actual recolectadas en cepellones de musgos, procedentes de distintas comunidades de ciprés (*Cupressus sempervirens* L.) en la isla de Creta (Grecia), fueron analizadas palinológicamente. Las muestras proceden de seis asociaciones fitosociológicas dominadas por el ciprés entre 23 y 1600 m asl, bajo regímenes de precipitación y temperatura diferentes. El objetivo de este trabajo es prover datos novedosos acerca de la lluvia polínica actual en las islas del Egeo, así como tratar éstos mediante análisis multivariantes (análisis de cluster jerárquico y análisis de correspondencias canónicas) y a partir de sus porcentajes polínicos. La discriminación de los espectros polínicos corresponde en gran medida a la diferenciación florística de la vegetación de los bosques de *Cupressus sempervirens* e indica la existencia de tres nuevas asociaciones.
Palabras clave: *Cupressus sempervirens*; Creta; Grecia; Palinología; Fitosociología; análisis multivariantes.

Introduction

The Mediterranean, common, or Italian cypress (*Cupressus sempervirens* L.) is a medium-size evergreen coniferous tree whose natural habitats are found in the semi-arid mountains around the eastern Mediterranean basin and the Middle East. It has been widely cultivated and naturalized elsewhere since historical periods and its natural range is unclear (Eckenwalder, 2009; Caudullo & De Rigo, 2016). Natural stands occur in the eastern Mediterranean basin over several geographically non-adjacent areas reaching eastwards the Caucasus and south-western Iran, from sea level (Crete) up to 2000 m asl in Turkey (Intini & Della Rocca, 2004). Its natural distribution comprises the Aegean islands (Greece), Cyprus, Turkey (south Anatolia), north-east Africa (Libya, Tunisia), and the Middle East (Iran, Jordan, Lebanon and Syria) (Farjon & Filer, 2013), where cypress occurs mostly as disjunct populations (Zohary, 1973; Roques *et al*., 1999). Two morphological varieties of cypress are known (Tutin *et al*., 1993): the wild type var. *horizontalis* (Miller) Aiton, which is widely represented by native populations and is characterized by a broad conical crown with the main branches forming a wide angle with the trunk; while the fastigiated var. *pyramidalis* Nymann (= var. *stricta* Aiton) is the most widely planted and cultivated since ancient times for its columnar and dense crown with main branches growing upwards close to the trunk (Zacharis, 1977; Farjon, 2010).

1 Grupo de Investigación Arqueobiología, Instituto de Historia, CCHS, CSIC. Albasanz 26-28. 28037 Madrid. Spain. E-mail: joseantonio.lopez@cchs.csic.es
2 University of Caen Normandy, CNRS, EPHE PSL, Université d'Angers, Université de Bretagne Occidentale, Université de Nantes, Université de Rennes 2, UMR LETG. Esplanade de la Paix. 14032 Caen. France. E-mail: arthur.glais@unicaen.fr
3 School of Biology, Aristotle University of Thessaloniki. P.O. Box 104. 54124 Thessaloniki. Greece. E-mail: tsiripid@bio.auth.gr
4 Department of Forestry and Natural Environment Management, Eastern Macedonia & Thrace Institute of Technology. 66100 Drama. Greece. E-mail: stsiftsi@bio.auth.gr
5 Departamento de Pharmacology, Pharmacognosy, and Botany, Facultad de Farmacia. Universidad Complutense. 28040 Madrid. Spain. E-mail: dsmata@ucm.es
6 LGP-UMR 8591 CNRS, Université de Paris Est-Créteil. 1 place Aristide Briand. 92195 Meudon Cedex. France. E-mail: laurent.lespez@u-pec.fr

Genetic and palaeobotanical data (Papageorgiou *et al*., 1993, 1994, 2005; Korol *et al*., 1997; Bagnoli *et al*., 2009; Manescu *et al*., 2011; Velitzelos *et al*., 2014) point out: i) high genetic differentiation between natural and domesticated cypress populations; ii) the reduction in allelic richness in Italian and Tunisian populations due to genetic drift originating from a long tradition of cypress cultivation and/or a drastic reduction in effective population sizes of natural cypress since the Tertiary; and, iii) that the present natural populations of Mediterranean cypress are just the remnants of an extensive cypress forest of the Pliocene, distributed throughout the central and eastern Mediterranean areas, which was progressively disappearing as a consequence of human activities (irrational felling, grazing and wildfires) and canker disease caused by *Seridium cardinale* (Wag.) Sutton & Gibson, particularly in the island of Crete (Papanastasis *et al*., 1990; Xenopoulos *et al*., 1990; Rackham & Moody, 1996). In Greece, the Mediterranean cypress is native only in Crete and some of the East Aegean islands (Samos, Rhodes, Kos, Symi, Milos, Chios, Kalymnos; perhaps also in Thasos and Samothraki) (Papageorgiou *et al*., 2005; Brofas *et al*., 2006; Dimopoulos *et al*., 2013). The Greek *Cupressus sempervirens* woods are included in the Natura 2000 network of Protected Natural Areas of Greece (Habitat 9290) and they are considered of high conservation value because they comprise an endemic and rare habitat type, which is important for endemic species and it faces several threats (Papastergiadou *et al.*, 1997; Dafis *et al.*, 2001; Dimopoulos *et al.*, 2006). *Cupressus sempervirens* is a pioneer species, growing quickly on most types of soils, including rocky and compact ones, such as calcareous, clayish, dry and poor soils (Xenopoulos *et al.*, 1990). It is adapted to the Mediterranean climate with dry and hot summers and rainy winters, as well as to the semi-arid climate in the eastern and interior areas of its range (Farjon, 2010). The Mediterranean cypress is able to tolerate prolonged drought and high temperatures. Particularly, the var. *horizontalis* is resistant to ignition because of the high ash content and the ability of the leaves to maintain a high water content during the summer (Della Rocca *et al*., 2015).

Although Cretan cypress forests have been relatively well studied from a phytosociological point of view, there are still a number of controversies among researchers as well as confusing syntaxonomic assignments. A first approach was done by Zohary & Orshan (1965), who described the *Cupresseto-Aceretum orientalis* association and its corresponding *cupressetosum* subassociation, also previously informally described by Rechinger & Rechinger-Moser (1951), limited to the highest altitudes. Later, Barbero & Quézel (1980) corrected the illegitimate nomenclature of Zohary & Orshan (1965), recognizing the new association *Luzulo nodulosae-Cupressetum sempervirentis* as the most widespread in the island between 1000–1100 m asl and even constituting the tree line over 1600–1700 m asl. They recognized three subassociations: the aforementioned *cupressetosum* in the supra-mediterranean bioclimatic belt, and the two new *pinetosum brutiae* (meso-mediterranean) and *berberidetosum creticae* (montane mediterranean belt).

In a later work, concerning orophilous communities from the central and eastern Mediterranean area, Brullo *et al.* (2001) described two new associations of *Cupressus sempervirens* woodlands with very open canopy in the Lefka Ori range: the first one in the lower and middle montane mediterranean belts at 1000–1400 m asl (*Daphno sericeae*-*Cupressetum sempervirentis*), and the second one at the timberline (1400–1800 m asl) in the upper montane to oro-mediterranean belts (*Junipero oxycedri*-*Cupressetum sempervirentis*). These two new communities have been considered by Bauer & Bergmeier (2011) as synonymous with the *Luzulo nodulosae-Cupressetum sempervirentis* association and the *Luzulo nodulosae-Cupressetum sempervirentis berberidetosum creticae* subassociation, respectively. Brullo *et al.* (2001) situate both new associations within the *Pino-Juniperetea* class due to the abundance of orophilous shrubs. More recently, Brofas *et al.* (2006) described five communities characterized by the constant presence of *Cupressus sempervirens* in combination with other tree or shrub species: *Quercus coccifera*, *Q. ilex*, *Erica arborea*, *Acer sempervirens* and *Pistacia lentiscus*. The former, with kermes oak, was found between the thermo- and the lower supra-mediterranean bioclimatic belts (120–800 m asl) and occasionally in the upper supra-mediterranean and montane mediterranean ones (850–1240 m asl) on limestone, marly conglomerates, schists or, more rarely flyschs. The one with lentisk occurs mainly in the thermo-mediterranean belt (10–300/350 m asl) and rarely extend to the meso-mediterranean one (250–550 m asl) on similar soil types. They also documented in their relevés the *Luzulo nodulosae-Cupressetum sempervirentis* association, but they were not able to distinguish the three subassociations described by Barbero & Quézel (1980); although they differentiate this association from the community formed by the cypress and *Acer sempervirens* precisely by the presence of the latter species in the lower and middle montane mediterranean belts (1100–1500 m asl) on hard limestone rocks and occasionally in the supra-mediterranean belt at 800 m asl on schists and even in the upper montane and oro-mediterranean ones (1500–1800 m asl) also on limestone. The authors consider the *Acer sempervirens*-*Cupressus sempervirens* community as a high altitude endemic woodland association restricted to Crete, although they do not clasiffy it in a certain syntaxonomical rank. In fact, from a bioclimatic and floristic point of view this community resembles the *Daphno sericeae*-*Cupressetum sempervirentis* association described by Brullo *et al.* (2001). Two other cypress communities cited by Brofas *et al.* (2006) with *Quercus ilex* and *Erica arborea* also occupies the thermo- and the meso-mediterranean bioclimatic belts (200–550 m asl), growing on relatively moist sites.

Finally, in the most recent work we know to deal with cypress communities, Bauer & Bergmeier (2011) make a detailed review of cypress mountain woodlands of western Crete above 500 m asl, although the authors do not use Brullo *et al.* (2001) and Brofas *et al.* (2006) relevés because they are considered incomplete. They cite the rare presence of cypress in relevés of the *Aceri sempervirentis-Quercetum calliprini* association in the Psiloritis range (900–1385 m asl), i.e. in mixed woodlands invariably composed by *Quercus coccifera* and *Phillyrea latifolia*, where the presence of *Quercus ilex* and *Acer sempervirens* is also occasional. Some inventories of this association resemble floristically those of the *Quercus coccifera*-*Cupressus sempervirens* community described by Brofas *et al.* (2006) that occasionally reaches the montane mediterranean belt. Bauer & Bergmeier (2011) also recognize in their relevés the *Luzulo nodulosae-Cupressetum sempervirentis cupressetosum* subassociation between the meso– and the supra-mediterranean belts (400–1070 m asl), which, unlike indicated by Brofas *et al.* (2006), incorporates *Acer sempervirens* but also *Pinus brutia*. They also recognize the two other subassociations described by Barbero & Quézel (1980): *berberidetosum creticae* (830–1480 m asl) and *pinetosum brutiae* (150–1075 m asl). Bauer & Bergmeier (2011) point out that there is a gradual transition between *Pinus brutia* and *Cupressus sempervirens* forests without obvious ecological evidence (Rechinger & Rechinger-Moser, 1951). In fact, pine forests other than included in the *pinetosum brutiae* subassociation occur on the lower slopes of the southern foothills of Crete. Among these, Barbero & Quézel (1980) described the *Irido cretensis-Pinetum brutiae* community for thermophilous woodlands located at lower altitudes (300−800 m asl), which often incorporate isolated *Cupressus sempervirens* trees.

In this paper, we study modern pollen samples from Crete to discriminate *Cupressus sempervirens* forest communities, that is, the exploration of how well local vegetation is represented in pollen samples-assemblages. The advantage of modern pollen rain studies is that cushion mosses collect the airborne pollen of the last 5−30 years (Pardoe *et al.*, 2010), while the floristic inventories depend intrinsically on the season of the year in which they are made. In this sense, multivariate analyses are a powerful tool in the comparison and diagnosis of different plant communities from their pollen content in Mediterranean European countries (Court-Picon *et al.*, 2006; Mazier *et al.*, 2006; López-Sáez *et al.*, 2010, 2013, 2015; Glais *et al.*, 2016). The main objectives of our study are (i) to explore how contemporary vegetation is depicted in surface pollen assemblages, (ii) to identify pollen indicators of *Cupressus sempervirens* forest syntaxa, and, (ii) to establish statistic relationships between pollen rain and vegetation patterns in order to use them for paleoecological reconstruction in future studies.

Material and Methods

Study area

The island of Crete is located south of the Aegean Sea in the southeastern part of the Mediterranean region (Figure 1). With 8336 km^2 (the maximum length is 269 km and the maximum width 60 km) is the largest island of Greece and the fifth largest island of the Mediterranean (Legakis & Kypriotakis, 1994). It is an extremely mountainous territory with four main massifs from west to east: Lefka Ori or White Mountains range (Pahnes: 2453 m asl), Psiloritis or Ida range (Timios Stravos: 2456 m asl), Asterousia range (Kofinas: 1231 m asl) and Dikti range (Spathí: 2148 m asl). Various calcarerous rocks (limestones and dolomites) dominate the mountain areas, whereas Neogene sediments (limestones, sandstones and marls) cover large areas of the lowlands. There are also ortho-quartzites, phyllites, flyschs, Quaternary rocks and alluvian deposits (Higgins & Higgins, 1996).

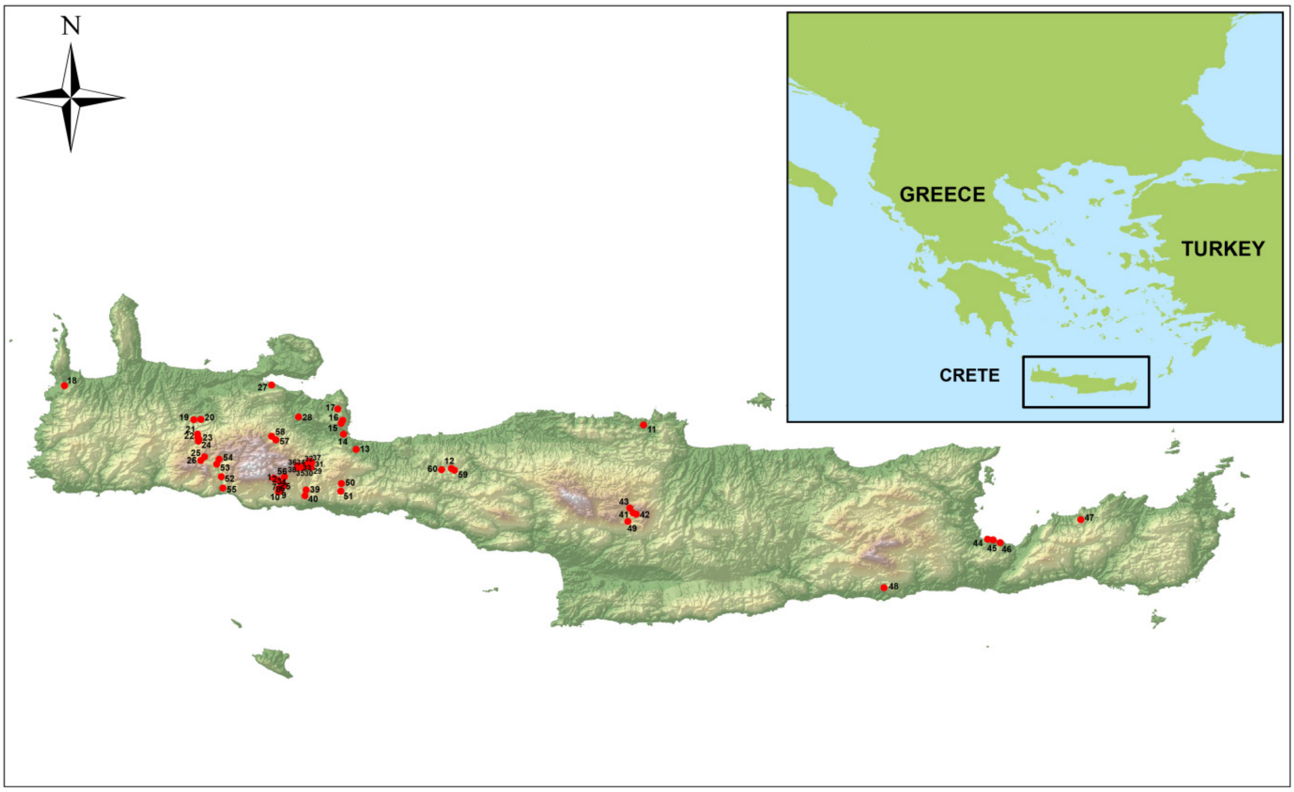

Figure 1. Map showing the surface pollen samples on Crete (Greece).

The Cretan climate is typically Mediterranean with hot and dry summers, and mild and wet winters. The mean annual rainfall is about 750 mm, and decreases from west (2118 mm on the Askifou upland, 740 m asl) to east (440 mm on the plain of Ierapetra, 10 m asl) and from north (Mediterranean pluviseasonal oceanic) to south (Mediterranean xeric oceanic), but increases with altitude (Naoum & Tsanis, 2004; Koutroulis *et al.*, 2011). There is also a slight increase (1–1.5ºC) in mean annual temperature from northwest to southeast and a decrease with altitude. The eastern and southern parts of the island are more arid than the western and northern ones, as there is higher precipitation in the northwestern coastal areas and lower in the southeastern part of the island (Chartzoulakis & Psarras, 2005). Crete belongs to the Cretan biogeogaphical subprovince, Graeco-Aegean province, Eastern Mediterranean subregion, Mediterranean region (Rivas-Martínez *et al.*, 2004).

Table 1. Site characteristics for the 60 modern pollen surface samples on the island of Crete. Abbreviations are: Lat. N: Latitude N; Long. E: Longitude E; TC: tree cover; GP: grazing pressure; TA: annual temperature; TM: max temperature of warmest month; Tm: min temperature of coldest month; PA: annual precipitation; PM: precipitation of wettest month; Pm: precipitation of driest month; BT: bedrock type (LD: limestone and dolomite; D: deposits; L: limestone; S: schists; F: flyschs).

Sample	Altitude (m asl)	Lat. N	Long. E	Aspect	TC	GP	TA	TM	Tm	PA	PM	Pm	BT
CS01	1600	35.26628	24.08713	W	1	3	10.9	22.4	-1.4	999.0	194.0	6.0	LD
CS02	1575	35.26383	24.09011	W	1	3	10.9	22.4	-1.4	999.0	194.0	6.0	LD
CS03	1525	35.26223	24.09747	SW	3	2	11.0	22.4	-1.3	997.0	194.0	6.0	LD
CS04	1312	35.25397	24.10791	S	4	2	12.0	23.3	-0.2	963.0	190.0	5.0	LD
CS05	1130	35.24908	24.11154	S	4	2	13.6	24.9	1.5	911.0	181.0	4.0	LD
CS06	1030	35.24264	24.09952	SE	4	2	14.7	26.0	2.5	865.0	173.0	3.0	LD
CS07	1005	35.24154	24.10394	SE	4	2	14.4	25.6	2.3	879.0	176.0	4.0	LD
CS08	925	35.23839	24.10145	SE	4	3	14.4	25.6	2.3	879.0	176.0	4.0	D
CS09	875	35.23489	24.09878	SE	4	3	15.6	26.7	3.6	804.0	163.0	3.0	D
CS10	837	35.23431	24.09785	S	4	4	15.6	26.7	3.6	804.0	163.0	3.0	D
CS11	55	35.39009	24.94583	NW	4	2	18.0	28.6	7.0	565.0	109.0	1.0	S
CS12	418	35.28882	24.49980	N	4	2	16.4	27.4	4.1	783.0	159.0	2.0	L
CS13	27	35.33333	24.27897	W	3	2	17.9	29.3	6.1	576.0	115.0	1.0	L
CS14	23	35.36890	24.24966	W	3	3	18.3	29.2	6.6	579.0	117.0	1.0	S
CS15	296	35.39367	24.24410	SE	3	3	17.4	28.2	5.8	664.0	135.0	2.0	LD
CS16	323	35.40058	24.24771	SE	3	3	17.2	28.0	5.7	675.0	137.0	2.0	L
CS17	284	35.42717	24.23641	S	3	2	17.4	28.0	6.4	656.0	133.0	2.0	L
CS18	178	35.48124	23.60171	SE	3	1	17.7	28.0	7.3	567.0	114.0	1.0	LD
CS19	348	35.40187	23.90172	W	3	3	16.4	28.0	4.4	653.0	131.0	2.0	LD
CS20	467	35.40316	23.91829	NW	4	3	16.2	27.9	4.2	671.0	135.0	2.0	L
CS21	950	35.36863	23.91020	NE	4	3	13.4	25.7	0.5	838.0	166.0	5.0	L
CS22	1008	35.36195	23.91130	NE	4	2	13.0	25.1	0.3	861.0	170.0	5.0	LD
CS23	1110	35.35596	23.91369	S	4	1	12.7	24.7	0.1	875.0	173.0	5.0	L
CS24	1077	35.35271	23.91283	S	4	1	12.7	24.7	0.1	875.0	173.0	5.0	LD
CS25	1428	35.31643	23.92660	S	4	2	12.5	24.4	0.3	880.0	176.0	5.0	L
CS26	1229	35.30792	23.91812	SE	4	2	12.8	24.6	0.8	872.0	175.0	5.0	L
CS27	67	35.48237	24.08233	SE	3	3	18.2	29.3	6.6	584.0	117.0	1.0	L
CS28	190	35.40837	24.14508	SE	3	3	17.7	29.0	5.6	613.0	123.0	1.0	LD
CS29	730	35.29179	24.17448	SE	4	2	13.8	25.8	1.4	893.0	178.0	4.0	LD
CS30	826	35.29258	24.17020	SE	5	1	13.8	25.8	1.4	893.0	178.0	4.0	D
CS31	957	35.30251	24.17552	SE	5	1	14.1	26.0	1.8	880.0	175.0	4.0	LD
CS32	1122	35.30161	24.16758	SE	4	1	13.1	24.9	0.9	932.0	185.0	5.0	L
CS33	1127	35.29942	24.16540	SE	5	1	12.8	24.6	0.5	938.0	186.0	5.0	S
CS34	1138	35.29508	24.15833	N	4	1	12.2	24.0	-0.1	957.0	188.0	5.0	L
CS35	1209	35.29118	24.15338	N	4	2	12.1	23.9	-0.1	954.0	188.0	5.0	S
CS36	1228	35.29522	24.14306	E	3	2	12.1	24.0	-0.2	961.0	188.0	6.0	L
CS37	1055	35.30538	24.17095	E	3	3	13.1	24.9	0.9	932.0	185.0	5.0	L
CS38	1217	35.29114	24.14364	E	3	3	12.2	24.0	-0.1	954.0	187.0	5.0	L
CS39	739	35.23943	24.16299	E	4	3	15.0	26.0	3.2	843.0	171.0	3.0	L
CS40	699	35.22589	24.16004	E	4	2	15.7	26.7	4.0	799.0	163.0	3.0	L
CS41	1347	35.18610	24.92163	SW	4	2	11.7	24.1	-1.4	1033.0	209.0	5.0	LD
CS42	1377	35.18327	24.92849	SW	4	1	11.9	24.1	-1.0	1033.0	210.0	4.0	LD
CS43	1406	35.19708	24.91408	SW	4	3	11.6	24.1	-1.6	1034.0	209.0	5.0	L
CS44	26	35.12477	25.74405	N	3	3	18.2	28.2	7.6	562.0	118.0	1.0	L
CS45	64	35.12318	25.75691	N	4	0	18.3	28.3	7.8	550.0	115.0	1.0	F
CS46	57	35.11705	25.77376	N	4	0	18.8	28.9	8.2	510.0	106.0	1.0	F
CS47	298	35.17038	25.96087	N	2	1	17.2	27.6	6.4	673.0	140.0	2.0	D
CS48	446	35.01228	25.50378	S	2	2	17.1	28.2	5.6	679.0	140.0	2.0	D
CS49	938	35.16627	24.90959	SW	4	1	13.5	25.4	0.7	1026.0	211.0	3.0	L

Sample	Altitude (m asl)	Lat. N	Long. E	Aspect	TC	GP	TA	TM	Tm	PA	PM	Pm	BT
CS50	977	35.25457	24.24462	N	4	1	13.7	25.0	1.8	923.0	186.0	4.0	L
CS51	735	35.23638	24.24345	N	4	2	14.9	26.2	3.2	855.0	174.0	3.0	L
CS52	529	35.26975	23.96583	W	5	1	15.4	26.9	4.1	724.0	149.0	3.0	L
CS53	486	35.29888	23.95535	S	5	1	15.3	27.7	2.6	709.0	146.0	3.0	L
CS54	1113	35.31020	23.96105	SE	5	0	12.1	23.8	-0.2	899.0	181.0	5.0	L
CS55	230	35.24334	23.96927	W	4	2	16.4	27.1	5.6	685.0	140.0	2.0	LD
CS56	1445	35.26970	24.11235	SE	1	3	11.1	22.7	-1.2	990.0	194.0	6.0	L
CS57	1239	35.35537	24.09234	N	2	2	12.2	24.9	-1.1	924.0	181.0	5.0	L
CS58	1242	35.36366	24.08257	W	3	2	12.6	25.5	-1.0	906.0	178.0	5.0	LD
CS59	515	35.28507	24.50669	NW	5	1	16.3	27.4	4.0	799.0	162.0	2.0	L
CS60	429	35.28638	24.47743	W	5	1	16.5	27.6	4.3	762.0	154.0	2.0	LD

Field methods – vegetation and pollen sampling

Vegetation and pollen samples were collected in 2017 at 60 locations on Crete (Figure 1). Sampling sites were chosen to cover a certain variety of vegetation types in the whole island of Crete, in a wide altitudinal range, although the aim was mainly to analyse modern pollen rain in order to sample plant communities dominated or co-dominated by *Cupressus sempervirens*. Moss polsters samples were collected at each location to provide modern pollen data, with positional and altitudinal data recorded using a portable Juno 3D Trimble Ltd. Global Positioning System (GPS) device. Moss samples were collected over an area of approximately 100 m^2 by taking multiple moss polsters from the concerned site to ensure an even representation, following Sugita (1994) and Hicks *et al.* (2001) recommendations. The subsamples were sealed in plastic bags and mixed into one sample per site. A relevé of vegetation was also made at each sampling site following the physotociological approach (Braun-Blanquet, 1979). Ten environmental variables were available for 60 sites (Table 1). Six of these were bioclimatic variables obtained from the WorldClim database (Fick & Hijmans, 2017) in a 30-sec resolution (approximately 1 km^2), while the other four were tree cover, altitude, bedrock type and grazing pressure. Tree cover was graded on an ordinal scale from 1 to 5 at each sampling point (100 m^2) as follows: 5 (75–100%), 4 (50–75%), 3 (25–50%), 2 (5–25%), 1 (>0–5%). Bedrock types were obtained from the geological map of Greece at a scale of 1: 500,000 (I.G.M.E., 1983) and confirmed during the field study. Grazing pressure was estimated on a scale of 0 to 4 (Court-Picon *et al.*, 2006).

Laboratory methods – pollen

Moss polsters samples of approximately 10 cm^3 were homogenized prior to extraction. The samples were sieved through 1 mm screens to remove larger particles (e.g., leaves, twigs, and gravel) and then processed following the standard protocol developed by Faegri & Iversen (1989). Samples were stored in glycerol, mounted on microscope slides and examined with a Nikon Eclipse 50i light-microscope (Melville, NY, U.S.A.) to identify pollen, spores and non-pollen palynomorphs. Routine counting was carried out at 400x magnification. Pollen grains, spores and non-pollen palynomorphs were identified according to Moore *et al.* (1991) and López-Sáez & López-Merino (2007) at the lowest currently possible taxonomical level. "Type" groups of several taxa that are morphologically indistinguishable were used. This has been the case of Cupressaceae species present in Crete (*Cupressus sempervirens*, *Juniperus* sp.), as they share the same characteristics (stenopalynous) under the light microscopy (Moore *et al.*, 1991; Kurmann, 1994; Hidalgo *et al.*, 1999). *Erica arborea* and *Erica manipuliflora* pollen types were palynologically discriminated according to the Pal-Dat Palynological Database (www.paldat.org). *Erica arborea*-type was defined as small-size tetrahedral tetrads (pollen unit 10–25 µm) of spheroidal shape; while *Erica manipuliflora*-type was defined as medium-size tetrahedral tetrads (pollen unit 26–50 µm) of isodiametric shape. *Pistacia lentiscus* and *P. terebinthus* were palynologically identified according to Burgaz *et al.* (1994). A minimum of 300 pollen grains were identified and counted for each sample. Pollen percentages were calculated using a pollen sum excluding spores and non-pollen palynomorphs, and presented as bars in a pollen diagram. Tilia and TGView (Grimm, 1992) and CorelDraw software were used to plot the pollen diagrams (Figures 2 and 3). The terms 'local' and 'regional' used in the text refer to different pollen source areas according to Prentice (1985).

Statistical analyses

To identify clusters of samples based on their pollen content and hece to define specific *Cupressus sempervirens* forest communities, we used multivariate analysis. Only palynomorph taxa present at > 3% in at least one of the samples were included. The analyses were performed on recalculated percentages after all modifications had been made. Classification was performed by hierarchical cluster analysis (HCA) using the matrix of the Euclidean distance and Ward's minimum variance method (Ward, 1963) with software PAST (Hammer *et al.*, 2001). The percentage values of the taxa were not transformed. The hierarchical relationships between clusters are illustrated by the dendrogram in Figure 4. Later, we used ordination analyses to estimate the relationships between environmental variables, pollen assemblages and palynomorph types, eliminating those samples that the HCA clearly differentiated as not belonging to cypress forests (clusters Aa1 and Ba2b). Canonical correspondence analysis (CCA) was used as a unimodal interpretation method, because a previously applied detrended correspondence analysis (DCA) pointed to a unimodal response (gradient length > 2 standard deviation of species turnover units) of palynomorph types (variables) instead of lineal responses of taxa (ter Braak & Prentice, 1988). CCA was performed using square-root transformation of the percentage of palynomorph taxa and down-weighting of rare taxa (Figures 5 and 6) with CANOCO version 4.5 (ter Braak & Šmilauer, 2002). Each environmental variable was entered separately into the analysis and its significance was assessed using the Monte Carlo permutation test with 999 permutations. The analysis was run with scaling for inter-sample distances to relate the gradient in pollen assemblages to explanatory variables. Forward selection of explanatory variables was used to provide a ranking of the importance of specific variables and to avoid co-linearity (ter Braak & Šmilauer, 2012). The results are presented in Tables 2 and 3. Correlations between CCA axes and environmental variables were calculated using the non-parametric Kendall coefficient in Statistica 9.1 software (http://www.statsoft.com) and are presented in Table 4.

Table 2. Percentage variance explained by each environmental variable in CCA (999 unrestricted Monte Carlo permutations with a Bonferroni type adjustement) with this variable as the sole constraining variable.

Environmental variables	Explain %	F value	*p*
Altitude	4.3	2.3	0.028
Tree cover	3.6	0.5	0.001
Grazing pressure	4.2	0.2	0.034
TA	4.4	2.4	0.005
TM	4.7	2.1	0.015
Tm	3.9	2.3	0.006
PA	4.1	2.4	0.021
PM	3.1	2.4	0.001
Pm	2.4	2.4	0.001

Table 3. Eigenvalues, correlations between pollen taxa and environmental variables and canonical coefficients of the first four CCA axes. All four eigenvalues reported are canonical and correspond to axes that are constrained by the environmental variables (total inertia = 0.914).

Axis	1	2	3	4
Eigenvalues	0.256	0.097	0.046	0.033
Pollen taxa-environmental correlations	0.910	0.741	0.669	0.659
Cumulative percentage variance of pollen taxa	28.0	38.6	43.7	47.3
Cumulative percentage variance of pollen taxa-environmental relation	54.2	74.7	84.5	91.5

Table 4. Correlation (Kendall's coefficient) between environmental variables and CCA axes 1 to 4.

	Altitude	TC	GP	TA	TM	Tm	PA	PM	Pm	CCA1	CCA2	CCA3	CCA4
Altitude	1												
TC	-0.215	1											
GP	0.082	-0.655	1										
TA	-0.974	0.150	-0.032	1									
TM	-0.963	0.200	-0.022	0.974	1								
Tm	-0.959	0.129	-0.064	0.987	0.930	1							
PA	0.961	-0.131	0.070	-0.957	-0.941	-0.954	1						
PM	0.951	-0.104	0.052	-0.943	-0.929	-0.939	0.997	1					
Pm	0.966	-0.147	0.034	-0.986	-0.961	-0.971	0.947	0.935	1				
CCA1	-0.936	0.012	-0.026	0.955	0.907	0.950	-0.955	-0.956	-0.956	1			
CCA2	-0.075	0.512	-0.140	0.099	0.127	0.020	0.099	0.133	-0.157	0	1		
CCA3	-0.176	0.582	-0.389	0.208	0.169	0.278	-0.182	-0.135	-0.147	0	0	1	
CCA4	0.107	-0.539	0.625	0.041	0.001	0.046	0.022	0.051	-0.060	0	0	0	1

Nomenclature

Taxonomic nomenclature and authorities follow Dimopoulos *et al.* (2013, 2016). Syntaxonomical scheme, nomenclature, and syntaxa authorities follow the compilation and proposals of Mucina *et al.* (2016).

Results

The pollen and non-pollen palynomorph percentage data of the 60 modern surface samples (Figure 1, Table 1) are summarized in two pollen diagrams (Figures 2 and 3). A total of 67 pollen and non-pollen palynomorph taxa were identified during the analysis and counts of the 60 surface samples collected.

The 60 modern surface pollen samples (hereinafter samples) were classified by means of HCA into twelve sample groups, which correspond to ecologically and floristically interpretable vegetation units. On the first division level, the dendrogram of the HCA performed on pollen data (Figure 4) shows a good differentiation between forests dominated by cypress trees (cluster B) and mixed woodland formations of cypress and other species or woodlands hosting scattered cypress trees (cluster A). This division is probably related to high pollen frequencies (> 20%) of *Cupressus/Juniperus* pollen type in samples from cluster B (Figure 2). The next two clusters within cluster A are distinguished on the basis of high percentages (> 25%) of *Quercus ilex/coccifera* (cluster Aa) and *Pistacia lentiscus* (cluster Ab) respectively (Figure 3). Inside cluster Aa, we can detach, at a smaller range, the sub-clusters Aa1 and Aa2; respectively separating samples with *Cupressus/Juniperus* values lower than 3% (regional origin; sub-cluster Aa1) and ~15% (local origin; sub-cluster Aa2). Relating to cluster B, the major segregation separates Ba and Bb clades. The main disjunction promoted here is due to the high percentages (> 50%) of *Cupressus/Juniperus* pollen type in cluster Bb. The division of cluster Ba produced two main clades (Ba1 and Ba2). The first cluster Ba1 includes samples with *Cupressus/Juniperus* values ranging from 25 to 50% (except sample CS10), while in cluster Ba2 samples these values are less than 25%. Inside cluster Ba1, the sub-clusters Ba1a and Ba1b are segregated by the high values (12−38%) of *Pinus brutia* in the first and the very low (< 1%) in the second one (Figure 2). At a lower range, the sub-cluster Ba1a is subdivided into three clades as abundant *Berberis cretica*, *Prunus* and *Rhamnus* (Ba1a-1) or phrygana (*Sarcopoterium spinosum*, *Thymbra capitata*, *Verbascum*, *Euphorbia acanthothamnos*) pollen taxa (Ba1a-2 and 3) (Figure 3). Likewise, the sub-cluster Ba1b is also subdivided into three smaller clades depending on the abundance of *Pistacia lentiscus* (Ba1b-1), *Daphne* and *Berberis cretica* (Ba1b-2) or phyrgana pollen taxa (Ba1b-3). Finally, cluster Bb is subdivided into two main clusters (Bb1 and Bb2), segregated by the abundance of *Berberis cretica* and *Phlomis* in the first, as well as *Pinus brutia*, *Euphorbia acanthothamnos*, *Sarcopoterium spinosum* and *Thymbra capitata* in the second one (Figures 2 and 3).

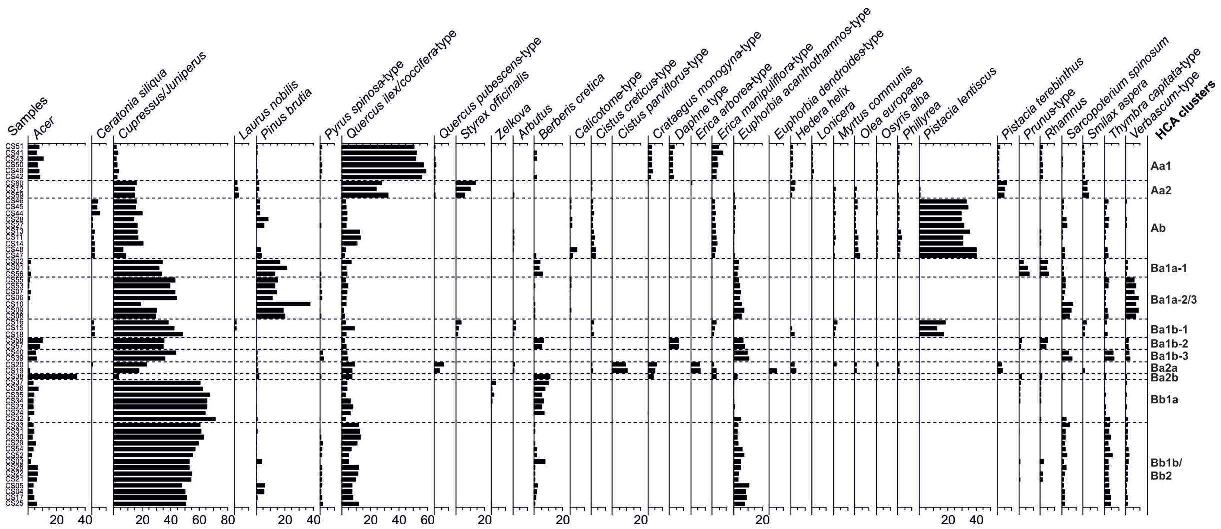

Figure 2. Percentage pollen diagram for trees and shrubs of the 60 surface samples on Crete.

The ordination of 53 sampling sites on the CCA biplot graph is shown in Figure 5, with arrows representing environmental variables, and their length linked to the correlation of the specific variable with the ordination axes. Thus, longer arrows indicate greater importance of the corresponding factor for sampling site variation. The samples corresponding to clusters Aa1 and Ba2b were not included in this analysis since they did not correspond to cypress forests. The first two axes of canonical correspondence analysis (CCA) explained 38.6% of the total pollen taxa variation and the first four axes 47.3% (Table 3). The first axis of the CCA explained almost 54.2% of the pollen taxa-environment relationship. The eigenvalue (0.256) corresponding to the first canonical axis is highly significant ($p < 0.001$), indicating significant difference in pollen assemblages among sampling sites. This CCA axis 1 seems to be strongly negatively correlated to altitude, PA, PM and Pm and positively correlated with TA, TM and Tm (Figure 5, Table 4). Many pollen taxa are discriminated along this axis (Figure 6); those displaying the highest species scores were typical of highland areas (negative values: e.g. *Prunus*, *Rhamnus*, *Zelkova*, *Daphne*, *Berberis vulgaris, Acer*) or maquis vegetation from lowlands (positive values: e.g. *Ceratonia siliqua*, *Prasium*, *Erica manipuliflora*, *Pistacia lentiscus*, *Cistus creticus*, *Calicotome*, *Olea europaea*, *Myrtus*). The second axis accounted for about 20% of the overall species-environment relationship ($r = 0.741$, $p < 0.001$) and was strongly associated with tree cover with high positive correlation, as well as with grazing pressure with low negative correlation (Figure

5, Table 4). Pollen taxa strongly associated with this axis are *Laurus*, *Pteridium*, *Pistacia terebinthus*, *Styrax*, *Ruscus*, *Smilax* and *Tamus* with positive correlation, and *Zelkova*, *Prunus* and *Rhamnus* with negative one (Figure 6). Another variable linked to human activities (e.g. grazing pressure), was also weakly correlated with this axis. The third axis (explaining 9.8% of the pollen taxa-environment relationship) seems to be fairly linked to tree cover and grazing pressure, and to a lesser extent to TA and Tm (Table 4).

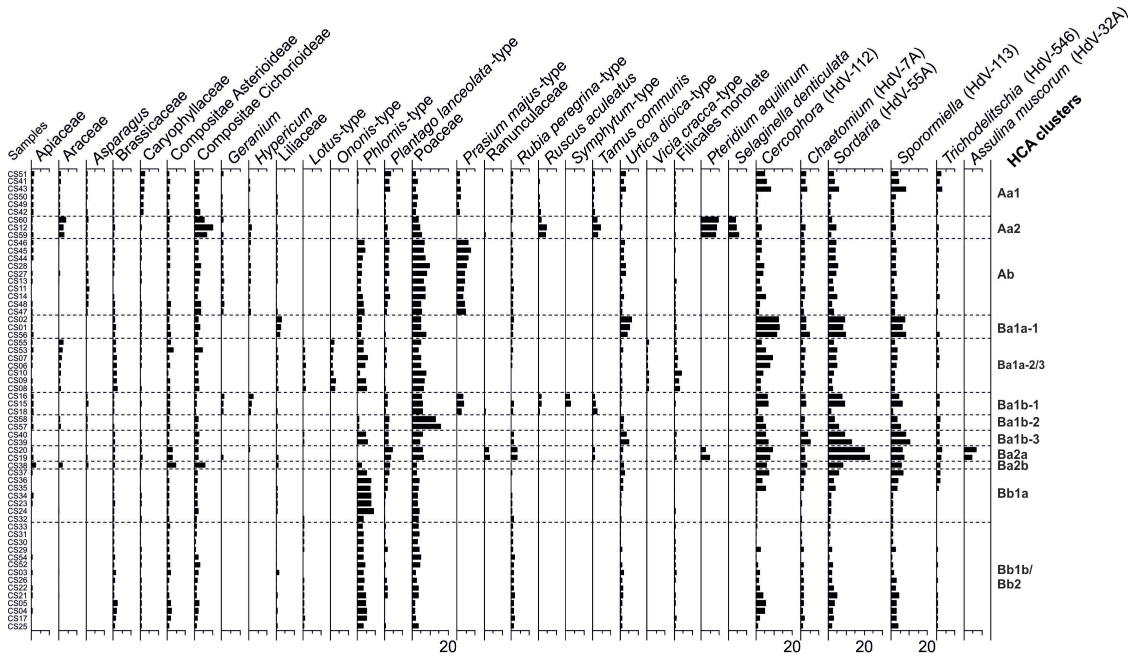

Figure 3. Percentage pollen diagram for herbs and non-pollen palynomorphs of the 60 surface samples on Crete.

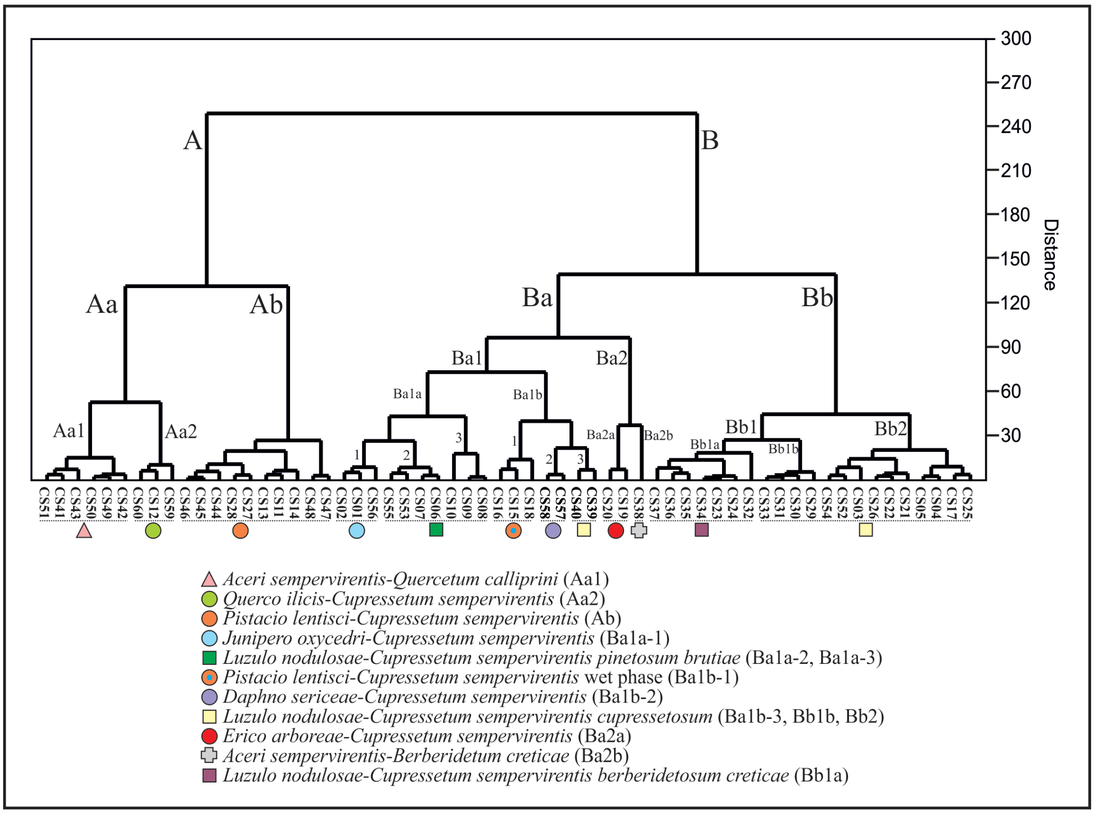

Figure 4. Hierarchical cluster analysis (HCA) dendrogram of the 60 modern pollen spectra.

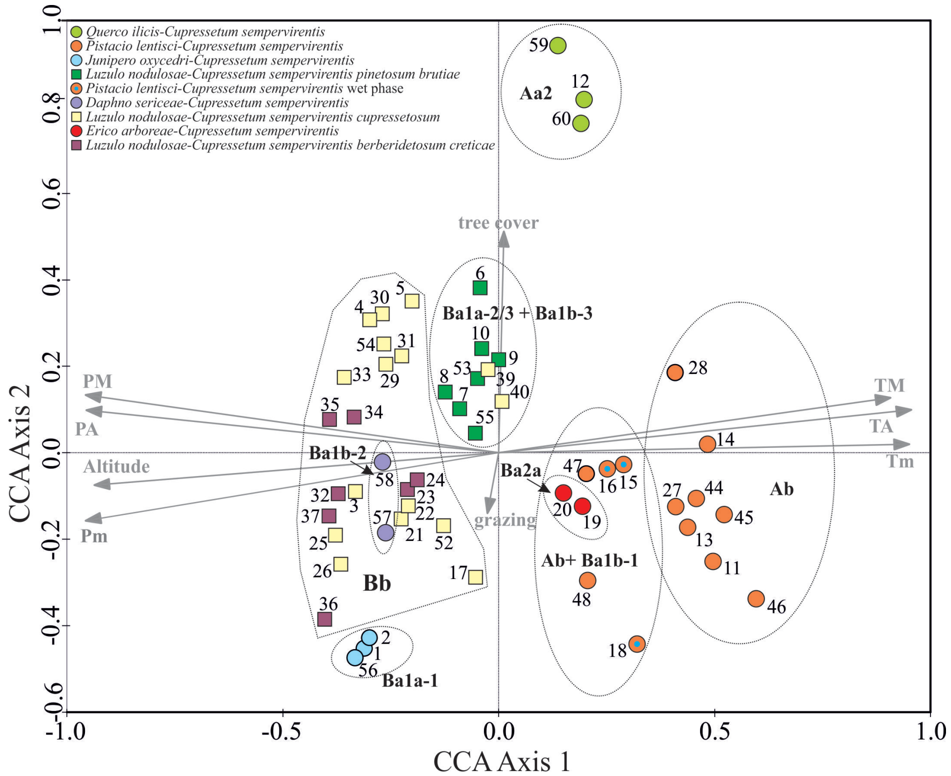

Figure 5. Ordination CCA-biplot of the first two canonical correspondence analysis axes of the 53 investigated modern surface pollen samples in the island of Crete. Vegetation units representing the plant communities defined by cluster analysis (Figure 4) are marked by different symbols and framed. Explanatory environmental variables are represented by gray arrows.

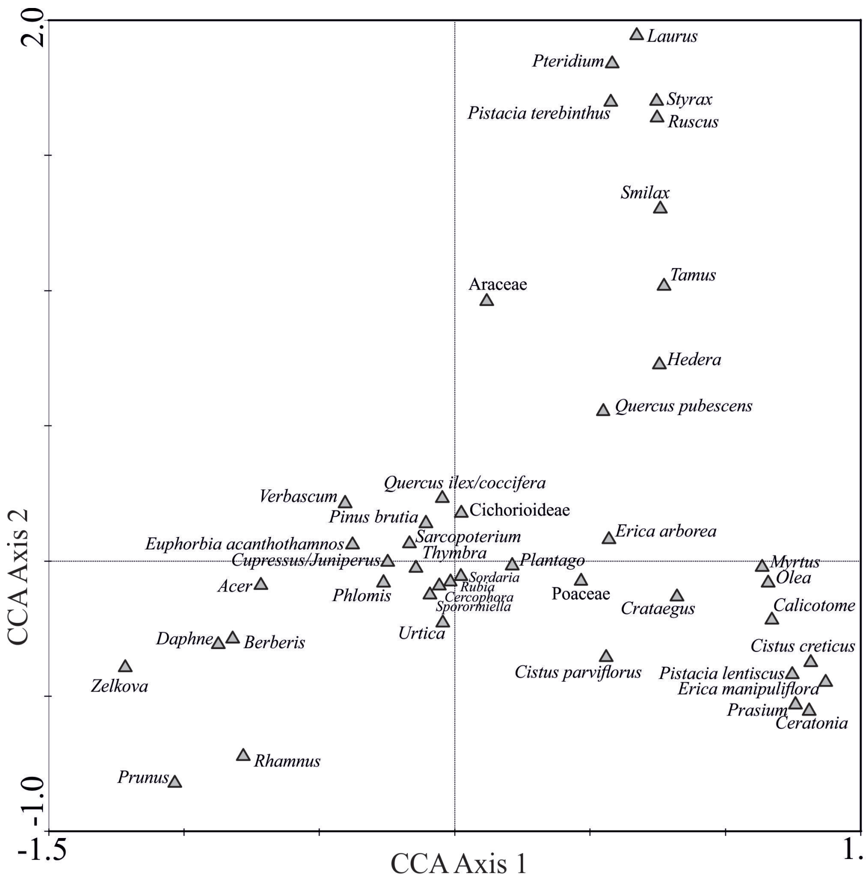

Figure 6. Ordination CCA-biplot of the first two canonical correspondence analysis axes of the main pollen and non-pollen palynomorph taxa.

Discussion

Cluster Ab of the HCA (Figure 4) represents thermo-mediterranean mixed woodlands dominated by *Pistacia lentiscus* and *Cupressus sempervirens*, growing on limestone and dolomite substrates, exceptionally on schists and flyschs, at low elevations (23−298 m asl) of northern Crete and punctually (meso-mediterranean belt) south of the island at 446 m asl (Figure 1, Table 1). Samples from cluster Ab are characterized by noticeable percentages of *Pistacia lentiscus* (30−40%), *Quercus ilex/coccifera* (2−13%) and *Cupressus/Juniperus* (7–19%), and significant frequencies (> 3%) of *Pinus brutia*, Poaceae, *Phlomis*, *Sarcopoterium spinosum*, *Thymbra capitata*, *Calicotome*, *Ceratonia siliqua*, *Erica manipuliflora*, *Olea europaea*, *Cistus creticus*, *Myrtus* and *Prasium majus* (Figures 2 and 3). Most of these pollen taxa are located on the positive side of CCA axis 1 (Figure 6), together with the samples of cluster Ab (Figure 5). All samples from cluster Ab are positively correlated with TA, TM and Tm, and negatively with PA, PM, Pm and altitude along CCA axis 1 (Figure 5). As a result of multivariate analyses (HCA, CCA), *Pistacia lentiscus*-*Cupressus sempervirens* woodland communities from Crete are very well discriminated from other cypress forests. This fact allows us to propose a new cypresswood association: *Pistacio lentisci-Cupressetum sempervirentis* Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova hoc loco* (Table 5, *holotypus*, relevé 8). It represents thermo(meso)-mediterranean xerophytic and thermophilous (PA: 510−679 mm; TA: 17.1−18.8 ºC; semi-arid to dry ombrotypes) cypress woodlands (Table 1). Floristically they are mainly characterized by *Cupressus sempervirens*, *Pistacia lentiscus*, *Prasium majus*, *Ceratonia siliqua*, *Erica manipulifora*, *Cistus creticus*, *Olea europaea*, *Myrtus communis*, *Phillyrea latifolia* and *Piptatherum miliaceum* (Table 5). This new association probably corresponds to the *Pistacia lentiscus*-*Cupressus sempervirens* community described by Brofas *et al.* (2006). Other pollen taxa with a constant presence and important values in samples from cluster Ab are pastoral indicators like *Plantago lanceolata* and *Urtica dioica*, and the coprophilous fungi *Cercophora*, *Chaetomium*, *Sordaria*, *Sporormiella* and *Trichodelitschia* (Figure 3) (López-Sáez & López-Merino, 2007). All these pollen/spore taxa have negative loadings in the CCA axis 2 (Figure 6), which is negatively correlated with grazing pressure (Figure 5, Table 4).

Cluster Aa1 of the HCA (Figure 4) represents woodland communities of mixed *Acer sempervirens* and *Quercus coccifera* formations, growing on calcareous substrates, at middle altitudes (735−1406 m asl) in the upper supra– and lower/middle montane mediterranean bioclimatic belts in the Lefka Ori and Psiloritis mountains (Figure 1, Table 1), corresponding to the *Aceri sempervirentis-Quercetum calliprini* community (Barbero & Quézel, 1980; Brullo *et al.*, 2004; Bauer & Bergmeier, 2011). The abundance of maple delimits the orophilous character of the community (Brullo *et al.*, 2001). This association occupies great extension in Crete, mainly in its northern half (Barbero & Quézel, 1980), often in N-SW expositions (Table 1). The most representative pollen taxa of these woodlands are *Quercus ilex/coccifera* (51−59%), *Acer* (6−11%), *Rhamnus*, *Erica manipuliflora, Hedera helix*, *Pistacia terebinthus*, *Crataegus monogyna* and *Daphne*, while *Cupressus/Juniperus* values are lower than 3.5% (Figure 2) due to the scarce presence of cypress trees in these woodlands or their regional character. These communities are subjected to strong pastoral pressure (Bauer & Bergmeier, 2011), and therefore the above-mentioned coprophilous fungi and anthropozoogenous taxa abound in cluster Aa1 samples (Figure 3).

Samples of cluster Aa2 are arranged in the same cluster (Aa) as those of cluster Aa1 (Figure 4) because they also have high values of *Quercus ilex/coccifera* (24−33%). However, both clusters differ because samples from Aa2 cluster have *Cupressus/Juniperus* percentages close to 15% (Figure 2), reflecting the local presence of cypress trees. Samples from cluster Aa2 are also characterized by noticeable values of *Pinus brutia* (1−2%), *Styrax officinalis* (6−13.6%), Compositae Cichorioideae (5−10%), *Pteridium aquilinum* (8−9%), *Pistacia terebinthus* (4.5−6.5%), Poaceae (4−6%), Araceae (2−4%), *Ruscus aculeatus* (2−4.3%), *Smilax aspera* and *Tamus communis* (2.5−4%), *Hedera helix* and *Laurus nobilis* (1−3%), *Selaginella denticulata* (4−5.5%), *Quercus pubescens*, *Myrtus communis, Asparagus* and *Hypericum* (Figures 2 and 3). Samples of cluster Aa2 appear clearly individualized in the CCA biplot with high loadings on the positive side of CCA axis 2 due to their high tree cover (4−5; Table 1), close to the relevant above-mentioned pollen indicator taxa (Figures 5 and 6). These Aa2 samples are placed in an intermediate position with respect to CCA axis 1 because their TA, TM, Tm, PA, PM and Pm values are equally intermediate between the total studied samples, although they are distributed with low positive values on CCA axis 1 due to their low altitude (418−515 m asl; Figure 5, Table 1). Samples from cluster Aa2 represent subhumid meso-thermophilous meso-mediterranean mixed forests codominated by holm oaks (*Quercus ilex*) and cypress trees (*Cupressus sempervirens*), growing on limestone and dolomite substrates in the northwestern part of the island of Crete (Figure 1). According to these facts, we propose a new association for these forests: *Querco ilicis-Cupressetum sempervirentis* Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova hoc loco* (Table 6, *holotypus*, relevé 1). The characteristic taxa of this new association are *Cupressus sempervirens*, *Quercus ilex*, *Hedera helix*, *Laurus nobilis*, *Ruscus aculeatus*, *Tamus communis* and *Styrax officinalis*. This new association corresponds to the *Quercus ilex*-*Cupressus sempervirens* community described by Brofas *et al.* (2006), although the authors did not give it any syntaxonomical rank. They cite that this community may also be present in the thermo-mediterranean bioclimatic belt (< 300 m asl), as in our case always in N, W and NW expositions on relatively moist sites (PA: 762–799 mm; TA: 16.3–16.5 ºC; lower subhumid ombrotype; Table 1).

Table 5. *Pistacio lentisci-Cupressetum sempervirentis* Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova* (*Ceratonio-Pistacion lentisci*, *Pistacio lentisci-Rhamnetalia alaterni*, *Quercetea ilicis*)

Altitude (m asl)	27	190	54	296	55	323	178	67	298	446	23	67	26
Aspect	W	SE	N	SE	NW	SE	SE	N	N	S	W	SE	N
Pollen sample number	CS13	CS28	CS45	CS15	CS11	CS16	CS8	CS46	CS47	CS48	CS14	CS27	CS44
N. species	17	21	22	22	24	24	24	27	27	27	27	27	27
Relevé N.	1	2	3	4	5	6	7	8	9	10	11	12	13
Characteristics													
Cupressus sempervirens	3	3	4	4	4	4	5	4	2	2	3	3	4
Pistacia lentiscus	3	4	4	1	2	2	2	4	4	3	4	4	2
Prasium majus	3	2	4	1	2	+	+	3	2	2	1	2	3
Ceratonia siliqua	1	+	2	+	+	+	+	2	1	1	1	+	2
Quercus coccifera	1	+	+	2	1	+	1	+	1	+	+	+	1
Asparagus acutifolius	1	+	+	+	.	+	.	1	1	+	.	+	+
Rubia peregrina	+	1	+	+	1	.	+	+	+	+	+	+	1
Achnatherum bromoides	.	·	1	.	+	+	.	1	1	1	+	+	+
Phillyrea latifolia	1	.	+	.	1	.	.	1	1	1	1	+	+
Myrtus communis	.	+	.	+	+	1	+	+	·	·	+	.	+
Olea europaea	1	.	1	·	+	.	.	1	1	2	+	·	+
Arbutus unedo	·	·	·	1	·	1	+	+	·	+	.	.	.
Styrax officinalis	·	·	·	1	·	2	1	·	·	·	1	2	.
Smilax aspera	·	·	·	+	·	1	+	·	·	·	+	+	.
Tamus communis	·	·	·	+	·	+	1	·	·	·	+	1	.
Ruscus aculeatus	·	·	·	1	·	1	+	·	·	·	.	.	.
Symphytum creticum	·	·	·	1	·	+	·	·	·	·	.	.	+
Hedera helix	·	·	·	+	·	·	1	·	·	·	.	+	.
Cyclamen creticum	·	·	·	·	·	+	·	·	+	+	·	.	·
Laurus nobilis	·	·	·	+	·	+	·	·	·	·	.	.	·
Arbutus andrachne	.	·	.	·	1	·	·	·	·	·	+	·	·
Others													
Piptatherum miliaceum	2	3	2	+	3	1	+	3	2	3	2	2	2
Erica manipuliflora	2	2	1	+	3	1	+	1	+	+	2	1	1
Cistus creticus	2	1	1	+	2	1	1	+	2	2	1	1	1
Plantago coronopus	2	1	+	+	1	+	+	+	+	+	1	1	+
Thymbra capitata	.	1	+	.	+	+	+	+	2	1	1	1	+
Osyris alba	1	+	+	.	+	.	.	1	1	+	+	1	+
Phlomis fruticosa	+	+	+	.	+	.	.	1	1	1	1	+	1
Geranium robertianum	.	·	·	+	+	+	+	+	+	+	+	+	+
Teucrium divaricatum	.	+	+	.	+	.	+	+	1	+	+	+	+
Crepis fraasii	.	+	+	.	+	.	.	1	1	+	+	+	+
Dactylis glomerata	+	+	.	.	+	.	+	·	+	+	+	+	+
Hypericum empetrifolium	·	+	.	1	.	1	+	+	+	·	+	+	+
Brachypodium retusum	.	·	+	·	+	+	.	1	+	+	+	.	+
Pinus brutia	·	1	+	.	.	.	.	1	+	+	·	+	+
Sarcopoterium spinosum	·	1	+	.	1	·	.	+	1	1	.	2	·
Plantago cretica	.	·	.	.	+	.	+	+	·	·	+	+	+
Calicotome villosa	·	·	·	·	.	·	·	·	+	2	·	·	·

Other species: Characteristics: *Berberis cretica* + in 9 and *Asparagus aphyllus* + in 12. Others: *Crucianella latifolia* + in 1; *Ranunculus velutinus* + in 7 and *Cynosurus echinatus* 1 in 11.

Localities: 1: Kournas lake; 2: between Agii Pantes and Neo Chorio; 3 and 13: Istro; 4: between Sellia and Likotinarera; 5: Fodele; 6: Kefalas; 7: Gramvousa; 8: between Istro and Pacheia Ammos, *holotypus ass*.; 9: Mesa Mouliana; 10: Sykologos; 11: Georgioupoli and 12: Suda.

Sub-cluster Ba1a-1 samples are characterized by *Cupressus/Juniperus* values ranging from 32 to 34.5% and high *Pinus brutia* percentages (13−21.5%), although they differ from those of sub-clusters Ba1a-2 and 3 (Figure 4) due to the high percentages of *Berberis cretica* (3.6−6.1%), *Prunus* (3−7%) and *Rhamnus* (4.5−6%) (Figure 2), reflecting the high altitude of these samples (1445–1600 m asl) in the upper montane to oro-mediterranean bioclimatic belts (Figure 1, Table 1). The three samples of sub-cluster Ba1a-1 are clearly separated from the rest with higher negative scores on CCA axis 2 (Figure 5), following the grazing pressure gradient and their low tree cover (Tables 1 and 4). Samples from sub-cluster Ba1a-1 in the CCA biplot are arranged close to the above-mentioned relevant pollen indicator taxa, that is, *Berberis cretica*, *Prunus* and *Rhamnus* (Figure 6). High values of anthropogenic pollen taxa (Compositae Cichorioideae, *Urtica dioica* 4−6%) and coprophilous fungi (*Sordaria* 8−9.5%, *Sporormiella* 6−8%, *Cercophora* 12−13%) in samples from sub-cluster Ba1a-1 (Figure 3) indicates that these cypress woodlands at higher altitudes are subjected to greater human impact, especially livestock grazing (López-Sáez & López-Merino, 2007). Instead, sub-cluster Ba1a-1 samples represent xero-mesophilous and orophilous (TA: 10.9−11.1 ºC; Table 1) woodland communities from the upper montane and oro-mediterranean bioclimatic belts of the Lefka Ori massif (Figure 1), corresponding to the *Junipero oxycedri-Cupressetum sempervirentis* association described by Brullo *et al.* (2001). Although their annual precipitation (PA) values are high (990−999 mm; Table 1), these cypress woodlands could be considered as xerophilous because they are covered by winter snow for at least 2–3 months and grow on sunny, windy and hardly sloping places on the southern slopes of the massif. In fact, these three samples of sub-cluster Ba1a-1 are located at close to the center of CCA axis 1 (although at its negative part) (Figure 5). Floristically, these cypress woodlands are characterized by orophilous spiny cushion-shaped dwarf shrubs such as *Juniperus oxycedrus* subsp. *oxycedrus*, *Berberis cretica*, *Prunus prostrata*, *Hypericum empetrifolium* subsp. *tortuosum* and *Rhamnus saxatilis* subsp. *prunifolia*, which justifies its inclusion within the *Pino-Juniperetea* class and the *Berberido creticae-Juniperion foetidissimae* alliance (Brullo *et al.*, 2001). This association usually considered as synonymous to that described by Barbero & Quézel (1980) and also recognized by Bauer & Bergmeier (2011) as *Luzulo nodulosae-Cupressetum sempervirentis berberidesotum creticae* within the *Quercetea ilicis* class. However it differs from *Luzulo nodulosae-Cupressetum sempervirentis berberidesotum creticae* by the absence of characteristics species of *Quercetea ilicis* and thermophilous taxa that tend to disappear in these open and high altitude cypress woodlands.

Table 6. *Querco ilicis-Cupressetum sempervirentis* Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova* (*Quercion ilicis*, *Quercetalia ilicis*, *Quercetea ilicis*)

Altitude (m asl)	418	429	515
Aspect	N	W	NW
Pollen sample number	CS12	CS60	CS59
Number of species	23	27	29
Relevé number	1	2	3
Characteristics s.l.			
Cupressus sempervirens	4	3	3
Quercus ilex	2	2	3
Styrax officinalis	2	3	1
Hedera helix	1	1	+
Laurus nobilis	1	+	1
Quercus coccifera	+	1	+
Pistacia terebinthus	+	+	+
Ruscus aculeatus	1	+	1
Tamus communis	1	+	+
Smilax aspera	+	+	1
Asparagus acutifolius	+	+	+
Myrtus communis	1	.	1
Olea europaea	+	.	+
Pistacia lentiscus	+	.	+
Phyllirea latifolia	.	+	+
Rubia peregrina	.	+	+
Cyclamen creticum	.	+	+
Cyclamen hederifolium	.	+	+
Arisarum vulgare	.	+	+
Others			
Pteridium aquilinum	1	1	1
Selaginella denticulata	1	+	1
Hypericum empetrifolium	1	+	+
Crepis fraasii	+	+	+
Plantago coronopus	+	+	+
Dactylis glomerata	+	.	+
Cistus creticus	+	+	.
Osyris alba	+	+	.
Piptatherum miliaceum	+	+	.
Teucrium divaricatum	.	+	+
Geranium robertianum	·	+	+

Other species: Characteristics: *Arbutus unedo* + in 3. Others: *Erica arborea* + in 2 and *Ranunculus velutinus* + in 3.

Localities: 1: Oros, *holotypus ass.*; 2: between Selli and Gouledianа and 3: between Kare and Ampelakion.

Samples from sub-clusters Ba1a-2 and Ba1a-3 (Figure 4) are characterized by noticeable values of phrygana pollen taxa (*Sarcopoterium spinosum* 1.5−8%, *Verbascum* 6−9%, *Thymbra capitata* 1−3%, *Euphorbia acanthothamnos* 3.5−7%), *Phlomis* (1.3−5.3%) and Araceae, as well as by low or null percentages of orophilous pollen taxa such as *Berberis*, *Prunus* or *Rhamnus* (Figures 2 and 3), reflecting the low altitude of these samples (230–1030 m asl) between the thermo– and the upper supra-mediterranean bioclimatic belts (Figure 1, Table 1). Both sub-clusters differ by higher values of *Cupressus/Juniperus* in the first (39−44% versus 30%) and *Pinus brutia* in the second one (20−38% versus 11.6−15%). Sub-clusters Ba1a-2 and Ba1a-3 represent upper dry to low subhumid meso-thermophilous (PA: 685−879 mm; TA: 14.4−16.4 ºC; Table 1) mixed cypress-pine forests, growing on limestone and dolomite substrates on the southern slopes of the Lefka Ori massif and the Samaria gorge (Figure 1), usually in S and SE expositions (Table 1). These mixed forests correspond to the *Luzulo nodulosae*-*Cupressetum sempervirentis* association and its corresponding *pinetosum brutiae* subassociation (Barbero & Quézel, 1980; Brullo *et al.*, 2004; Bauer & Bergmeier, 2011). Floristically, this subassociation is characterized by the abundance of thermophilous elements and phrygana species (*Phlomis fruticosa*, *Euphorbia acanthothamnos*, *Verbascum spinosum*, *Quercus coccifera*, *Biarum davisii*, *Lithodora hispidula*, *Erica manipuliflora*, *Genista acanthoclada*) and by the endemics *Ononis verae* and *Paeonia clusii* (Barbero & Quézel, 1980; Bergmeier, 1995; Bauer & Bergmeier, 2011). On CCA axis 2 (positive values) both sub-clusters Ba1a-2 and Ba1a-3 are grouped and individualized from the rest of samples (Figure 5), probably due to their high tree cover. Because these forests extend over a wide altitudinal range (Table 1), their samples are placed in an intermediate position along CCA axis 1, close to the aforementioned phrygana pollen taxa (Figures 5 and 6). Sample CS10, unlike the rest of the B cluster samples, has *Cupressus/Juniperus* values of less than 20% (Figure 2). This sample is characterized by the extralocal presence of *Pinus brutia* (38%) and local values of phrygana pollen taxa, particularly of *Sarcopoterium spinosum*, *Verbascum* and *Euphorbia acanthothamnos*. For these reasons, this sample is grouped within sub-cluster Ba1a-3 both in the dendrogram and CCa plot (Figures 4 and 5).

The division of sub-cluster Ba1b provides three main groups (Figure 4). First, it separates mixed thermo-mediterranean *Pistacia lentiscus*-*Cupressus sempervirens* forests (Ba1b-1) from pure cypress forests (Ba1b-2 and 3). Then, the following clustering discriminates between northwestern lower montane mediterranean (Ba1b-2) and southwestern lower supra-mediterranean (Ba1b-3) cypress forests (Figure 4), corresponding to the northern and southern slopes of the Lefka Ori massif respectively (Figure 1). Sub-cluster Ba1b-1 represents northwestern thermo-mediterranean (178−323 m asl) forests dominated by *Cupressus sempervirens* trees but with an important *Pistacia lentiscus* cover, growing on limestone and dolomite substrates (Figure 1, Table 1). Samples from sub-cluster Ba1b-1 have pollen spectra similar to those described for cluster Ab, that is, high values of *Pistacia lentiscus* (12−18%), *Quercus ilex/coccifera* (2.5−9%), Poaceae (5−6%) and significant frequencies (> 2%) of *Erica manipuliflora*, *Myrtus* and *Prasium majus* (Figures 2 and 3). In fact, sub-cluster Ba1b-1 samples are located on the positive side of CCA axis 1, grouped with those of cluster Ab (Figure 5). However, both clusters are differentiated by: (i) high percentages (38−48.5%) of *Cupressus/Juniperus* in Ba1b-1 samples, which justifies their inclusion in cluster B; (ii) very low or zero values of phrygana pollen taxa (*Euphorbia acanthothamnos*, *Sarcopoterium spinosum*, *Verbascum*, *Thymbra capitata*, *Calicotome*) and thermophilous elements (*Olea europaea*, Araceae, *Ceratonia siliqua*, Cistus *creticus*) in Ba1b-1 samples; and, (iii) noticeable frequencies of certain humid, ombrophilous and mesophilous elements exclusive to the sub-cluster Ba1b-1, such as *Arbutus*, *Laurus nobilis*, *Hedera helix*, *Tamus communis*, *Smilax aspera*, *Ruscus aculeatus*, *Hypericum*, *Geranium* and *Styrax officinalis* (Figures 2 and 3). In short, Ba1b-1 sub-cluster samples correspond to a wet facies of the *Pistacio lentisci-Cupressetum sempervirentis* association described above, characterized by a floristic composition (Table 5, relevés 11−13) where species such as *Arbutus unedo*, *Styrax officinalis, Smilax aspera*, *Symphytum creticum*, *Ruscus aculeatus*, *Rubia peregrina*, *Tamus communis* and *Hedera helix* appear in deep moist soils representing well-developed cypress forests of northwest Crete (Brofas *et al.*, 2006). High percentages of coprophilous fungi (*Cercophora*, *Chaetomium*, *Sordaria*, *Sporormiella*; Figure 3) are indicative of the strong pastoral pressure to which these low altitude cypress forests are subjected.

Samples from sub-clusters Ba1b-2 and Ba1b-3 (Figure 4) are characterized by high percentages of *Cupressus/Juniperus* (35−35.6% and 36−44% respectively) and noticeable values of *Acer* (5−10%), *Quercus ilex/coccifera*, *Euphorbia acanthothamnos* and *Verbascum* (Figure 2). However, they are discriminated both in the HCA and CCA axes 1 and 2 (Figures 4 and 5) by the following features (Figures 2 and 3): (i) higher percentages of orophilous taxa such as *Berberis cretica* (5−7%), *Daphne* (6%), *Rhamnus* (4−5.3%), *Prunus* (1.3−1.6%) and Poaceae (13−16%) in Ba1b-2 samples, reflecting its higher altitude (1239–1242 m asl) in the lower montane mediterranean bioclimatic belt (Figure 1, Table 1); (ii) higher values of thermophilous taxa such as *Phlomis* (4.7−5.6%), *Thymbra capitata* (6−6.3%), *Sarcopoterium spinosum* (4.5−7.3%), *Pyrus spinosa* (2−2.5%) and *Rubia peregrina* (1.4%) in Ba1b-3 samples, reflecting equally its low altitude (699−739 m asl) in the lower supra-mediterranean belt (Figure 1, Table 1). Therefore, sub-cluster Ba1b-2 samples represent xerophilous and orophilous (PA: 906−924 mm; TA: 12.2−12.6 ºC; Table 1) cypress woodland communities from the lower montane mediterranean bioclimatic belt on the northern slopes of the Lefka Ori massif (Figure 1), corresponding to the *Daphno sericeae*-*Cupressetum sempervirentis* association described by Brullo *et al.* (2001), growing on mature soils or around dolines in N and W expositions. This community is replaced by the aforementioned *Junipero oxycedri-Cupressetum sempervirentis* community at a higher altitude in high sloping rocky surfaces. Although cypress is the dominant arboreal species, along with scattered kermes oak and maples, this community is characterized by low tree cover (2–3, Table 1) and a shrubby layer dominated by *Daphne sericea*, *Berberis cretica*, *Prunus prostrata*, *Hypericum empetrifolium* subsp. *tortuosum*, *Euphorbia acanthothamnos* and *Rhamnus saxatilis* subsp. *prunifolia*, which indicates also its inclusion within the *Pino-Juniperetea* class (Brullo *et al.*, 2001).

Along CCA axis 1 there seems to be an altitudinal distribution of sub-cluster Ba1b samples: sub-cluster Ba1b-1 samples (178−323 m asl) are located at the positive side of the CCA axis 1, negatively correlated with altitude; sub-cluster Ba1b-3 samples (699−739 m asl) are grouped in an intermediate position along CCA axis 1 near zero; while sub-cluster Ba1b-2 samples (1239−1242 m asl) are clearly located on the CCA axis 1 with negative values –as cluster Bb samples– and positively correlated with altitude (Figure 5). In fact, sub-cluster Ba1b-2 samples are located close to the pollen indicator taxa of the *Daphno sericeae-Cupressetum sempervirentis* community, namely *Daphne* and *Berberis* (Figure 6). They are also located on the CCA axis 2 with negative values due to both their low tree cover and the high grazing pressure they suffer (Figure 5), which leads to the abundance of coprophilous fungi (*Sordaria*, *Spormiella*, *Cercophora*) and anthropozoogenous pollen taxa (*Urtica*, *Plantago lanceolata*) in their pollen spectra (Figure 3).

Instead, sub-cluster Ba1b-3 samples represent xero-thermophilous (PA: 799−843 mm; TA: 15−15.7 ºC; Table 1) cypress woodland communities from the lower supra-mediterranean bioclimatic belt on the southern slopes of the Lefka Ori massif (Figure 1). They correspond to the *Luzulo nodulosae-Cupressetum sempervirentis* association and its corresponding *cupressetosum sempervirentis* subassociation (Rechinger & Rechinger-Moser, 1951; Zohary & Orshan, 1965; Barbero & Quézel, 1980; Brullo *et al.*, 2004; Bauer & Bergmeier, 2011). This community is floristically characterized by dense cypress forests, *Quercus coccifera*, *Acer sempervirens*, *Luzula nodulosa*, *Asperula rigida*, *Pyrus spinosa* and *Berberis cretica*, although it still maintains a dense phrygana vegetation cover, particularly of *Phlomis cretica*, *Thymbra capitata* and *Euphorbia acanthothamnos* (Barbero & Quézel, 1980; Bergmeier, 1995; Brofas *et al.*, 2006; Bauer & Bergmeier, 2011). As mentioned above, within the Ba1 cluster the respective sub-clusters Ba1a and Ba1b are separated by the greater or lesser abundance of *Pinus brutia* pollen (Figures 2 and 4). However, the sub-clusters Ba1a-2/3 and Ba1b-3 are grouped along CCA axis 2, having positive values (Figure 5). Both represent the same *Luzulo nodulosae-Cupressetum sempervirentis* association although different subassociations (*pinetosum brutiae* and *cupressetosum sempervirentis*, respectively). These facts may be due to several factors: (i) its high tree cover (both groups of samples are positively correlated with tree cover along CCA axis 2) with *Cupressus/Juniperus* values above 30% (Figure 2); (ii) although the majority of samples are located on the supra-mediterranean bioclimatic belt, phrygana pollen taxa are abundant in their pollen spectra (Figure 2), which justifies their intermediate position along CCA axis 1 (Figure 5); (iii) both groups of samples share the same exposition (predominantly south and east) and similar TA and PA values (Table 1), intermediate with respect to the rest of the samples, that is, probably the same ombrotype, which again justifies their intermediate position along CCA axis 1.

Cluster Ba2 comprises modern pollen samples characterized by *Cupressus/Juniperus* values below 25% and noticeable percentages of *Quercus ilex/coccifera* (7−9%). The division of cluster Ba2 provides two main sub-clusters (Ba2a and Ba2b), which differ by a greater percentage of *Cupressus/Juniperus* in the first (18−23%) with respect to the second (4%) (Figures 2 and 4). Probably, the only sample of the Ba2b sub-cluster (CS38) is included within the Ba cluster due to high values of *Acer* (34%) and *Berberis cretica* (11%), as well as low percentages of phrygana pollen taxa (Figures 2 and 3). Sub-cluster Ba2b represent upper subhumid mesophilous (PA: 954 mm; TA: 12.2 ºC; Table 1) middle montane mediterranean woodlands (1217 m asl) dominated by *Acer sempervirens* growing on calcareous rocky sites (limestones), corresponding to the *Aceri sempervirentis-Berberidetum creticae* association; whose characteristic species are *Acer sempervirens*, *Berberis cretica*, *Crataegus monogyna* and *Rosa pulverulenta* (Zohary & Orshan, 1965; Barbero & Quézel, 1980; Brullo *et al.*, 2004). According to Brullo *et al.* (2001), this community can reach the oro-mediterranean bioclimatic belt close to the treeline (2100 m asl). Probably, the presence of *Euphorbia acanthothamnos* (2.1%) in sample CS38 would allow us to assign it to the *euphorbietosum acanthothamni* subassociation described by the previous authors. The high altitude at which this community develops allows certain orophilous chameaphytes such as *Prunus prostrata* and *Rhamnus saxatilis* subsp. *prunifolia* to be frequent. Both pollen taxa are present in the pollen assemblage of this sample (*Rhamnus* 0.9%; *Prunus* 1.8%), as well as *Crataegus monogyna* (3.3%). As attested by Bergmeier (2002), *Acer sempervirens* is commonly heavily browsed by goats and the spiny *Berberis cretica* is selectively undergrazed and therefore frequently the dominant species, while the herbaceous layer contains many perennial nitrophytes supported by the dung that is left behind by the sheep seeking the shade of the maple trees. In fact, sample CS38 is also characterized by high values of coprophilous fungi such as *Sordaria* (8.2%) and *Sporormiella* (5.7%), as well as by anthropozoogenous pollen taxa such as *Urtica dioica* (2%) and *Plantago lanceolata* (2.7%) (Figure 3). The presence of cypress trees in this community is sporadic, hence its low percentage (4%) indicating its regional origin.

Sub-cluster Ba2a is discriminated both in the HCA and CCA (Figures 4 and 5) by the following features (Figures 2 and 3): (i) high percentages of *Cupressus/Juniperus* (18−23%) and *Quercus ilex/coccifera* (7.4−9%); (ii) high values of coprophilous fungi (*Sordaria* 20−23%, *Sporormiella* 6−7%, *Cercophora* 8−9%, *Trichodelitschia* 2%) and anthropozoogenous pollen taxa (*Plantago lanceolata* 3.5−4.5%, *Urtica dioica* 1−2%); (iii) significant percentages of meso-thermophilous taxa such as *Erica* *arborea* (6–6.5%), *Cistus parviflorus* (9–10%), *Crataegus monogyna*, *Pteridium aquilinum*, *Pistacia terebinthus*, *Ceratonia siliqua*, *Myrtus communis*, *Erica manipuliflora*, *Olea europaea*, *Cistus creticus*, *Arbutus*, *Osyris alba*, *Phillyrea*, *Rubia peregrina*, *Smilax aspera*, *Tamus communis*, *Hedera helix* and *Euphobia dendroides*; (iv) the identification in their two samples of the testate amoeba *Assulina muscorum* (4.6–7.1%). Floristically, sub-cluster Ba2a represents upper dry meso-thermophilous (PA: 653–671 mm; TA: 16.2–16.4 ºC; Table 1) meso-mediterranean (348–467 m asl) mixed forests codominated by cypress trees (*Cupressus sempervirens*) and tree heaths (*Erica arborea*), growing on limestone and dolomite substrates in the northwestern part of the island of Crete in scattered nuclei (Figure 1). They are characterized by *Cupressus sempervirens*, *Erica arborea*, *Arbutus unedo*, *Cistus parviflorus*, *Cyclamen creticum*, *Erica manipuliflora* and *Pteridium aquilinum*; although other elements such as *Crataegus monogyna*, *Myrtus communis*, *Quercus coccifera*, *Q. pubescens* and *Rubia peregrina* are also frequent. This fact allows us to propose a new cypresswood association: *Erico arboreae-Cupressetum sempervirentis* Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova hoc loco* (Table 7, *holotypus*, relevé 4). These forests were studied by Brofas *et al.* (2006) without assigning in any specific syntaxon, but pointing out their differences with other thermo– and meso-mediterranean Cretan cypress forests. The presence of *Assulina muscorum* in the samples of sub-cluster Ba2b is due to the fact that this type of forest is developed mainly in moist and ombrophilous sites, where this thecamoeba can grow on mosses (López-Sáez *et al.*, 1998). High values of coprophilous fungi and anthropozoogenous pollen taxa are significant of the strong impact of livestock activities on these low altitude forests (López-Sáez & López-Merino, 2007). Samples from Ba2a sub-cluster are arranged close to the relevant pollen indicator taxa (Figure 6). They are placed close to some samples from Ab (CS47) and Ba1b-1 (CS15 and CS 16) clusters (*Pistacio lentisci-sempervirentis*) on both CCA axes (Figure 5) due to their palynological affinities (Figures 2 and 3), mainly because of the significant presence in their pollen spectra of some of the aforementioned meso-thermophilous pollen taxa (*Ceratonia siliqua*, *Myrtus communis*, *Erica manipuliflora*, *Olea europaea*, *Cistus creticus*, *Rubia peregrina*, *Smilax aspera*, *Tamus communis*, *Hedera helix*).

Table 7. *Erico arboreae-Cupressetum sempervirentis* Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova* (*Quercion ilicis*, *Quercetalia ilicis*, *Quercetea ilicis*)

Altitude (m asl)	433	447	450	467	348
Aspect	NW	NW	NW	NW	W
Pollen sample number	-	-	-	CS20	CS19
Number of species	18	19	20	22	24
Relevé number	1	2	3	4	5
Characteristics s.l.					
Cupressus sempervirens	3	4	4	4	3
Erica arborea	4	4	3	3	3
Quercus coccifera	1	+	1	+	+
Crataegus monogyna	1	1	1	+	+
Quercus pubescens	1	+	1	1	+
Rubia peregrina	+	+	+	1	+
Hedera helix	1	+	.	+	1
Cyclamen creticum	.	+	+	1	+
Phillyrea latifolia	.	+	+	+	+
Tamus communis	.	+	+	+	+
Myrtus communis	.	+	+	+	.
Smilax aspera	.	+	+	.	+
Pistacia terebinthus	+	.	.	+	+
Arbutus unedo	+	.	·	+	+
Olea europaea	+	.	.	+	.
Asparagus acutifolius	.	+	+	.	.
Acer sempervirens	.	.	+	.	+
Others					
Pteridium aquilinum	+	1	1	1	2
Erica manipuliflora	1	+	+	+	1
Cistus parviflorus	+	+	.	1	+
Ranunculus velutinus	.	+	+	1	1
Brachypodium retusum	+	.	·	+	+
Plantago coronopus	+	.	.	+	+
Cistus creticus	.	.	+	+	+
Hypericum empetrifolium	+	+	.	.	.
Teucrium divaricatum	+	.	+	.	.
Osyris alba	+	.	.	+	.
Geranium robertianum	+	·	·	.	+

Other species: Characteristics: *Asparagus aphyllus* + in 3 and *Euphorbia dendroides* + in 5. Others: *Poa bulbosa* + in 3.

Localities: 1–2: Lakkoi-Agios Antonios; 3–4: Karanos, *holotypus ass.* inv. 4; 5: Orthouni.

The division of cluster Bb provides three main clusters (Figure 4). First, it separates samples with *Cupressus/Juniperus* values above 60% (cluster Bb1) from others with percentages below 60% (cluster Bb2). Then, the following division of cluster Bb1 discriminates between samples with higher values of *Berberis cretica* (5−10%) (sub-cluster Bb1a) and those with higher percentages of *Quercus ilex/coccifera* (> 10%) and phrygana pollen taxa (*Sarcopoterium spinosum*, *Euphorbia acanthothamnos*, *Thymbra capitata*) (sub-cluster Bb1b). Sub-cluster Bb1a samples represent low to subhumid and orophilous (PA: 875−961 mm; TA: 12.1−13.1 ºC; Table 1) cypress woodlands communities from the lower montane mediterranean bioclimatic belt (1055−1228 m asl) on the northern slopes of the Lefka Ori massif in predominantely E and SE expositions (Figure 1, Table 1), corresponding to the *Luzulo nodulosae*-*Cupressetum sempervirentis* association and its *berberidetosum creticae* subassociation (Barbero & Quézel, 1980; Bauer & Bergmeier, 2011). This community is the vicariant of the *cupressetosum sempervirentis* subassociation described above at higher altitude or even at lower altitudes on degraded or deep clay soils. Floristically, the characteristic species of this association are *Berberis cretica*, *Prunus prostrata*, *Rosa pulverulenta* and *Rhamnus saxatilis* subsp. *prunifolia*, whose corresponding pollen taxa are documented in their pollen samples (Figure 2). Interestingly, in some samples of this sub-cluster Bb1a *Zelkova* pollen is identified, which probably corresponds to the endemic species *Zelkova abelicea*, one of the most prominent Tertiary relict trees of the Mediterranean region (Kozlowski *et al.*, 2014).

Finally, samples from sub-cluster Bb1b and cluster Bb2 represent xero-thermophilous (PA: 656−997 mm; TA: 11−17.4 ºC; Table 1) cypress woodland communities from the lower supra– to the lower/middle montane mediterranean belts (529−1525 m asl) of the Lefka Ori massif (Figure 1), exceptionally in the thermo-mediterranean one (284 m asl), growing mainly on limestone and dolomite substrates, sometimes on schists, in dominant S and SE expositions (Table 1). Both group of samples (Bb1b and Bb2) correspond to the aforementioned *Luzulo nodulosae-Cupressetum sempervirentis cupressetosum sempervirentis* subassociation (sub-cluster Ba1b-3). They are located in different clusters (Figure 4) due to the aforementioned differences in their *Cupressus/Juniperus* percentage (Figure 2). They are grouped together (also with the samples from Bb1a sub-cluster) along CCA axis 1 with negative values (Figure 5), mainly reflecting their geographical distribution at mid and high altitudes. In short, Ba1b-3 and Bb1b/Bb2 samples correspond to the same community despite being located in very different clusters (Ba and Bb respectively). All of them share floristic affinities, characterized by high constancy in their floristic composition of *Quercus coccifera*, *Acer sempervirens*, *Luzula nodulosa*, *Asperula rigida* and *Pyrus spinosa*, maintaining a dense phrygana vegetation cover (Barbero & Quézel, 1980; Bergmeier, 1995; Brofas *et al.*, 2006; Bauer & Bergmeier, 2011). In fact, they all have pollen spectra where phrygana pollen taxa are abundant, mainly *Euphorbia acanthothamnos*, *Phlomis*, *Sarcopoterium spinosum*, *Verbascum* and *Thymbra capitata* (Figures 2 and 3). *Berberis cretica* and *Acer sempervirens* are also constant species both in the flora and the pollen spectra of samples of the three mentioned clusters, although with lower percentages than in the aforementioned *berberidetosum creticae* subassociation (sub-cluster Bb1a). As mentioned, the Ba and Bb clusters are differentiated by the percentage of *Cupressus/Juniperus* pollen, higher than 50% in the second; probably because the presence of *Pinus brutia* pollen is notable in the two samples of cluster Ba1b-3 coming from the Samaria gorge (Figures 1 and 2).

Conclusions

Our study provides a set of modern surface pollen data spectra which contributes to improving the lack of data from the Aegean islands. Our results clearly demonstrate that it is possible to obtain distinct pollen and non-pollen palynomorph markers for the *Cupressus sempervirens* forests of the island of Crete. These distinctions are related to specific climatic or geographic conditions, as well as to different degrees of human impact. Classification of modern pollen samples, by means of HCA, indicated the existence of twelve vegetation units, eight of which were ranked as associations and four as subassociations. CCA ordination diagrams of modern pollen samples and pollen/non-pollen palynomorph taxa indicated that palynological differentiation was attributed mainly to factors such as altitude, annual temperature, annual precipitation, tree cover and grazing pressure. On the first CCA axis orophilous tree and shrub pollen taxa (*Zelkova*, *Prunus*, *Rhamnus*, *Berberis*, *Daphne*) are separated from low-elevation meso-thermophilous taxa (*Myrtus*, *Olea*, *Calicotome*, *Cistus creticus*, *Pistacia lentiscus*, *Erica manipuliflora*, *Prasium*, *Ceratonia*, *Laurus*, *Ruscus*, *Smilax*, *Tamus*, *Hedera*, *Quercus pubescens* and *Erica arborea*) located at the positive side of the axis, following an altitudinal gradient and increasing precipitation (negative values) or increasing temperature (positive values). On the second CCA axis pollen taxa from tree species (*Laurus*, *Quercus pubescens*, *Pinus brutia* and *Quercus ilex/coccifera*) are located on the positive side (increasing tree cover), while most shrubs and herbs are located on the negative side of CCA axis 2.

Our modern pollen rain studies and multivariate analyses allow us to discriminate the peculiarities of six *Cupressus sempervirens* forest communities on the island of Crete (Greece), proposing three new phytosociological associations: *Pistacio lentisci-Cupressetum sempervirentis*, *Querco ilicis-Cupressetum sempervirentis* and *Erico arboreae-Cupressetum sempervirentis*.

Although Bauer & Bergmeier (2011) does not recognize the two new associations proposed by Brullo *et al.* (2001) as *Daphno sericeae-Cupressetum sempervirentis* and *Junipero oxycedri-Cupressetum* *sempervirentis*, considering them synonymous with the *Luzulo nodulosae-Cupressetum sempervirentis* community, our study shows that the associations referred by Brullo *et al.* (2001) are recognizable by their pollen spectra and are distinguished in both the HCA and the CCA. However, it is true that *Daphno sericeae-Cupressetum sempervirentis* modern pollen samples show some overlap with those of the *Luzulo nodulosae-Cupressetum sempervirentis* on both CCA axes. Future studies and the analysis of a higher number of modern pollen samples may contribute to shed light on these potential synonyms.

Syntaxonomical scheme

Quercetea ilicis Br.-Bl. ex A. Bolòs et O. de Bolòs in A. Bolòs y Vayreda 1950
Quercetalia ilicis Br.-Bl. ex Molinier 1934
Quercion ilicis Br.-Bl. ex Molinier 1934
Querco ilicis-Cupressetum sempervirentis Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova*
Erico arboreae-Cupressetum sempervirentis Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova*
Quercetalia calliprini Zohary 1955
Quercion calliprini Zohary 1955
Aceri sempervirentis-Quercetum calliprini Brullo et al. 2004
Aceri sempervirentis-Cupression sempervirentis Barbero et Quézel ex Quézel et al. 1993
Luzulo nodulosae-Cupressetum sempervirentis (Zohary & Orshan 1965) Barbero & Quézel 1980
cupressetosum Zohary & Orshan 1965
pinetosum brutiae Barbero & Quézel 1980
berberidetosum creticae Barbero & Quézel 1980
Pistacio lentisci-Rhamnetalia alaterni Rivas-Martínez 1975
Ceratonio-Pistacion lentisci Zohary & Orshan 1959
Pistacio lentisci-Cupressetum sempervirentis Sánchez-Mata, Tsiripidis & López-Sáez *ass. nova*
Pino-juniperetea Rivas-Martínez 1964
Berberido creticae-Juniperetalia excelsae Mucina in Mucina et al. 2016
Berberido creticae-Juniperion foetidissimae Brullo et al. 2001
Aceri sempervirentis-Berberidetum creticae Barbero & Quézel 1980
Junipero oxycedri-Cupressetum sempervirentis Brullo et al. 2001
Daphno sericeae-Cupressetum sempervirentis Brullo et al. 2001

Acknowledgements

This study is part of the international PALEOMEX-INEE Research Program, itself a component of the Mediterranean Integrated Studies at Regional and Local Scales (MISTRALS) of the CNRS, France.

Bibliography

Bagnoli, F., Vendramin, G.G., Buonamici, A., Doulis, A.G., González-Martínez, S.C., La Porta, N., Magri, D., Raddi, P., Sebastiani, F. & Fineschi, S. 2009. Is Cupressus sempervirens native in Italy? An answer from genetic and palaeobotanical data. Mol. Ecol. 18: 2276–2286.
Barbero, M. & Quézel, P. 1980. La végétation forestière en Crete. Ecol. Mediterr. 5: 175–210.
Bauer, E.M. & Bergmeier, E. 2011. The mountain woodlands of western Crete – plant communities, forest goods, grazing impact and conservation. Phytocoenologia 41: 73–105.
Bergmeier, E. 1995. Die Höhenstufung der Vegetation in Südwest-Kreta (Griechenland) entlang eines 2450 m-Transektes. Phytocoenologia 25: 317–361.
Bergmeier, E. 2002. The vegetation of the high mountains of Crete: a revision and multivariate analysis. Phytocoenologia 32: 205–249.
Braun-Blanquet, J. 1979. Fitosociología. Bases para el estudio de las comunidades vegetales. H. Blume. Barcelona.
Brofas, G., Karetsos, G., Dimopoulos, P. & Tsagari, C. 2006. The natural environment of Cupressus sempervirens in Greece as a basis for its use in the Mediterranean region. Land Degrad. Develop. 17: 645–659.
Brullo, S., Giusso del Galdo, G. & Guarino, R. 2001. The orophilous communities of the Pino-Juniperetea class in the Central and Eastern Mediterranean area. Feddes Repert. 112: 261–308.
Brullo, S., Guarino, R., Minissale, P., Scelsi, F. & Spampinato, G. 2004. Indagine fitosociologica sulla vegetazione forestale dell'Egeo meridionale. Colloq. Phytosociol. 28: 401–466.
Burgaz, M.E., Güemes, J. & Roselló, M.J. 1994. Estudios palinológicos de flora autóctona valenciana: Anacardiaceae, Capparaceae y Coriariaceae. In: La Serna-Ramos, I. (Ed.). Polen y Esporas: Contribución a su conocimiento. Pp. 9–18. Universidad de La Laguna, Tenerife.

Caudullo, G. & De Rigo, D. 2016. Cupressus sempervirens in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., De Rigo, D., Caudullo, G., Houston Durrant, T. & Mauri, A. (Eds.). European Atlas of Forest Tree Species. Pp. e01afb4. Publ. Off. EU. Luxembourg.

Chartzoulakis, K. & Psarras, G. 2005. Global change effects on crop photosynthesis and production in Mediterranean. The case of Crete, Greece. Agric. Ecosyst. Environ. 106: 147−157.

Court-Picon, M., Buttler, A. & de Beaulieu, J.L. 2006. Modern pollen/vegetation/land-use relationships in mountain environments: an example from the Champsaur valley (French Alps). Veget. Hist. Archaeobot. 15: 151−168.

Dafis, S., Papastergiadou, E., Lazaridou, M. & Tsiafouli, M. 2001. Technical guide for the identification, description and mapping of habitat types in Greece. Greek Centre of Biotopes-Wetlands, Athens.

Della Roca, G., Hernando, C., Madrigal, J., Danti, R., Moya, J., Guijarro, M., Pecchioli, A. & Moya, B. 2015. Possible land management uses of common cypress to reduce wildfire initiation risk: a laboratory study. J. Environ. Manage. 159: 68−77.

Dimopoulos, P., Bergmeir, E. & Fischer, P. 2006. Natura 2000 habitat types of Greece evaluated in the light of distribution, threat and responsibility. Biol. Environ. 106B: 175−187.

Dimopoulos, P., Raus, T., Bergmeier, E., Constantinidis, T., Iatrou, G., Kokkini, S., Strid, A. & Tzanoudakis, D. 2013. Vascular plants of Greece: An annotated checklist. Botanischer Garten und Botanisches Museum Berlin-Dahlem, Freie Universität Berlin & Hellenic Botanical Society, Berlin and Athens.

Dimopoulos, P., Raus, T., Bergmeier, E., Constantinidis, T., Iatrou, G., Kokkini, S., Strid, A. & Tzanoudakis, D. 2016. Vascular plants of Greece: An annotated checklist. Supplement. Willdenowia 46: 301−347.

Eckenwalder, J.E. 2009. Conifers of the World. The Complete Reference. Timber Press, Portland.

Faegri, K. & Iversen, J. 1989. Textbook of Pollen Analysis. Wiley, Chichester.

Farjon, A. 2010. A Handbook of the World's Conifers. Brill, Leiden.

Farjon, A. & Filer, D. 2013. An Atlas of the World's Conifers. An analysis of their distribution, biogeography, diversity and conservation status. Brill, Leiden.

Fick, S.E. & Hijmans, R.J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37: 4302−4315.

Glais, A., Papageorgiou, A.C., Tsiripidis, I., Abel-Schaad, D., López-Sáez, J.A.& Lespez, L. 2016. The relationship between vegetation and modern pollen assemblages on Mount Paggeo (NE Greece). Lazaroa 37: 105−123.

Grimm, E.C. 1992. Tilia version 2. Illinois State Museum. Research and Collection Center. Springfield.

Hamer, Ø., Harper, D.A.T. & Ryan, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. Paleontol. Electron. 4: 1−9.

Hicks, S., Tinsley, H., Huusko, A., Jensen, C., Hättestrand, M., Gerasimidis, A. & Kvavandze, E. 2001. Some comments on spatial variation in arboreal pollen deposition: first records from the Pollen Monitoring Programme (PMP). Rev. Palaebot. Palynol. 117: 183−194.

Hidalgo, P.J., Galán, C. & Domínguez, E. 1999. Pollen production of the genus Cupressus. Grana 38: 296−300.

Higgins, M.D. & Higgins, R. 1996. A geological companion to Greece and the Aegean. Gerald Duckworth & Co. London.

I.G.M.E. 1983. Geological map of Greece, 1: 500,000. IGME, Athens.

Intini, M. & Della Rocca, G. 2004. Il cipresso comune (Cupressus sempervirens L.): caratterische botaniche, distribuzione, ecología. Centro Promozione Pubblicità, Firenze.

Korol, L., Kara, N., Isik, K. & Schiller, G. 1997. Genetic differentiation among and within natural and planted Cupressus sempervirens L. eastern Mediterranean populations. Silvae Genet. 46: 151−155.

Koutroulis, A.G., Vrohidou, A.E.K. & Tsanis, I.K. 2011. Spatiotemporal characteristics of meteorological drought for the island of Crete. J. Hydrometeorol. 12: 206−226.

Kozlowski, G., Frey, D., Fazan, L., Egli, B., Bétrisey, S., Gratzfeld, J., Garpi, G. & Pirintsos, S. 2014. The Tertiary relict tree Zelkova abelicea (Ulmaceae): distribution, population structure and conservation status on Crete. Oryx 48: 80−87.

Kurmann, M.H. 1994. Pollen morphology and ultrastructure in the Cupressaceae. Acta Bot. Gallica 141: 141−147.

Legakis, A. & Kypriotakis, Z. 1994. A biogeographical analysis of the island of Crete, Greece. J. Biogeogr. 21: 441−445.

López-Sáez, J.A., Alba-Sánchez, F., López-Merino, L. & Pérez-Díaz, S. 2010. Modern pollen analysis: a reliable tool for discriminating Quercus rotundifolia communities in Central Spain. Phytocoenologia 40: 57−72.

López-Sáez, J.A., Alba-Sánchez, F., Sánchez-Mata, D., Abel-Schaad, D., Gavilán, R.G. & Pérez-Díaz, S. 2015. A palynological approach to the study of Quercus pyrenaica forest communities in the Spanish Central System. Phytocoenologia 45: 107−124.

López-Sáez, J.A. & López-Merino, L. 2007. Coprophilous fungi as a source of information of anthropic activities during the Prehistory in the Amblés Valley (Ávila, Spain): the archaeopalynological record. Rev. Esp. Micropal. 39: 103−116.

López-Sáez, J.A., Sánchez-Mata, D., Alba-Sánchez, F., Abel-Schaad, D., Gavilán, R.G. & Pérez-Díaz, S. 2013. Discrimination of Scots pine forests in the Iberian Central System (Pinus sylvestris var. iberica) by means of pollen analysis. Phytosociological considerations. Lazaroa 34: 191−208.

López-Sáez, J.A., van Geel, B., Farbos-Texier, S. & Diot, M.F. 1998. Remarques paléoécologiques à propos de quelques palynomorphes non-polliniques provenant de sédiments quaternaires en France. Rev. Paléobiol. 17: 445−459.

Manescu, C., Hamamouch, N., Maios, C., Harfouche, A., Doulis, A.G. & Aravanopoulos, F.A. 2011. Linkage mapping of the Mediterranean cypress, Cupressus sempervirens, based on molecular and morphological markers. Genet. Mol. Res. 10: 1891−1909.

Mazier, F., Galop, D., Brun, C. & Buttler, A. 2006. Modern pollen assemblages from grazed vegetation in the western Pyrenees, France: a numerical tool for more precise reconstruction of past cultural landscapes. Holocene 16: 91−103.
Moore, P.D., Webb, J.A. & Collinson, M.E. 1991. Pollen analysis (2nd ed.). Blackwell Scientific Publications. London.
Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.P., Raus, T., Čarni, A., Šumberová, K.,Willner, W., Dengler, J., Gavilán-García, R., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Valachovič, M., Schaminée, J.H.J., Lysenko, T., Didukh, Y.P., Pignatti, S., Rodwell, J.S., Capelo, J., Weber, H.E., Solomeshch, A., Dimopoulos, P., Aguiar, C., Hennekens, S.M. & Tichý, L. 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Appl. Veg. Sci. 19 (Suppl. 1): 3−264.
Naoum, S. & Tsanis, I.K. 2004. Orographic precipitation modelling with multiple linear regression. J. Hydrol. Eng. 9: 79−102.
Papageorgiou, A.C., Bergmann, F., Gillet, E. & Hattemer, H.H. 1993. Genetic analysis of isozyme variation in Mediterranean cypress (Cupressus sempervirens L.). Silvae Genet. 42: 109−111.
Papageorgiou, A.C., Finkeldey, R., Hattemer, H.H. & Xenopoulos, S. 2005. Genetic differences between autochthonous and breeding populations of common cypress (Cupressus sempervirens L.) in Greece. Eur. J. For. Res. 124: 119−124.
Papageorgiou, A.C., Panetsos, K.P. & Hattemer, H.H. 1994. Genetic differentiation of natural Mediterranean cypress (Cupressus sempervirens L.) populations in Greece. For. Genet. 1: 1−12.
Papanastasis, V.P., Kyriakakis, S. & Ispikoudis, J. 1990. Forestry and grazing practices in Crete. In: Grove, A.T., Moody, J. & Rackham, O. (Eds.). Stability and change in the Cretan landscape. Pp. 42−46. Corpus Christi College. Cambridge.
Papastergiadou, E., Dafis, S., Dimopoulos, P. & Lazaridou, T. 1997. Syntaxonomic typology of Greek habitats. Folia Geobot. Phytotax. 32: 335−341.
Pardoe, H., Giesecke, T., Van Der Knaap, W., Svitasvká-Svobodová, H., Kvavadze, E., Panajitoidis, S., Gerasimidis, A., Pidek, I., Zimny, M., Święta-Musznicka, J., Latalowa, M., Noryśkiewicz, A., Bozilova, E., Tonkov, S., Filipa-Marinova, M., Van Leeuwen, J., Kalniņa, I. 2010. Comparing pollen spectra from modified tauber traps and moss samples: examples from a selection of woodlands across Europe. Veg. Hist. Archaeobot. 19: 271−283.
Prentice, I.C. 1985. Pollen representation, source area, and basin size: toward a unified theory of pollen analysis. Quat. Res. 23: 76−86.
Rackham, O. & Moody, J.A. 1996. The making of the Cretan landscape. Manchester University Press. Manchester.
Rechinger, K.H. & Rechinger-Moser, F. 1951. Phytogeographia Aegea. Denkschriften Österr. Akad. Wiss. Köln.
Rivas-Martínez, S., Penas, A. & Díaz, T.E. 2004. Bioclimatic & Biogeographic Maps of Europe. University of León, León.
Roques, A., Markalas, S., Roux, G., Pan, Y., Sun, J. & Raimbault, J.P 1999. Impact of insects damaging seed cones of cypress, Cupressus sempervirens, in natural stands and plantations of southeastern Europe. Ann. For. Sci. 56: 167−177.
Sugita, S. 1994. Pollen representation of vegetation in Quaternary sediments: theory and method in patchy vegetation. J. Ecol. 82: 881−897.
ter Braak, C.J.F. & Prentice, I.C. 1988. A theory of gradient analysis. Adv. Ecol. Res. 18: 271−317.
ter Braak, C.J.F. & Šmilauer, P. 2002. CANOCO Reference manual and Canodraw for Windows user's guide: software for canonical community ordination. Biometris, Wageningen.
Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. 1993. Flora Europaea, vol. I. Cambridge University Press. Cambridge.
Velitzelos, D., Bouchal, J.M. & Denk, T. 2014. Review of the Cenozoic floras and vegetation of Greece. Rev. Palaeobot. Palynol. 204: 56−117.
Ward, J.H. 1963. Hierarchical grouping to optimize an objective function. J. Am. Stat. Assoc. 58: 236−244.
Xenopoulos, S., Andréoli, C., Panconesi, A., Pinto Ganhão, J. & Tuset, J.J. 1990. Importance of cypress. In: Ponchet, J. (Ed.). Progress in EEC Research on Cypress Diseases. Pp. 1−13. Commission of the European Communities Report EUR 12493. Luxembourg.
Zacharis, A. 1977. Forests of Crete from Antiquity to today. Ministry of Agriculture, Athens.
Zohary, M. 1973. Geobotanical Foundations of the Middle East, vol. 2. Gustav Fischer Verlag, Stuttgart.
Zohary, M. & Orshan, G. 1965. An outline of the geobotany of Crete. Isr. J. Bot. 14: 1−49.