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Review of Palaeobotany and Palynology 185 (2012) 79–92

Contents lists available at SciVerse ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Research paper

Modern vegetation, pollen and climate relationships on the Mediterranean island of Cyprus

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ARTICLE INFO

Article history:
Received 2 April 2012
Received in revised form 7 August 2012
Accepted 12 August 2012
Available online 21 August 2012

Keywords:
Cyprus
discriminant analysis
Mediterranean islands
modern pollen–vegetation relationships
pollen–climate relationships
surface soil samples

ABSTRACT

This research investigates patterns of plant species distributions, modern pollen deposition, and climate on the island of Cyprus in the eastern Mediterranean, and explores the potential for using these modern pollen–vegetation–climate relationships for paleoenvironmental interpretation. Vegetation and pollen data were collected at 56 locations along elevational gradients from the southern coast across the Troodos Mountains, to the Kyrenia Range, and to the northern coast of Cyprus. Elevation, mean annual precipitation and mean annual temperature were interpolated for each sample locale. Discriminant analysis, cluster analysis, non-metric multi-dimensional scaling and indices of plant-pollen fidelity and dispersibility are used to characterize the vegetation and pollen of Cyprus.

The main vegetation types in Cyprus — oak forests, pine forests, orchards, and coastal scrub and salt lake vegetation can be distinguished in modern pollen samples; samples from disturbed garigue vegetation could not be separated from surrounding vegetation types. Pollen taxa demonstrate clear relationships with climatic variables. *Pinus*, Cyperaceae, *Cistus*, *Quercus* and *Prunus* are found associated with greater amounts of precipitation and higher elevations. Higher temperatures are linked particularly to Cupressaceae, *Olea*, *Cerealia*-type, Liguliflorae, and Chenopodiaceae pollen. The majority of the pollen taxa show moderate to moderately high fidelity, signifying the close link between the vegetation of Cyprus and its pollen. Many pollen taxa also reflect high dispersibility, which in some cases demonstrates over representation in the pollen rain. The relationships between the main modern pollen taxa of Cyprus and broad climatic variables can provide the basis for interpreting paleoenvironmental records.

1. Introduction

An understanding of the relationship between contemporary vegetation, modern pollen rain and climate is essential for the interpretation of fossil pollen spectra to characterize past vegetation and paleoclimates. Many studies demonstrate the value of this approach in a variety of geographic settings (e.g., Anderson, 1970; Birks, 1973; Markgraf et al., 1981; Prentice et al., 1987; Jackson, 1990; Fall, 1992; Islebe and Hooghiemstra, 1995; Ren and Beug, 2002; Ma et al., 2008; Marcos and Mancini, 2012). Investigations of taxonomic over- and under-representation of pollen types have been explored (e.g., Davis, 1984), including the calculation of palynological indices of dispersibility and fidelity (McGlone and Meurk, 2000) to help understand the patterns of pollen deposition and modern vegetation.

Studies of modern pollen rain have a long tradition in the eastern Mediterranean region. Surface pollen data, often collected as modern analogs for paleoenvironmental interpretations based on fossil pollen data, come from forested areas in Greece (Bottema, 1974; Gerasimides et al., 2006), Turkey (van Zeist et al., 1970, 1975; Vermoere et al., 2001; Kaniewski et al., 2007) and Iran (Wright et al., 1967; Ramezani et al., 2008; Djamali et al., 2009). Similarly, modern pollen studies from more arid regions in the Levant often are designed to support the interpretation of fossil pollen data (e.g., Horowitz and Baum, 1967; Rossignol, 1969; Weinstein, 1976; Bottema and Barkoudah, 1979; El-Moslimany, 1990; Horowitz, 1992; Davies and Fall, 2001). On the island of Cyprus, however, no previous studies compare extant vegetation with its modern pollen rain. Although the vegetation of the Mediterranean reflects a legacy of human impact, modern plant species distributions retain portions of their natural distributions (Zohary, 1973), thereby reflecting contemporary climatic conditions. Thus, the spatial distribution of modern pollen can be linked to the vegetation that produced it, as well as to climatic conditions.

2. Vegetation and climate of Cyprus

2.1. Climate

The climate of Cyprus is decidedly Mediterranean; relatively mild, moist winters stand in sharp contrast to hot, dry summers. Seasonal variability in precipitation is compounded by variations in annual

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http://dx.doi.org/10.1016/j.revpalbo.2012.08.002

rainfall, leading occasionally to multi-year droughts. The Troodos Mountains rise to over 1950 m, drawing increased precipitation off the Mediterranean Sea as air rises over this massif. The lower elevation Kyrenia Range (reaching just over 1000 m) running along the northern coast of Cyprus similarly supports a moister climate at higher elevation. The mean annual precipitation for Cyprus is about 480 mm, with values as high as 1100 mm at the top of the Troodos, about 550 mm in the Kyrenia Range, and as low as 300 mm on the Mesoria Plain (Tsintides et al., 2002). Snow generally occurs only at elevations above about 1000 m. The island's topography similarly affects temperatures, with mean daily values reaching 29 °C in summer along the coasts and on the central Mesoria plain, and cooler daily means of about 22 °C in the mountains.

2.2. Vegetation of Cyprus

The flora of Cyprus and the eastern Mediterranean is characterized by relatively high biodiversity, with many areas in which species are endangered (e.g., Quézel, 1995, 1999). Like most Mediterranean islands and coastal areas, Cyprus has experienced millennia of human exploitation. As a result, much of the original pine and oak forests have been modified heavily (Pons and Quézel, 1998). The landscape has been transformed by deforestation, fire and the introduction of domestic animals and agriculture, particularly intensive arboriculture. Hence, most vegetation communities have evolved in concert with human manipulation. Coastal Mediterranean forests often have been altered, particularly in stature, to become maquis or garigue (Burnie, 1995). Maquis is defined here as forest vegetation that has not fully regenerated and is comprised of evergreen shrubs or small trees (up to 3–5 m high). Common maquis shrubs include *Myrtus communis*, *Genista*, and *Calcycotome*. Similarly, garigue is composed of low-growing evergreen shrubs up to about 50 cm high. Throughout the Mediterranean region characteristic plants of garigue include *Thymus* and *Cistus*, both of which are unpalatable to goats (Burnie, 1995). Cyprus represents a mixture of regenerated forests, extensive areas of maquis and garigue, and orchards and agricultural fields amid a landscape of villages, towns and cities. Aside from the capital of Lefkosia (Nicosia), most of the larger towns and cities and new tourist developments are in coastal environments. Some of the lands surrounding mountain villages appear to be regenerating, as shrubs and forest species take over former fields and orchards (particularly olive and almond), as observed similarly in the western Mediterranean (e.g., Pons and Quézel, 1998). The exceptions to this forest regeneration are well-maintained vineyards and fruit orchards. In spite of this landscape modification, the potential vegetation of Cyprus is still reflected in its remnant forests and pockets of natural vegetation (Quézel and Barbéro, 1985).

2.2.1. Conifer forests

Two species of *Pinus* dominate the forests of Cyprus (Barbéro et al., 1998). *Pinus nigra pallasiana* (black pine) dominates the highest elevation pine forests of the Troodos Mountains from about 1400 m elevation to their summit at Mt. Olympus (1952 m). Tsintides (1998) notes that *Pinus nigra* can grow as low as about 1200 m elevation in wetter locations. Understory plants in the black pine forest include *Sorbus aria*, *Juniperus foetidissima*, *Rosa canina canina*, *Berberis cretica*, *Alyssum cypricum*, *Hypericum repens*, *Cotoneaster racemiflorus*, *Cistus cretica*, *Rubus sanctus* and *Pterocephalus multiflorus*. *Pinus brutia* (Calabrian pine) is a component of the black pine forest below about 1750 m elevation, which becomes a co-dominant below about 1600 m elevation. *Pinus nigra* grows in the Troodos Mountains where annual precipitation ranges between 800 and 1000 mm (falling mainly as snow) and winter temperatures drop to −10 °C (Tsintides, 1998).

Pinus brutia forests are found in the Troodos Mountains and foothills primarily between about 600–1200 m elevation, and from about 300–800 m elevation in the Kyrenia Range. Individual *Pinus brutia* trees can be found growing as low as sea level and up to about 1750 m elevation. Common trees and shrubs within the *Pinus brutia* forests in the Kyrenia Range of northern Cyprus are *Cupressus sempervirens*, *Genista spaeceolata*, *Sarcopoterium spinosum*, *Cistus* sp., *Olea europaea*, *Asphodelus* sp., *Lithodora* sp., *Pistacia lentiscus*, *Pistacia terebinthus*, *Rhamnus oleoides*, *Arbutus andrachne* and *Crataegus azarolus*. *Pinus brutia* dominates some forest stands accompanied by relatively few understory species, which include *Cistus* spp., grasses and occasional *Pistacia* spp. shrubs. In other parts of the Troodos Mountains and the southern part of Cyprus, *Pinus brutia* grows amid a wide range of species, including *Cistus* spp., *Pistacia terebinthus*, *Crataegus azarolus*, *Myrtus communis*, *Rhus coriaria*, *Ceratonia siliqua*, *Helichrysum italicum*, *Ptilostemon chamaepeuce*, *Rubia* cf. *tenuifolia*, *Pterocephalus multiflorus*, *Calicotome villosa* and *Rhamnus oleoides*.

The endemic tree *Cedrus brevifolia* (Cyprus cedar) has a restricted geographical distribution in the Cedar Valley of the Paphos Forest from 900 to 1400 m elevation (Tsintides et al., 2002). It is now planted extensively along roads, villages and monuments in the forests of the Troodos Mountains. Its relative, the exotic *Cedrus libani* (Cedar of Lebanon), is planted occasionally in the mountains. The evergreen tree *Cupressus sempervirens* (Mediterranean cypress) is indigenous to Cyprus. *Cupressus sempervirens* is planted widely in Cyprus, but also occurs naturally in forests, particularly in the Kyrenia Range where it grows alone or with *Pinus brutia* (Tsintides et al., 2002).

2.2.2. Oak forests

Two evergreen species dominate the oak forests of Cyprus, *Quercus alnifolia* (golden oak) and *Quercus coccifera* (holly or Kermes oak). A third species, *Quercus infectoria*, is less common than the other two today, but was noted historically in both the Troodos and Kyrenia mountains as growing up to 1400 m elevation (Meikle, 1985). *Quercus alnifolia* is endemic to Cyprus and grows only on the ultrabasic igneous substrates of the Troodos Mountains (Meikle, 1985). *Quercus alnifolia* generally grows between about 800 and 1500 m elevation. This oak is found with *Pinus brutia* in drier locales, but forms dense stands with other evergreen maquis species in wetter places with deeper soils (Barbéro and Quézel, 1979; Meikle, 1985). *Quercus coccifera*, distributed widely through the Mediterranean region, is closely related to *Quercus calliprinos* (Palestine oak) to the degree that in Cyprus it is classified occasionally as *Q. coccifera* subsp. *calliprinos*. *Quercus coccifera* grows primarily on limestone substrates and is common in a wide range of habitats. *Quercus coccifera* can grow from the coastal plain in southern Cyprus up to about 1400 m elevation in the Troodos Mountains, sometimes on igneous soils within the elevational range of *Quercus alnifolia*. Where they grow together, these two oaks can hybridize (Neophytou et al., 2007). Much of the elevational range of the oak forests of southern Cyprus has been converted to *Vitis vinifera* vineyards and fruit orchards.

2.2.3. Maquis and Garigue

Maquis vegetation generally occurs in areas with about 450–1000 mm of annual precipitation. Common species include *Juniperus phoenicea*, *Pistacia lentiscus*, *Ceratonia siliqua*, *Olea europaea*, *Cistus* spp. and *Salvia fruticosa*, with occasional *Pinus brutia* trees (Tsintides, 1998). At higher elevations in the Troodos Mountains, the maquis blends into the oak forests, where it is dominated by *Quercus alnifolia*, *Arbutus andrachne*, *Pistacia terebinthus*, *Quercus coccifera* and *Crataegus azarolus*.

Garigue vegetation consists of shrubs growing from sea level up into the Troodos Mountains. Characteristic plants include *Genista spaeceolata*, *Calycotome villosa*, *Cistus* spp., *Lithodora hispidula*, *Prasium majus*, *Pterocephalus multiflorus*, *Ephedra fragilis*, *Thymus capitatus*, *Fumana* spp., *Asperula cypria* and *Lavandula stoechas*, with scattered *Pistacia* spp., *Ceratonia siliqua* and *Pinus brutia* (Tsintides, 1998). On the drier, eroded slopes of the Mesoria Plain, and around Lefkosia and Larnaca, garigue plants consist of *Crataegus azarolus*, *Ziziphus lotus*, *Noaea mucronata*, *Phagnalon rupestre*, *Thymus capitatus*, *Fumana* spp., *Sarcopoterium spinosum*, *Asparagus stipularis*, *Helianthemum obtusifoilum* and *Asperula cypria* (Tsintides, 1998).

2.2.4. Coastal and wetland vegetation

Coastal vegetation is characterized by the low plants *Limonium* spp., *Echium angustifolium*, *Medicago maritima*, *Cakile maritima*, *Centaurea aegialophila* and *Verbascum sinuatum*. Exotic species near the coasts also occur as groves of introduced *Eucalyptus*, *Acacia* and *Tamarix*. The salt tolerant plants *Salicornia*, *Arthrocnemum*, *Suaeda* and *Juncus* dominate the edges of salt lakes and marshes.

Platanus orientalis, *Alnus orientalis*, *Laurus nobilis*, *Nerium oleander*, *Rubus sanctus*, *Arundo donax*, *Mentha* spp. and *Juncus* spp. grow along streams. A small montane marsh in the Troodos Mountains fed by the Almyrolivado Spring provides a habitat for *Calamagrostis epigejos*, *Juncus littoralis*, *Poa pratensis*, *Polypogon semiverticillatus*, *Schoenus nigricans* and *Carex* spp., along with the endemic species *Brachypodium firmifolium*, *Taraxacum holmboei* and *Crocus cyprius*.

2.2.5. Orchards

Orchards at lower elevations in Cyprus are dominated by *Citrus* groves. *Ceratonia* (carob) and *Olea* (olive) also are common at low to mid-elevations. *Cupressus sempervirens* (cypress) is planted commonly around olive and citrus orchards. Fruit trees in the genera *Prunus* (almond and cherry, primarily) and *Vitis* (grape) are found on mid-elevation mountain slopes; while *Ficus carica* (fig) generally grows at lower elevations.

3. Material and methods

3.1. Field methods — vegetation and pollen sampling

Vegetation and pollen samples were collected in the summers of 2008 and 2009 at 56 locations on the island of Cyprus (Fig. 1). Sample locales were chosen to cover a variety of vegetation types, ranging from coastal scrub to orchards to the forested landscapes of the higher elevations. Surface soil samples were collected at each locale to provide modern pollen data. These samples incorporated 15–20 subsamples of the uppermost soil collected in a circular area approximately 10 m in diameter. In forest environments some of the samples contained leaf litter or moss. Sample points were located with a Garmin hand-held GPS; additional data on aspect, substrate and perennial plant cover were noted at each point. Perennial plant species were recorded at each location over an area of about 100 m diameter. In heterogeneous landscapes like Cyprus, relevant pollen source areas of about 50–100 m from a sample locale have been shown to adequately reflect the local vegetation (Jackson, 1990; Sugita, 1994). These sample locations were arrayed along a series of vegetation transects covering the full elevational range of the island, starting below sea level on the Akrotiri Peninsula south of Limassol, at sea level near Cape Kiti south of Larnaca and near Cape Greko, and extending to the top of the Troodos Massif (Table 1). An additional transect was collected in northern Cyprus along the Kyrenia Range and north coast (Table 2). Plants were identified in the field; nomenclature follows *Trees and Shrubs in Cyprus* (Tsintides et al., 2002), *Flora of Cyprus* (Miekle, 1985) and *An Illustrated Flora of North Cyprus* (Viney, 1994).

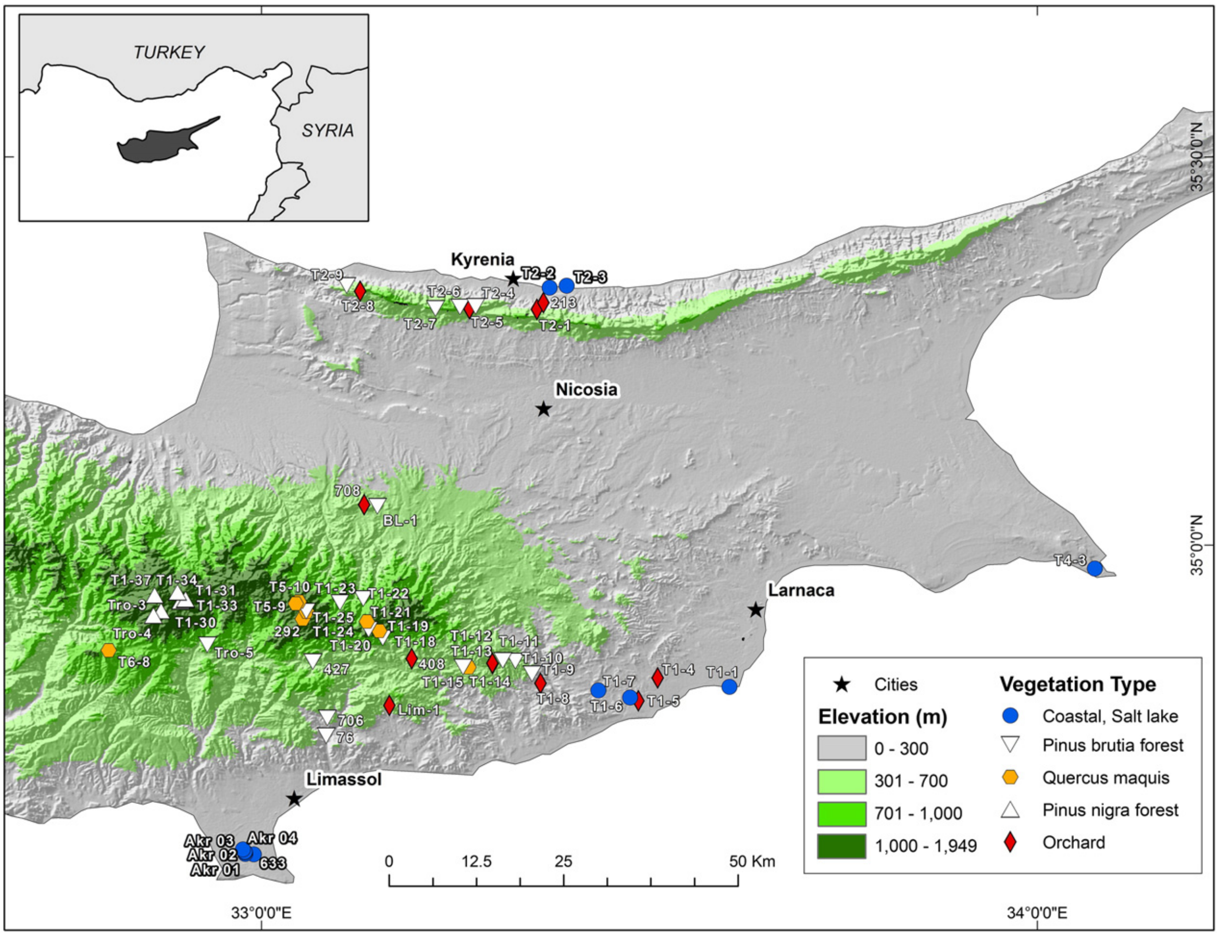

Fig. 1. Map of Cyprus showing locations of modern pollen samples by vegetation types.

Table 1
Modern pollen samples from the Troodos Mountains and southern coast of Cyprus (arranged by elevation). Note: #/Obser/model = discriminant analysis sample number/observed group/modeled group.

Field sample	#/Obser/model	Elevation	Longitude (E)	Latitude (N)	Vegetation type & location
	Main plant species				
Akr-4	1/1/1	−5 m	32 58 33.82	34 36 34.7	Salt lake, Akrotiri Peninsula
	No vegetation, 50 m further out on dry lake from Akr-3				
Akr-3	x/1/1	−5 m	32 58 42.2	34 36 16.92	Salt lake, Akrotiri Peninsula
	No vegetation (a few dead *Atriplex* sp. plants seen further out onto playa)				
Akr-2	3/1/3	0 m	32 58 43.03	34 36 12.96	Salt lake, edge, Akrotiri Peninsula
	Salicornia fruticosa, *Polygonum* sp., *Tamarix* sp., Cyperaceae, *Pistacia lentiscus*, *Eucalyptus* sp. (exotic tree, planted as windbreak along road), *Plantago* sp. and *Atriplex* cf. *semibaccata* at basin edge				
Akr-1	4/1/1	0 m	32 58 44.26	34 36 5.98	Salt lake, flats south of dry lake basin, Akrotiri Peninsula
	Salicornia fruticosa, *Zygophyllum album*, *Anthrocnemum macrostachyum*, Cyperaceae, Poaceae, *Polygonum* cf. *equisetiforme*, *Eucalyptus* (exotic tree, planted along road), *Plantago* sp. in dunes				
633	6/1/1	5 m	32 59 23.89	34 36 4.03	Coastal/orchard near Monastery, Akrotiri
	Citrus x paradisi (exotic, planted), *Pistacia lentiscus*, *Malva parvifolia*, Poaceae				
T1-1	7/1/1	8 m	33 36 11.3	34 49 1.7	Coastal, cliff above beach at Cape Kiti, south coast
	Atriplex halimus, *Acacia pycnantha* (exotic, planted), *Eucalyptus* sp. (exotic, planted), *Polygonum equisetiforme*, *Noaea macronata*, *Helianthemum* cf. *stipulatum*, *Anthrocnemum* cf. *macrostachyum*, *Thymus capitatus*, *Rhamnus oleoides*, *Fumaria thymifolia*, Papilionaceae				
T1-5	9/6/1	24 m	33 29 8.63	34 47 57.37	Olive orchard and fields surrounded by cypress
	Pistacia sp., *Ceratonia siliqua*, *Crataegus azarolus*, *Thymus capitatus*, *Ferula communis*, *Rhamnus oleoides*, *Noaea macronata*, *Olea europaea*, *Thymelaea hirsuta*, *Capparis spinosa*, *Asphodelus* sp., *Asparagus acutifolius*, *Helichrysum conglobatum*, *Anchusa* cf. *azurea*, *Ziziphus lotus*, *Cupressus sempervirens*, *Eucalyptus* sp. (exotic, planted), *Ephedra fragilis*, *Lonicera etrusca*				
T4-3	10/1/1	39 m	34 4 27.1	34 58 10.9	Coastal, open juniper scrub near Cape Greko
	Juniperus phoenicea, *Thymus capitatus*, *Rhamnus oleoides*, *Ephedra fragilis* subsp. *campylopoda*, *Asparagus spinosa*, *Olea europaea*				
T1-6	11/2/1	41 m	33 28 30.18	34 48 12.06	Garigue/coastal, surrounded by fields and orchards
	Pistacia sp., *Crataegus azarolus*, *Asparagus acutifolius*, *Helichrysum* sp., *Pinus brutia*, *Rhamnus oleoides*, *Prosopis farcta*, *Olea europaea*, *Calycotome villosa*, *Capparis spinosa*, *Noaea macronata*, *Sarcopoterium spinosa*, *Inula viscosa*, *Hypericum* sp., *Punica granatum*, *Ferula communis*				
T1-4	12/6/6	56 m	33 30 38.52	34 49 44	Olive orchard with cypress fields, s of Kivisili
	Olea europaea (planted), *Cupressus sempervirens* (planted), *Asparagus acutifolius*, *Eucalyptus* sp. (exotic, planted), *Rhamnus oleoides*, *Asparagus stipularis*, *Capparis spinosa*				
T1-7	13/2/1	98 m	33 26 2.47	34 48 44.86	Garigue near Kofinou
	Calycotome villosa, *Genista spaeceolata*, *Sarcopoterium spinosum*, *Olea europaea*, *Echium angustifolium*, *Hypericum* sp., *Zizyphus lotus*, *Pistacia* sp., *Cistus* sp., *Capparis spinosa*, *Crataegus azarolus*, *Ceratonia siliqua*, *Ferula communis*, *Pallensis spinosa*, *Asparagus acutifolius*, *Asparagus stipularis*, *Noaea macronata*, *Anchusa* cf. *azurea*, *Asphodelus* cf. *aestivus*, *Helichrysum* sp., *Inula viscosa*, *Eucalyptus* sp. (exotic, planted), *Reseda* cf. *orientalis*, *Pistacia lentiscus*, Brassicaceae, *Fumaria* sp.				
76	14/2/3	124 m	33 5 0.13	34 45 14.69	Garigue
	Cistus sp., *Thymus capitatus*, *Calycotome villosa*, *Pistacia lentiscus*, *Sarcopoterium spinosum*, *Helichrysum* sp., *Genista spaeceolata*, *Asphodelus* sp., Poaceae, *Phagnalon rupestre*, a few small *Pinus brutia*, *Olea europaea*, *Ceratonia siliqua*				
T1-8	16/6/6	163 m	33 21 34.92	34 49 19.24	Orchards and maquis above Skarinou
	Pistacia sp., *Ceratonia siliqua*, *Rhamnus oleoides*, *Sarcopoterium spinosum*, *Thymus capitatus*, *Calycotome villosa*, *Olea europaea*, *Cistus* sp., *Asphodelus* sp., *Capparis spinosa*, *Pistacia terebinthus*				
T1-9	18/3/3	272 m	33 20 55.5	34 50 1.93	*Pinus brutia* forest/maquis
	Ptilostemon chamaepeuce, *Ceratonia siliqua*, *Genista spaeceolata*, *Cistus* sp., *Sarcopoterium spinosum*, *Helichrysum* sp., *Asphodelus* sp., *Pistacia terebinthus*, *Rhamnus oleoides*, *Asparagus acutifolius*, *Pinus brutia*, *Pistacia* sp., *Thymus capitatus*, *Lithodora* sp.				
706	19/3/3	273 m	33 5 5.5	34 46 37.45	*Pinus brutia* forest/maquis
	Cistus sp., *Calycotome villosa*, *Genista spacelata*, *Sarcopoterium spinosum*, *Pinus brutia*, *Ceratonia siliqua*, *Rhamnus oleoides*, *Thymus capitatus*, *Pistacia lentiscus*, *Olea europaea*, *Micromeria myrtifolia*, *Lithodora hispidula*				
T1-12	22/6/6	416 m	33 17 52.04	34 50 50.28	Orchard/maquis
	Cistus sp., *Teucrium creticum*, *Ptilostemon chamaepeuce*, *Olea europaea*, *Lithodora hispidula*, *Sarcopoterium spinosa*, *Ceratonia siliqua*, *Pistacia terebinthus*, *Rubus sanctus*, *Pistacia* sp., *Calycotome villosa*, *Helianthemum obustifolium*, *Inula viscosa*, *Asphodelus* sp.				
T1-13	21/6/6	416 m	33 17 51.29	34 50 51.68	Orchard/maquis
	Phragmites australis, *Cistus* sp., *Calycotome villosa*, *Inula viscosa*, *Daucus carota*, *Ptilostemon chamaepeuce*, *Rubus sanctus*, Cyperaceae, *Polygonum* sp., *Pistacia* sp., *Pistacia terebinthus*, *Sarcopoterium spinosa*, *Olea europaea*, *Acacia* sp. (exotic, wattle type), *Helichrysum* sp., *Ferula communis*, *Tamarix* sp., *Genista spaeceolata*, *Capparis spinosa*, *Eucalyptus* sp. (exotic), *Echinops* sp., *Nerium oleander*, Poaceae, *Centaurea* sp.				
708	24/6/6	428 m	33 7 56.5	35 3 7.78	Orchard/maquis
	Olea europaea, *Cistus* sp., *Phagnalon rupestre*, *Rhamnus oleoides*, *Sarcopoterium spinosum*, *Pinus brutia*, *Inula viscosa*, Papilionaceae, *Capparis spinosa*, *Noaea micronata*, Poaceae				
BL-1	25/2/3	443 m	33 8 57.88	35 2 59.93	Garigue
	Thymus capitatus, *Cistus* sp., *Sarcopoterium spinosum*, Poaceae, *Ziziphus lotus*, *Pistacia lentiscus*, *Crataegus azarolus*, Papilionaceae, *Quercus coccifera*				
T1-14	26/4/4	452 m	33 16 0.44	34 50 32.32	*Quercus* maquis
	Quercus coccifera, *Pistacia lentiscus*, *Pistacia* sp., *Cistus* sp., *Rhamnus oleoides*, *Ferula communis*, *Asparagus acutifolius*, *Capparis spinosa*, *Inula viscosa*, *Arbutus andrachne*, *Sarcopoterium spinosa*, *Ceratonia siliqua*, *Ptilostemon chamaepeuce*, *Calycotome villosa*, *Teucriumcreticum*, *Olea europaea* (orchard nearby), *Prunus dulcis* (orchard nearby), Brassicaceae, Papaveraceae, *Astragalus*, *Rubia* cf. *tenuifolia*, cf. *Rhamnus alaternus*				
T1-15	23/3/3	467 m	33 15 35.14	34 50 34.62	*Pinus brutia* forest
	Cistus sp., *Ceratonia siliqua*, *Ptilostemon chamaepeuce*, *Helichrysum* sp., *Pinus brutia*, *Thymus capitatus*, *Olea europaea*, *Genista spaeceolata*, *Pistacia terebinthus*, *Pistacia* sp., *Lavandula stoechas*, *Teucriumcreticum*, *Lithodora* sp., *Rhamnus oleoides*, *Asphodelus* sp., *Fumana* sp.				
Lim-1	27/6/6	477 m	33 9 53.42	34 47 55.66	Olive orchard
	Olea europea, *Cistus* sp., *Pinus brutia*, *Thymus capitatus*, *Genista* sp., *Lavandula stoechas*, *Prunus dulcis*				
408	29/6/6	487 m	33 11 37.43	34 51 13.1	Orchard/maquis
	Cistus sp., *Sarcopoterium spinosum*, *Olea europaea*, *Pistacia lentiscus*, *Pistacia terebinthus*, *Helichrysum italicum*, *Rhamnus oleoides*, *Quercus coccifera*, *Ceratonia siliqua*, *Calycotome villosa*, Poaceae				
T1-10	28/3/3	496 m	33 19 37.52	34 51 1.98	*Pinus brutia* forest/maquis
	Genista spaeceolata, *Helichrysum* sp., *Ptilostemon chamaepeuce*, *Ceratonia siliqua*, *Micromeria myrtifolia*, *Cistus* sp., *Sarcopoterium spinosum*, *Pinus brutia*, *Inula viscosa*, *Thymus capitatus*, *Pallensis spinosa*, *Rubia tenuifolia*, *Echinops* sp., *Cupressus sempervirens*, *Acacia* sp. (exotic), *Nerium oleander*, Brassicaceae, Apiaceae, *Plantago* sp., *Lithodora* sp., *Pinus canariensis* (exotic, planted)				

Table 1 (*continued*)

Field sample	#/Obser/model	Elevation	Longitude (E)	Latitude (N)	Vegetation type & location
	Main plant species				
T1-11	30/2/2	542 m	33 18 39.49	34 51 4.43	Garigue/maquis
	Genista spaeceolata, *Pistacia terebinthus*, *Sarcopoterium spinosa*, *Inula viscosa*, *Ceratonia siliqua*, *Helichrysum* sp., *Capparis spinosa*, *Lithodora hispidula*, *Micromeria myrtifolia*, *Rubia* cf. *tenuifolia*, *Cupressus sempervirens* (planted), *Ferula communis*, *Pinus brutia* (planted), *Acacia* (exotic), *Nerium oleander*, *Calycotome villosa*, *Ptilostemon chamaepeuce*, *Asparagus acutifolia*, *Cistus* sp., *Olea europaea* (planted), *Echinops* sp., *Teucriumcreticum*, *Daucus carota*, Alhagi sp.				
427	31/3/3	605 m	33 3 57.85	34 50 58.99	*Pinus brutia* forest
	Pinus brutia, *Cistus* sp., *Pistacia* sp., *Calycotome villosa*, *Helichrysum italicum*, *Hypericum repens*				
T1-18	36/3/3	757 m	33 9 22.39	34 52 48.9	*Pinus brutia* forest
	Pinus brutia, *Cistus* sp., *Pistacia terebinthus*, *Crataegus azarolus*, *Rhus coriaria*, *Ceratonia siliqua*, *Helichrysum italicum*, *Ptilostemon chamaepeuce*, *Rubia* cf. *tenuifolia*, cf. *Centaurea*, *Pterocephalus multiflorus*, *Calycotome villosa*, *Juglans* sp., *Prunus dulcis*, *Cercis siliquastrum*				
T1-22	37/3/3	769 m	33 7 52.03	34 55 51.31	*Pinus brutia* forest
	Pinus brutia, *Quercus alnifolia*, *Rhus coriaria*, *Pistacia terebinthus*, *Cistus* sp., *Acer obustifolium*, *Rhamnus oleoides*, *Ptilostemon chamaepeuce*, *Polygonum* sp., *Capparis spinosa*, *Silene vulgaris*, *Daucus carota*, *Pterocephalus multiflorus*, *Helichrysum italicum*, *Stachys* cf. *cretica*, *Micromeria myrtifolia*, *Heliotropium* cf. *dolosum*, *Asparagus acutifolius*, *Echinops* sp.				
Tro-5	39/3/5	809 m	32 55 48.11	34 52 17.26	Burned *Pinus brutia* forest
	Pinus brutia, *Myrtus communis*, *Pistacia* sp., *Quercus coccifera*, Leguminosae (cf. *Vicia* or *Colutea*), *Inula viscosa*, *Eucalyptus* (exotic, planted along road), Papaveraceae, *Robinia pseudoacacia*, Boraginaceae				
T1-23	40/3/3	864 m	33 6 4.25	34 55 33.1	*Pinus brutia* forest
	Pinus brutia, *Cupressus sempervirens* (planted), *Polygonum* sp. *Capparis spinosa*, *Prunus dulcis*, *Inula viscosa*, *Echinops* sp., *Ptilostemon chamaepeuce*, *Pterocephalus multiflorus*, *Avena* sp., *Cistus* sp., *Ailanthus glandulosa* (planted), *Quercus* sp., *Nerium oleander* (planted), *Pinus* sp. (planted)				
T1-19	41/4/4	886 m	33 9 6.62	34 53 22.02	*Quercus* maquis
	Rhus coriaria, *Quercus alnifolia*, *Pistacia terebinthus*, *Crateagus azarolus*, *Helichrysum italicum*, *Cistus* sp., *Ptilostemon chamaepeuce*, *Lithodora* sp., *Capparis spinosa*, *Rubus sanctus*, *Pterocephalus mutliflorus*, *Micromeria myrtifolia*, *Echinops* sp., *Ficus carica*, *Euphorbia* sp., *Vicia* sp., *Platanus orientalis*, *Pinus brutia* (in area)				
T6-8	42/4/4	980 m	32 48 10.8	34 51 51.6	*Quercus* maquis and vineyards near Omodos
	Vitis vinifera, *Ceratonia siliqua*, *Olea europaea*, *Prunus dulcis*, *Cistus sp.*, *Genista spaeceolata*, *Odonites cypria*, *Pterocephalus multiflora*, *Rhamnus oleoides*, *Helichrysum conglobatum*, *Rubia tenuifolia*, *Quercus coccifera*, *Lithodora hispidula*, *Ephedra fragilis*, *Teucrium divaricum*, *Rhus coriaria*, *Fumana arabica*, *Ferula communis*, *Crataegus azarolus*, *Pistacia terebinthus*				
T1-21	43/4/4	1059 m	33 8 8.56	34 54 5.47	*Quercus* maquis
	Quercus alnifolia, *Cistus* sp., *Rhus coriaria*, *Pistacia terebinthus*, *Lonicera etrusca*, *Pterocephalus multiflorus*, *Ptilostemon chamaepeuce*, *Rubus sanctus*, Brassicaceae, *Avena* sp., *Pinus brutia* (in area), *Prunus dulcis* (in area), *Vitis vinifera*				
T1-20	44/3/3	1129 m	33 8 17.34	34 53 28.25	*Pinus brutia* forest
	Pinus brutia, *Pistacia terebinthus*, *Quercus alnifolia*, *Cistus* sp., *Rhus coriaria*, *Helichrysum italicum*, *Pterocephalus multiflorus*, *Acer obustifolium*, *Micromeria myrtifolia*, *Capparis spinosa*, *Ficus carica*, *Vicia* sp., *Crataegus azarolus*, *Echinops* sp., *Vitis vinifera* (on slopes)				
T1-24	45/4/3	1173 m	33 3 29.2	34 54 51.3	*Quercus* maquis
	Quercus alnifolia, *Cistus* sp., *Juniperus foetidissima*, *Pistacia terebinthus*, *Helichrysum italicum*, *Polygonum* sp., *Inula viscosa*, *Rhus coriaria*, *Pterocephalus multiflorus*, Apiaceae, *Pinus brutia* (roadside), *Silene vulgaris*, *Echinops* sp., *Brassica* sp., *Rubia tenuifolia*, Brassicacae, *Cupressus sempervirens*, *Ferula communis*, *Genista spaeceolata*				
T1-25	46/3/3	1202 m	33 3 28.15	34 54 53.53	*Pinus brutia* forest/maquis
	Pinus brutia, *Quercus alnifolia*, *Crataegus azarolus*, *Cistus* sp., *Pistacia terebinthus*, *Acer obustifolium*, *Echinops* sp., *Micromeria myrtifolia*, *Vicia* sp., *Genista spaeceolata*, *Asphodelus* sp., Apiaceae, *Ephedra fragilis*, *Silene vulgaris*, *Pyrocantha* sp., *Cupressus sempervirens*, *Echium* cf. *angustifolium*, *Robinia* sp., *Prunus dulcis* (on terraces), *Vitus vinifera* (on terraces)				
292	47/4/4	1280 m	33 3 11.3	34 54 16.74	*Quercus* maquis
	Quercus coccifera calliprinos, *Pistacia terebinthus*, *Pinus brutia*, *Cistus creticus*, *Arbutus andrachne*, *Rosa canina canina*, *Rhus coriaria*, *Pterocephalus multiflorus*, *Micromeria* sp., *Lonicera etrusca*, *Vitus vinifera* (in area)				
T5-9	48/4/4	1290 m	33 2 39.2	34 55 28.5	*Quercus* maquis, cherry and walnut orchards
	Prunus avium (planted), *Juglans regia*, *Quercus alnifolia*, *Cistus* cf. *creticus*, *Helichrysum italicum*, *Crataegus azarolus*, *Acer obtusifolium*, *Rosa canina*, *Vitis vinifera*, *Rhus coriaria*, *Silene vulgaris*				
T5-10	49/4/4	1330 m	33 2 53.3	34 55 37.5	*Quercus* maquis, almond trees and vineyards
	Quercus alnifolia, *Prunus dulcis*, *Acer obtusifolium*, *Vitis vinifera*, *Rhus coriaria*, *Pistacia terebinthus*, *Crataegus azarolus*, *Lonicera etrusca*, *Cistus* cf. *creticus*, *Pterocephalus multiflorus*, *Alyssum* cf. *cypricum* (*Pinus brutia* nearby)				
Tro-4	50/5/5	1452 m	32 51 38.27	34 54 33.16	*Pinus nigra* forest, Gerokamia Overlook
	Pinus brutia, *Pinus nigra pallastiana*, *Arbutus andrachne*, *Robinia pseudoacacia*, *Cistus* sp., *Cedrus brevifolia* (planted), *Quercus* sp., *Sequoiadendron giganteum* (exotic, planted), *Nerium oleander* (planted), *Silene vulgaris*, *Rubia tenuifolia*, Apiaceae, Poaceae				
T1-33	51/5/5	1590 m	32 53 45.06	34 55 38.93	*Pinus nigra* forest, Troodos Mountains
	Pinus nigra pallastiana, *Sorbus aria*, *Juniperus foetidissima*, *Pinus brutia*, Pteridophyta, *Berberis cretica*, *Rosa canina canina*, *Alyssum cypricum*, Cyperaceae, Poaceae				
Tro-3	52/5/5	1592 m	32 52 13.44	34 54 53.64	*Pinus nigra* forest, Kalidonia Trail
	Pinus brutia, *Pinus nigra pallastiana*, *Alnus orientalis*, *Rosa canina*, *Quercus alnifolia*, *Berberis cretica*, *Sorbus aria*, *Prunus dulcis*, *Prunus avium*, *Silene vulgaris*, *Rosa* sp., Pteridophyta, *Epilobium* sp., *Viola sieheana*, *Prunus serotina*, *Platanus orientalis*, *Rubus sanctus*, *Ulmus glabra*, *Juglans* sp. Nearby drier slopes with *Calycotome villosa*, *Cistus* sp., *Quercus coccifera*, Brassicaceae				
T1-31	53/5/5	1597 m	32 54 7.49	34 55 48.43	*Pinus nigra* forest, Troodos Mountains
	Pinus nigra pallastiana, *Juniperus foetidissima*, *Pinus brutia*, *Cedrus brevifolia*, *Rubus sanctus*, *Cistus creticus*, *Rosa canina canina*, *Berberis cretica*, *Pterocephalus multiflorus*, *Hypericum repens*, *Juncus* sp., Poaceae, *Alyssum cypricum*, Cyperaceae				
T1-30	54/5/5	1613 m	32 54 6.41	34 55 45.55	*Pinus nigra* forest, Troodos Mountains
	Pinus nigra pallastiana, *Cedrus brevifolia* (planted), *Pinus brutia*, *Quercus alnifolia*, *Berberis cretica*, *Sorbus aria*, *Alyssum cypricum*, Brassicaceae, *Rubus sanctus*, *Juniperus* sp., *Pterocephalus multiflorus*, *Euphorbia* sp.				
T1-34	55/5/3	1721 m	32 53 30.19	34 56 20.8	*Pinus nigra* forest, Troodos Mountains
	Pinus nigra pallasiana, *Pinus brutia*, *Pistacia terebinthus*, *Quercus alnifolia*, *Alyssum cypricum*, Pteridophyta, *Berberis cretica*, *Sorbus aria*, *Euphorbia* sp., *Cistus* sp., *Juniperus* sp.				
T1-37	56/5/3	1919 m	32 51 43.92	34 56 6.36	*Pinus nigra* forest, Troodos near summit
	Sorbus aria, *Juniperus foetidissima*, *Pinus nigra pallastiana*, *Rosa canina canina*, *Berberis cretica*, *Alyssum cypricum*, *Hypericum repens*, Poaceae, Lamiaceae				

Table 2
Modern pollen samples from Kyrenia Range and northern coast, Cyprus (listed by elevation). Note: #/Obser/model = discriminant analysis sample number/observed group/modeled group.

Field sample	#/Obser/model	Elevation	Longitude (E)	Latitude (N)	Vegetation type & location
	Main plant species				
T2-3	5/1/1	9 m	33 23 35.48	35 20 1.43	Coastal scrub, rocky coast east of Kyrenia
	Thymus capitatus, *Pistacia lentiscus*, *Noaea micronata*, *Limonium* cf. *virgatum*, Asteraceae, *Anchusa* cf. *azurea*, *Asphodelus* sp., *Allium* sp., *Alhagi* sp., *Asparagus stipularis*, *Stachys* sp., with *Phragmites australis* (exotic) and *Inula viscosa* in drainage area				
T2-2	8/1/1	23 m	33 22 16.68	35 19 52.97	Coastal, *Acacia* windbreak inland from north coast
	Acacia cf. *saligna* (exotic, planted), *Pistacia atlantica*, *Olea europaea*, *Ceratonia siliqua*, *Pistacia terebinthus*, *Daucus carota*, *Ficus carica*, *Punica granatum*, *Thymus capitatus*, *Plantago* sp.				
213	15/6/6	123 m	33 21 47.88	35 18 43.88	Old olive orchard below Bellapais
	Olea europaea, *Ceratonia siliqua*, *Crataegus azarolus*, *Cupressus sempervirens*, *Pistacia terebinthus*, *Pistacia atlantica*, *Pistacia lentiscus*, *Sarcopoterium spinosum*, Poaceae, *Cistus* sp., *Echinops* sp.				
T2-9	20/3/3	299 m	33 6 35.03	35 20 2.80	*Pinus brutia* forest, north slope of Kyrenia Range
	Pinus brutia, *Cupressus sempervirens*, *Olea europaea*, *Calycotome villosa*, *Genista spaeceolata*, *Sarcopoterium spinosum*, *Cistus* sp., *Asphodelus* sp., *Lithodora* sp., *Pistacia lentiscus*				
T2-1	17/6/1	301 m	33 21 18.25	35 18 12.17	Orchard and cypress, above Bellapais
	Olea europaea, *Cistus* sp., *Helichrysum* sp., *Calycotome villosa*, *Crataegus azarolus*, *Pinus brutia*, *Ceratonia siliqua*, *Pistacia atlantica*, *Cupressus sempervirens*, *Thymus capitatus*, *Asphodelus* sp., *Echinops* sp., *Micromeria myrtifolia*, *Pistacia terebinthus*, *Sarcopoterium spinosum*, Poaceae, *Capparis spinosa*, Asteraceae				
T2-4	32/3/3	597 m	33 16 33.53	35 18 26.14	*Pinus brutia* forest, Kyrenia Range, St. Hilarian
	Pinus brutia, *Arbutus andrachne*, *Pistacia terebinthus*, *Cistus* sp., *Helichrysum* sp., *Cupressus sempervirens*, *Olea europaea*, *Thymus capitatus*, Poaceae, *Inula viscosa*, *Micromeria myrtifolia*				
T2-5	33/6/1	645 m	33 16 5.38	35 18 14.87	Orchard/pine and cypress forest, Kyrenia Range
	Cupressus sempervirens, *Pinus brutia*, *Cistus* sp., *Rhamnus oleoides*, *Pistacia terebinthus*, *Olea europaea*, *Rhus coriaria*, *Ceratonia siliqua*, *Arbutus andrachne*, *Pistacia lentiscus*, *Thymus capitatus*, *Lithodora* sp.				
T2-8	34/6/1	667 m	33 7 37.78	35 19 36.77	Orchard/maquis/pine forest, Kyrenia Range
	Cistus sp., *Genista spaeceolata*, *Sarcopoterium spinosum*, *Thymus capitatus*, *Crataegus azarolus*, *Olea europaea*, *Cupressus sempervirens*, *Asphodelus* sp., *Pistacia terebinthus*, *Ceratonia siliqua*, *Pinus brutia*				
T2-7	35/3/3	693 m	33 13 26.87	35 18 16.09	*Pinus brutia* forest, Kyrenia Range
	Pinus brutia, *Cupressus sempervirens*, *Asphodelus* sp., *Lithodora* sp., *Cistus* sp., *Rhus coriaria*, *Rhamnus oleoides*, *Crataegus azarolus*				
T2-6	38/3/5	784 m	33 15 20.81	35 18 23.22	*Pinus brutia* forest, crest of Kyrenia Range
	Pinus brutia, *Cupressus sempervirens*, *Cistus* sp., *Asphodelus* sp., *Hypericum repens*, *Arbutus andrachne*, *Pistacia terebinthus*, *Thymus capitatus*, *Lithodora* sp.				

3.2. Laboratory methods — pollen

Surface soil samples of approximately 10 cm^3 were homogenized prior to extraction. Two *Lycopodium* spore tablets (University of Lund), each containing about 13,000 spores, were added to each sample prior to chemical treatment in order to calculate pollen and spore concentrations (Stockmarr, 1971). The samples were sieved through 1 mm screens to remove larger particles (e.g., leaves, twigs, and gravel) and then processed with successive treatments of 10% HCl, 48% HF, concentrated HCl, acetolysis mixture and 5% KOH (Moore et al., 1991).

Samples were stored in glycerol, mounted on microscope slides and examined with a Leitz light-microscope to identify pollen and spores. Pollen generally was counted at 400× magnification, with more difficult identifications made under oil immersion at 1000× magnification. Pollen identifications were based on comparisons with pollen reference material, using photographs of pollen from plants collected in the Mediterranean region (original pollen slides from the Biologisch-Archaeologisch Instituut, Groningen; photographs taken by the author at the Australian National University), as well as published photographs in pollen reference atlases (Moore et al., 1991; Reille, 1992, 1995, 1998). A minimum of 400 pollen grains were identified and counted for each sample (pollen sums range 400–1300; mean = 500 pollen grains). Pollen percentages were calculated excluding spores and indeterminant pollen grains (i.e., those that were broken, concealed, corroded, crumpled or degraded *sensu* Cushing, 1967). Both *Pinus brutia* and *Pinus nigra* trees produce *Pinus sylvestris*-type pollen (Beug, 2004), and thus were not differentiated. Poaceae pollen was identified as *Cerealia*-type if the pollen grains were greater than 37 μm in size and had a thickened annulus around the pore. *Cerealia*-type pollen includes pollen from cultivated cereals (i.e., *Triticum* and *Hordeum*) and from some wild grasses (Beug, 2004). Pollen and spore concentrations (grains/cm^3) were calculated based on the ratio of the added, exotic *Lycopodium* spores to the modern pollen grains counted per cm^3 of each soil sample.

3.3. Numerical analyses

Quantitative analyses were used to evaluate the relationships between surface pollen and its contemporary vegetation for future application in paleoenvironmental reconstruction (Birks and Gordon, 1985). Discriminant analysis provides a particularly valuable tool for evaluating the a priori classification of surface pollen samples based on observed vegetation types (Liu and Lam, 1985; Fall, 1992; Reese and Liu, 2005; Ma et al., 2008; Marcos and Mancini, 2012). Pollen frequencies used in the discriminant analyses, including nine tree types (*Alnus*, *Ceratonia*, *Citrus*, Cupressaceae, *Olea*, *Pinus*, *Pistacia*, *Prunus* and *Quercus*) and twelve shrub or herb taxa (Asteraceae, Brassicaceae, *Cerealia*-type, Chenopodiaceae, *Cistus*, Cyperaceae, *Ephedra*, Laminaceae, Liguliflorae, Poaceae, *Plantago* and *Sarcopoterium*-type). Each of the 56 surface pollen samples was assigned to one of six vegetation types: 1) coastal or salt lake, 2) garigue, 3) *Pinus brutia* forest, 4) *Quercus* maquis, 5) *Pinus nigra* forest or 6) orchard (dominated primarily by *Prunus* and *Olea*). The pollen spectrum for each sample and the centroid for each vegetation type were plotted according to the first two canonical discriminant functions using PASW Statistics (version 18.0) (SPSS Inc., 2009).

Hierarchical cluster analysis was used as an exploratory tool to classify the pollen taxa according to their dissimilarity (PASW Statistics version 18.0, SPSS Inc., 2009). This method provides a valuable means of revealing groupings within multivariate modern pollen data (Birks, 1973; Markgraf et al., 1981). Non-metric multi-dimensional scaling subsequently evaluated the relationship between relative frequencies of pollen taxa and three environmental variables (elevation, mean annual precipitation and mean annual temperature). Non-metric multi-dimensional scaling (NMS), implementing the "autopilot" mode in PC-ORD 14.4 (McCune and Grace, 2002), utilized the Bray-Curtis method to calculate the distance matrix for ordination. Previous studies (e.g., Oswald et al., 2007; Ma et al.,

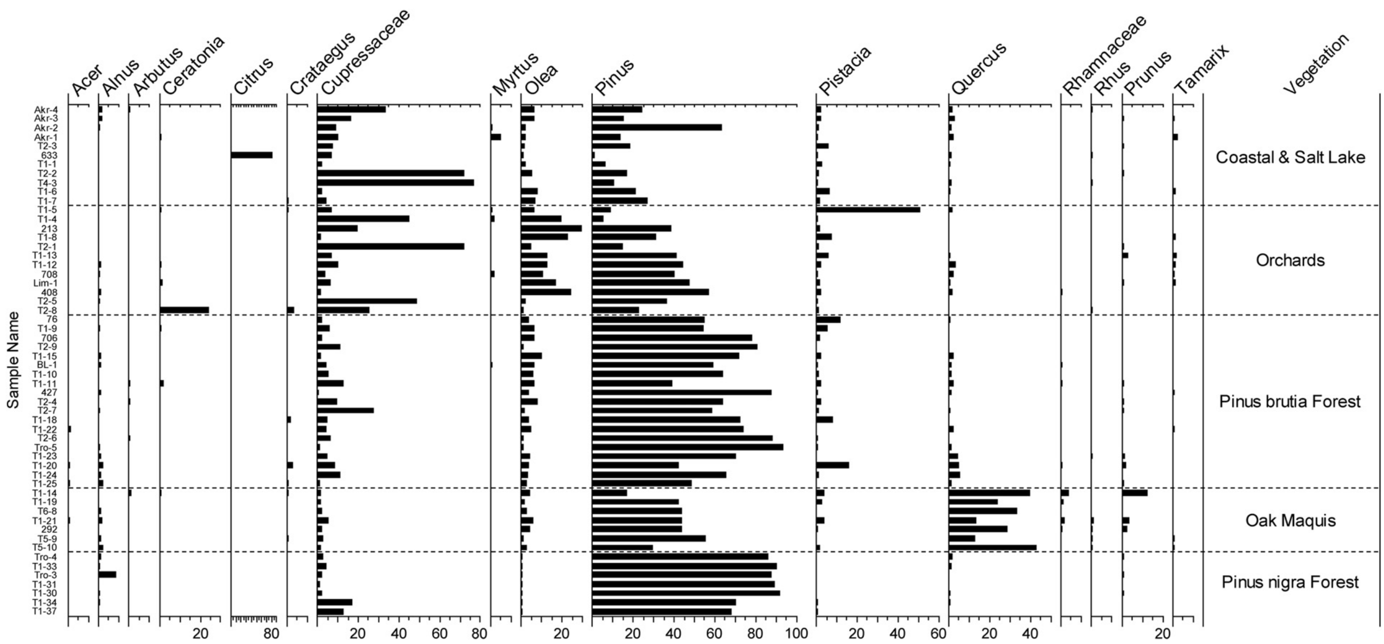

Fig. 2. Arboreal pollen percentages found in the 56 modern pollen samples organized by vegetation types (note scale change for *Citrus* pollen).

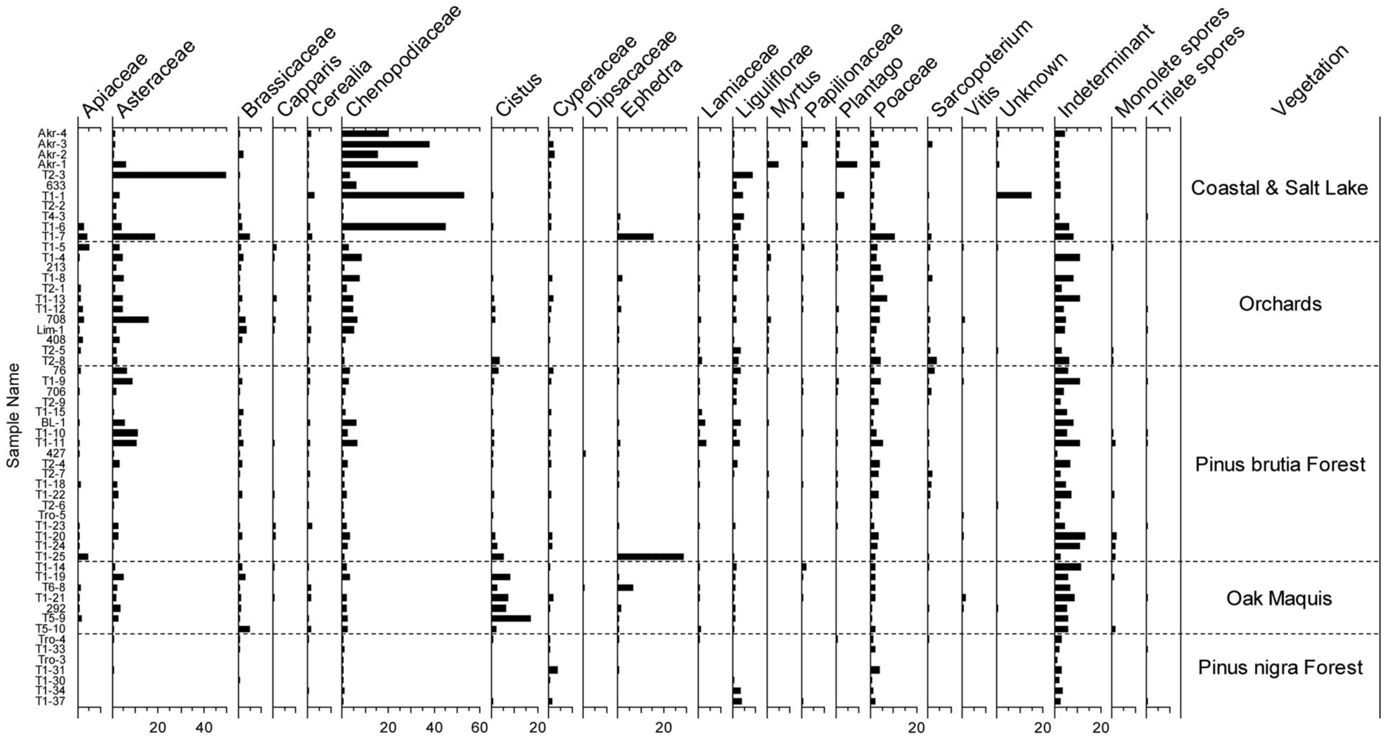

Fig. 3. Pollen percentages for shrub and herb taxa found in the 56 modern pollen samples organized by vegetation types (indeterminant taxa and fern spores are calculated outside the terrestrial pollen sum).

Table 3
Classification results for the modern pollen samples by discriminant analysis for six vegetation groups. [# (%)]; # = number of samples classified as predicted; % = percentage of samples classified as predicted.

Vegetation group (n)	Predicted group					
	Coastal/salt lake	Garigue	*Pinus brutia* forest	*Quercus* maquis	*Pinus nigra* forest	Orchard
Coastal/salt lake (9)	8 (88.9%)	0	1 (11.1%)	0	0	0
Orchard (12)	4 (33%)	0	0	0	0	8 (66.7%)
Garigue (5)	2 (40%)	1 (20%)	2 (40%)	0	0	0
Pinus brutia forest (15)	0	0	13 (86.7%)	0	2 (13.3%)	0
Quercus maquis (8)	0	0	1 (12.5%)	7 (87.5%)	0	0
Pinus nigra forest (7)	0	0	2 (28.6%)	0	5 (71.4%)	0

2008) demonstrate the advantages of this technique for linking palynological data to environmental gradients. A spatial climate model for Cyprus was created using WorldClim, a set of climate layers on a roughly 1 km^2 grid (Hijmans et al., 2005). Mean annual temperature and mean annual precipitation were modeled for each of the modern pollen sample locations. Pollen frequencies for sixteen taxa were used in the cluster and NMS analyses, including tree taxa, Cupressaceae, *Olea*, *Pinus*, *Pistacia*, *Prunus* and *Quercus*, and shrub or herb taxa, Asteraceae, Brassicaceae, *Cerealia*-type, Chenopodiaceae, *Cistus*, Cyperaceae, Liguliflorae, Poaceae, *Plantago* and *Sarcopoterium*-type.

In addition, the presence or absence of pollen taxa was compared with their source plants through the calculation of fidelity or dispersibility indices (McGlone and Meurk, 2000). These fidelity and dispersibility indices expand on the classic study by Davis (1984) to determine over- and under-representation of plants by their pollen. A broadened array of 35 pollen taxa, including many less common types, provides the data for these indices. The fidelity index is calculated as the number of sites at which a taxon appears in both the modern vegetation and in the surface pollen, expressed as a percentage of the total number of sites at which the plant was present. Fidelity = (# sites with plant + pollen/# sites with plant) × 100. The dispersibility index is calculated as the number of sites at which a taxon appears in the surface pollen but is absent in the modern vegetation, expressed as a percentage of all the sites at which the taxon was absent in the modern vegetation. Dispersibility = (# sites with pollen, but without plant/# sites without plant) × 100.

4. Results and discussion

4.1. Representation of Cypriot vegetation by pollen

Pollen percentage data for trees (Fig. 2) and shrub and herb taxa (Fig. 3) show variations by vegetation type. Coastal and salt lake vegetation is dominated by pollen from the Chenopodiaceae and Asteraceae families. Other herbaceous taxa include moderate amounts of Liguliflorae-type, *Plantago* and Poaceae (including *Cerealia*-type) pollen. Trees are represented either by spikes in locally produced pollen (e.g., *Citrus* and Cupressaceae), or local and long-distance pollen (e.g., *Pinus*). Surface samples from orchards have the highest percentages of *Olea* pollen (up to 29%) and moderate to high amounts of Cupressaceae pollen, with *Ceratonia* pollen abundant in one sample, and moderate amounts of *Pinus* pollen. Herbaceous taxa include low amounts of Asteraceae, Chenopodiaceae and Poaceae pollen.

Forests are distinctive according to their pollen spectra. Surface samples from *Pinus brutia* forests have high amounts of *Pinus* pollen, moderate Cupressaceae and low, but consistent amounts of *Olea*, *Pistacia* and *Quercus* pollen. Herbaceous taxa also are represented. Surface samples from oak forests are quite distinct, with the highest percentages of *Quercus* pollen (12–43%), moderate *Pinus*, *Prunus* and *Cistus* pollen, and lower amounts of *Pistacia* and *Olea* pollen. The higher elevation *Pinus nigra* forest samples are characterized by very high *Pinus* values (68–92%), moderate Cuppresaceae pollen and low herbaceous pollen percentages. Pollen spectra from the *Pinus nigra* forest are distinguished by the near absence of pollen from *Pistacia*, *Oak* and *Olea* trees, taxa that are common in the *Pinus brutia* forest samples.

4.2. Discriminant analyses of pollen spectra

The modern pollen samples are distinguished according to vegetation types, based on the results of discriminant analysis. An initial discrimination based on six vegetation types (the five mentioned above with the addition of garigue vegetation) is statistically significant (*Wilk's Lambda* = 0.020; $F = 17.489$; $p < 0.0001$) (Table 3). The taxa that contribute the most to this discrimination are *Olea*, *Pinus*, *Quercus* and *Cistus*. The first and second discriminant functions (*R canonical*: 0.933 *and* 0.862) were statistically significant and explained 65.7% and 28.2% of the total variance, respectively. The *Quercus* maquis is distinguished most clearly from the other five vegetation groups. Function 1 serves to clearly segregate seven of the eight maquis samples from the other five vegetation types, while one maquis sample lies more closely to the *Pinus brutia* forest group.

Samples from the two types of pine forests, distinguished by *Pinus brutia* vs. *Pinus nigra*, overlap but have clearly segregated group centroids. The *Pinus nigra* samples are grouped tightly, while *Pinus brutia* samples are more dispersed. This patterning reflects the more restricted high elevation distribution of *Pinus nigra* compared to the broader elevational range of *Pinus brutia* across Cyprus. Although both *Pinus brutia* and *Pinus nigra* produce *Pinus sylvestris*-type pollen (Beug, 2004) their pollen spectra differ (see Figs. 2 and 3), and they

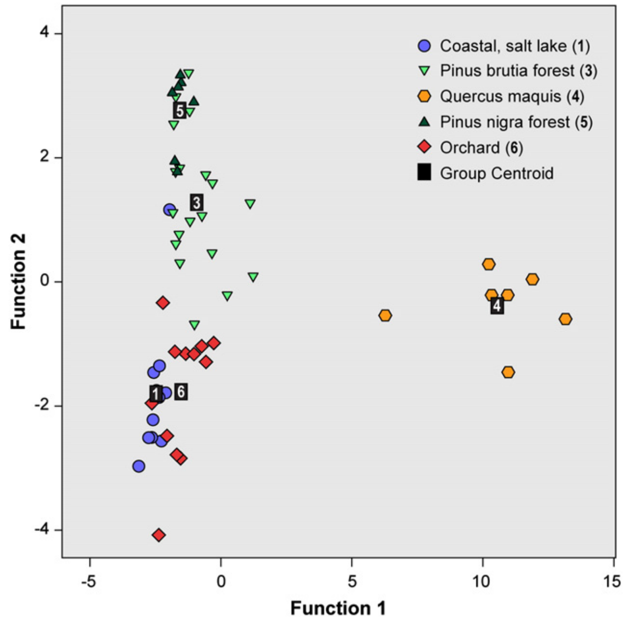

Fig. 4. Discriminant analysis plot of 56 modern pollen samples classified according to five vegetation types, including reclassification of six pollen samples (garigue, group 2 removed).

Table 4
Classification results for the modern pollen samples by discriminant analysis for five vegetation groups; Group 2 (garigue) eliminated. [# (%)]; # = number of samples classified as predicted; % = percentage of samples classified as predicted.

Vegetation type (n)	Predicted group				
	Coastal/salt lake	*Pinus brutia* forest	*Quercus* maquis	*Pinus nigra* forest	Orchard
Coastal/salt lake (11)	8 (72.7%)	1 (9.1%)	0	0	2 (18.2%)
Orchard (12)	1 (8.3%)	1 (8.3%)	0	0	10 (83.3%)
Pinus brutia forest (19)	0	16 (84.2%)	0	3 (15.8%)	0
Quercus maquis (7)	0	0	7 (100%)	0	0
Pinus nigra forest (7)	0	2 (28.6%)	0	5 (71.4%)	0

are shown to be distinct from one another based on the discriminant analysis.

Similarly, coastal/salt lake and orchard vegetation types overlap, with more nearly coincident group centroids than those plotted for the two pine groups. Many of the orchards in Cyprus grow in coastal environments or at the lower elevations of former *Pinus brutia* forests. Interestingly, the samples from garigue vegetation overlap with those of other vegetation types, particularly those from the *Pinus brutia* forest that lies in close proximity.

Tabulated results for the six vegetation types relating the classification of samples according to vegetation groups observed in the field to those predicted by discriminant analysis show the highest rates of agreement (>86%) for three groups: coastal/salt lake, *Pinus brutia* forest and *Quercus* maquis (Table 3). *Pinus nigra* and orchards also show agreement for a majority of samples, at somewhat lower rates of agreement (67–71%). In keeping with the discriminant analysis dispersal of the garigue type, the observed and predicted classifications do not agree for four of five garigue samples. Thus, garigue vegetation does not provide a clear palynological signal. These results were used to modify the discriminant analysis by eliminating the garigue vegetation type and reclassifying the five garigue and one of the *Quercus* maquis samples into the remaining five vegetation types.

A second discriminant analysis evaluated the same pollen spectra, now reclassified into five vegetation groups (Fig. 4). The discrimination between the pollen spectra of these five vegetation types again is significant (*Wilk's Lambda* = 0.006; $F = 28.262$; $p < 0.0001$). The taxa providing the greatest contributions are *Olea*, *Pinus*, *Quercus*, *Cistus* and *Chenopodiaceae*. The first and second discriminant functions (*R canonical*: 0.973 *and* 0.870) were statistically significant, and explained 81.0% and 14.2% of the total variance, respectively. Several salient patterns are apparent, with clear analytical distinctions between the major vegetation types. *Quercus* maquis stands quite distinct from all other groups. *Pinus nigra* and *Pinus brutia* overlap, but with separated group centroids. The coastal/salt lake and orchard groups overlap slightly. The second discriminant analysis leads to revised relationships between observed and predicted classifications (Table 4). The *Quercus* maquis and the two pine forest groups show rates of agreement comparable to the previous iteration of the discriminant analysis (compare to Table 3), while the rate of agreement for the orchard type is enhanced considerably. Interestingly, and perhaps unexpectedly, the coastal/salt lake vegetation type shows less classification agreement than in the previous analysis (two samples observed as coastal now are predicted to be orchard, while one sample observed as coastal is once again predicted as *Pinus brutia* forest).

4.3. Relationships between pollen taxa

Cluster analysis of the 16 main pollen types (based on squared Euclidean distance) utilized the pollen data standardized as Z-scores. The results show four main clusters, plus segregation of two individual outlying pollen taxa (Fig. 5). The two pollen types displaying the greatest similarity, *Quercus* and *Prunus*, cluster with *Cistus* (Cluster 1) and are interpreted as an oak forest group with almond orchards. A second cluster (Cluster 2) consists of Asteraceae and Liguliflorae

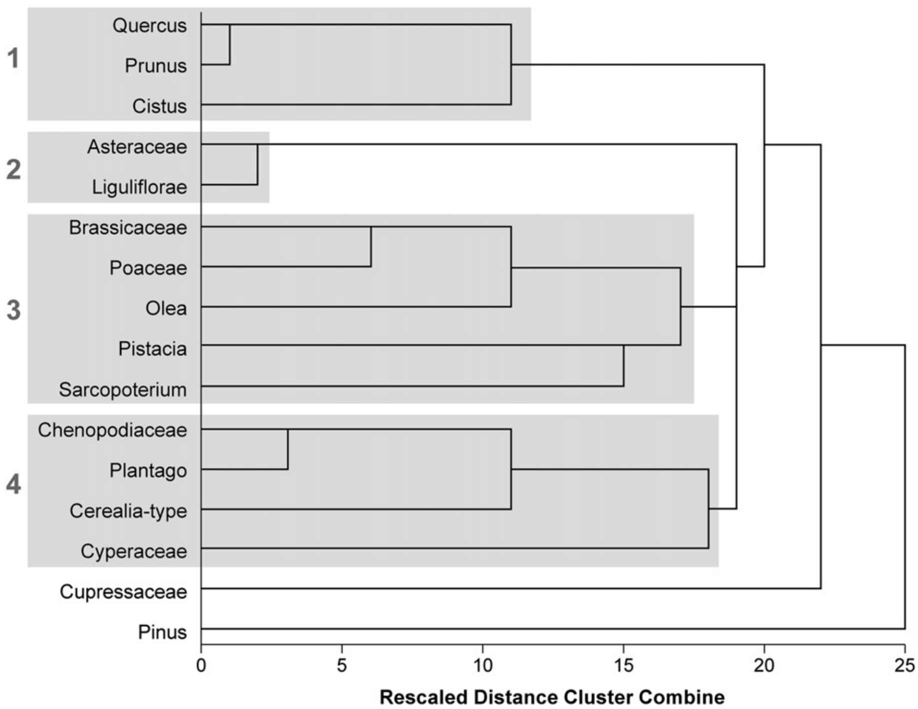

Fig. 5. Hierarchical cluster analysis dendrogram of pollen taxa using squared Euclidean distance.

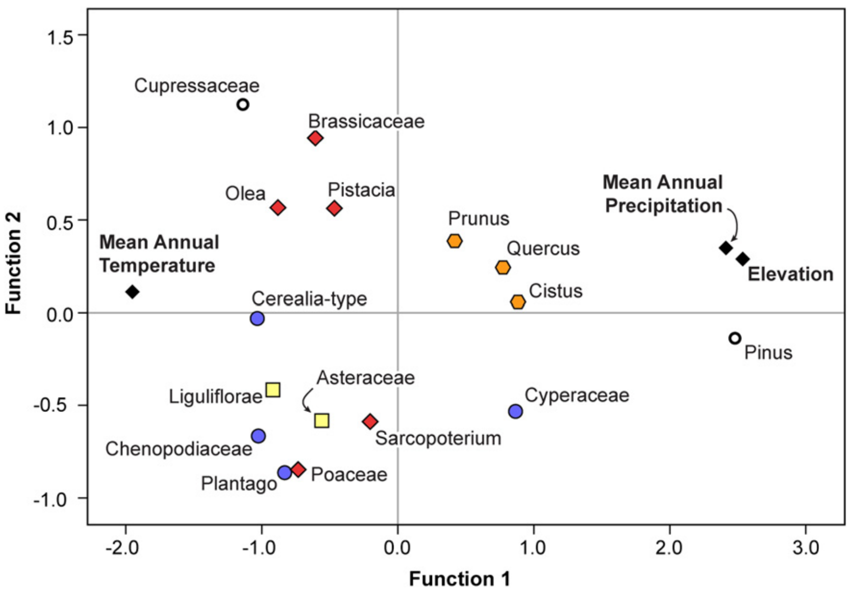

Fig. 6. Non-metric multi-dimensional scaling of pollen taxa and three envirnonmental variables (mean annual temperature, mean annual precipitation and elevation) using a derived stimulus configuration based on Euclidean distance.

pollen, consistent with a grouping of disturbance taxa. Cluster 3 incorporates five pollen types with intermediate levels of clustering (based on their rescaled distance values) consistent with an orchard taxa group, indicative primarily of olive orchards. A fourth cluster (Cluster 4) includes tightly clustered Chenopodiaceae and *Plantago* pollen, plus *Cerealia*-type and Cyperaceae clustered at greater distances, reflecting a low elevation group of taxa found on salt lakes or in coastal environments. The high distance values for Cupressaceae and *Pinus* pollen, relative to the four clusters above, as well as to each other, set them apart as individual analytical outliers. High distance values link Cupressaceae only remotely with Cluster 1 and, even more distantly, the other three clusters. *Pinus* pollen emerges as the most distinct outlier, based on an even greater analytical distance from Cupressaceae and from Clusters 1–4. *Pinus* and Cupressaceae pollen are common in all surface samples in Cyprus.

4.4. Relationships between pollen taxa and environmental variables

The results for non-metric multi-dimensional scaling (Fig. 6) amplify the analytical relationships between the 16 pollen types considered above, plus sample-by-sample data for elevation, mean annual temperature and mean annual precipitation derived from WorldClim (Hijmans et al., 2005). Functions 1 and 2 explain 53.8% and 19.1% of the variance, respectively, reflecting the influences of temperature,

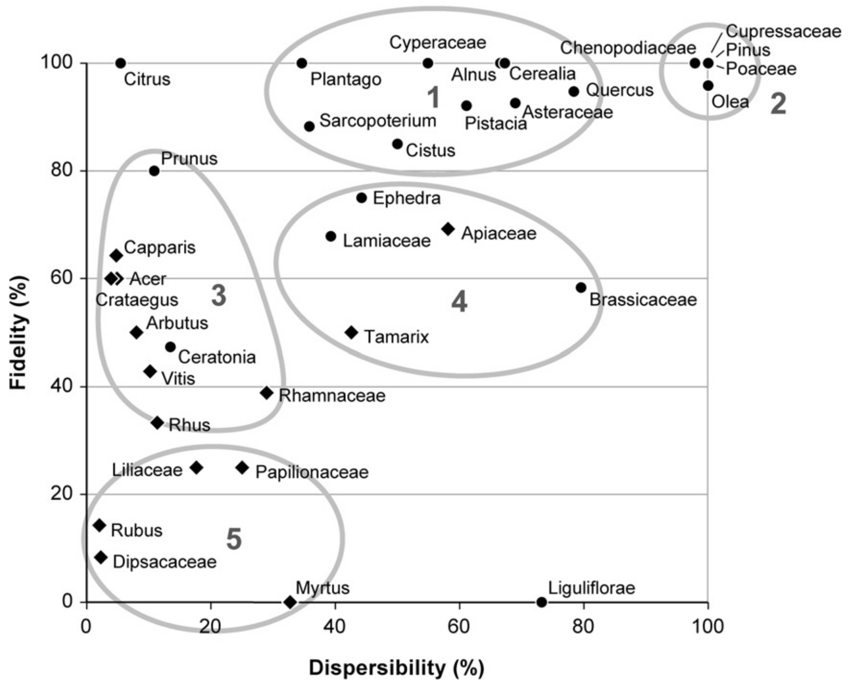

Fig. 7. Pollen taxa plotted by dispersibility index (percent presence of pollen at sites without parent taxon) vs. fidelity index (percent presence of pollen at sites with parent taxon). Five patterns are identified (circled on graph): (1) taxa with high fidelity and moderate dispersibility; (2) taxa with very high fidelity and very high dispersibility; (3) taxa with moderate fidelity and low dispersibility; (4) moderate fidelity and moderate dispersibility; and (5) taxa with low fidelity and low dispersibility. Taxa used in the discriminant analysis shown with a dot (other taxa shown with a diamond symbol).

on the one hand, and elevation and precipitation, on the other. The close association of elevation and mean annual precipitation suggests, not surprisingly, that these two variables are linked closely. The divergence of some pollen types away from a simple linear opposition of temperature vs. precipitation (e.g., as indicated by Function 2) hints at the potential influence of non-climatic factors, such as human activities (Jacques et al., 2008; Finsinger et al., 2010; Poska et al., 2011).

The most striking relationship is reflected by the close correlation between *Pinus* pollen, elevation and mean annual precipitation. This is consistent with the dominance of *Pinus* forests at the highest elevations in Cyprus and where precipitation is greatest. This result affirms the likelihood that other similarities between taxa shown in Fig. 6 also can be related to these broad climatic variables of temperature and precipitation. Along with *Pinus*, also arrayed on the positive side of dimension 1 towards greater precipitation and higher elevation, are Cyperaceae and the pollen group of *Cistus*, *Quercus* and *Prunus*. *Cistus* is a common understory plant in both the *Pinus* and *Quercus* forests at middle to higher elevations. Similarly, almond and cherry orchards (*Prunus*) grow on land once dominated by *Pinus brutia* and *Quercus* forests. Human activities over time may have reduced the geographic range of *Pinus brutia* forests, particularly at lower elevations. Thus, in this analysis the relationship between *Pinus* pollen and mean annual precipitation may be exaggerated, and any direct transfer function built between *Pinus* pollen and amount of precipitation may be biased (e.g., Finsinger et al., 2010).

Two distinct pollen groups display relationships to mean annual temperature and precipitation. The strongest patterning characterizes shrub and herb taxa common at lower elevation in association with higher temperature and lower precipitation, including plants in the Chenopodiaceae, Asteraceae and Poaceae families, along with Liguliflorae, *Plantago* and *Sarcopoterium*. At a slight remove, *Cerealia*-type pollen similarly associates more strongly with higher mean annual temperatures, and lower elevation and precipitation. Another distinct set of relationships among pollen types is reflected in a more linear distribution of mostly tree taxa: *Pinus*, *Cistus*, *Quercus*, *Prunus*, *Pistacia*, *Olea*, Brassicaceae and Cupressaceae (*Cistus* and Brassicaceae being the exceptions as non-trees). Again, *Pinus* (followed by *Cistus* and *Quercus*) reflects the strongest association with high elevation and precipitation, and relatively low mean annual temperatures. Moving along this gradient away from *Pinus* and *Cistus*, the taxa *Pistacia*, Brassicaceae, *Olea* and Cupressaceae associate sequentially with increasing temperature, lower elevations and lower amounts of precipitation. Cupressaceae (*Juniperus phoenicea* and *Cupressus sempervirens*) and *Olea*, in particular, are found commonly in warmer environments at lower elevations.

4.5. Fidelity and dispersibility of pollen

Comparison of 35 pollen taxa from Cyprus according to fidelity (higher fidelity indicates more frequent co-occurrence of both plant and pollen) and dispersibility (higher dispersibility indicates more frequent presence of pollen in sample locales where the plant is absent) produces five distinct patterns and two outliers (Fig. 7). The relationship between fidelity and dispersibility is strongly linked to the plant's pollination strategy. Many plants in Mediterranean ecosytems are insect pollinated, mainly by bees and flies, which also are pollen consumers (Petanidou and Vokou, 1990). Thus, even the insect pollinated plants may be moderate pollen producers. Also, in Mediterranean ecosystems, bees occasionally visit the wind-pollinated species, e.g., *Quercus coccifera* (Petanidou and Vokou, 1990). Plants in this study with the lowest dispersibility tend to be insect pollinated, while most of the plants with the highest dispersibility are wind-pollinated and may be over represented in modern pollen samples. Forest and woodland species in Cyprus are mainly wind pollinated, whereas the maquis and shrub lands have many more taxa that are insect pollinated.

Group 1 represents those pollen taxa with high fidelity and moderate dispersibility. Plants in this group are common in Cyprus, their pollen is reasonably well dispersed, and display a mixture of wind and insect pollination mechanisms. *Sarcopoterium*, *Cistus*, Cyperaceae and many of the Asteraceae are insect pollinated taxa. *Plantago*, *Alnus*, *Cerealia*-type, *Pistacia*, *Quercus* and some of the Asteraceae are wind pollinated (although many of these plants are also visited by insects). Thus, plants in Group 1 are well represented in the pollen rain and are good indicators that source plants grow nearby.

Plants in Group 2, Cupressaceae, *Pinus*, Chenopodiaceae, Poaceae and *Olea*, all have very high fidelity between source plants and pollen deposition. These pollen taxa are found in virtually every surface pollen sample collected. Plants represented by these pollen types are common in Cyprus, wind pollinated (a few of the Chenopodiaceae may also be insect pollinated), and generally over represented in pollen spectra. *Citrus*, an outlier in this comparison of indices stands in sharp contrast to Group 2. While it also shows 100% fidelity between plant and pollen, it is insect dispersed and has extremely low dispersibility, only being found in sample where *Citrus* trees grow.

Pollen taxa in Groups 3 and 5 have dispersibility indices below 40% and are pollinated predominantly by insects. Interestingly, two of the taxa in Group 3, *Ceratonia* and *Vitis*, while mainly insect pollinated also can be pollinated by wind. Pollen from these cultivated plants is found in pollen records; in addition, wild *Vitis* is an abundant pollen producer (e.g., van Zeist et al., 2009). Pollen taxa in Group 3 demonstrate moderate to high (in the case of *Prunus*) fidelity between plants and pollen. Plants in Group 4 (*Ephedra*, Apiaceae, Lamiaceae, Brassicaceae and *Tamarix*) are represented reasonably well in the pollen record with moderate dispersibility, generally reflecting the locale in which source plants grow. Plants in this group generally are insect pollinated (with the exception of *Ephedra*), but are well represented in pollen diagrams from the eastern Mediterranean region (van Zeist et al., 2009). Plants in both Groups 3 and 5 display low dispersibility and thus may not contribute substantially to the modern pollen rain. Taxa in Group 5, which have both low fidelity and dispersibility, include Liliaceae, Papilionaceae, *Rubus*, Dipsacaceae and *Myrtus*. These taxa would be rare in a pollen record. In particular, this characteristic would make recognition of garigue vegetation problematic, since two common plants in this landscape, *Calycotome* and *Genista*, produce Papilionaceae pollen. Of particular note, while pollen from the insect pollinated shrub *Myrtus* was found in low numbers in Cypriot samples, its pollen was not recovered from locations where the plant grew. The second outlier in this analysis, Liguliflorae, is a relatively common pollen taxon with high dispersibility, and often is associated with human disturbance (e.g., Bottema, 1975). Liguliflorae plants were not recorded in the vegetation (perhaps due to our sampling strategy of recording perennial vegetation in summer when the ephemeral plants in the Liguliflorae family are not apparent).

5. Conclusions

The major vegetation types in Cyprus are distinct in their pollen rain. In particular, pollen spectra from the *Quercus* forests and maquis differ most substantially from all other vegetation types. Samples from the high elevation *Pinus nigra* forests, which are geographically isolated at the uppermost elevations in the Troodos, form a tight cluster and are distinct from samples collected in the broader elevational range of the *Pinus brutia* forests. The only vegetation type that could not be distinguished from others was the garigue (or maquis which did not have *Pinus* or *Quercus*), possibly due to the fact that two main constituent plant taxa, *Calycotome villosa* and *Genista sphaceolata* (both Papilionaceae), disperse pollen very poorly. While the non-forest vegetation surrounding the salt lakes and in coastal settings overlaps palynologically with orchard vegetation, it is distinct from all the natural forest types. Today, orchards are primarily replacing either low coastal vegetation or lower elevation *Pinus brutia* forest stands. Ancient orchards would be dominated primarily by pollen from *Olea europaea*, *Ficus carica* and *Vitis vinifera* (both *Ficus* and *Vitis* are under-represented by pollen; e.g., Tinner et al., 2009), and hence would produce a signal similar to today's olive orchards.

The majority of the pollen taxa in Cyprus show moderate to moderately high fidelity, demonstrating the close link between source vegetation and its pollen. While some plant taxa are relatively under-represented by their pollen, the dominant plant species in the vegetation (*Pinus nigra*, *Pinus brutia*, *Quercus alnifolia*, *Juniperus phoenicea*, *Cupressus sempervirens*, *Pistacia* spp., *Olea europaea*, Chenopodiaceae and Poaceae) all are well represented palynologically.

Pollen taxa grouping indicated by cluster analysis demonstrates the strong palynological signal of *Quercus* stands, disturbance types as exemplified by Liguliflorae and Asteraceae, orchards, and lower elevation non-forest vegetation. The relationship between the main pollen taxa in Cyprus and three environmental variables – elevation, mean annual precipitation and mean annual temperature – provides a means to link specific pollen taxa with climatic variables. *Pinus*, Cyperaceae, *Cistus*, *Quercus* and *Prunus* show the strongest correlation with greater elevations and higher amounts of precipitation. Pollen from Cupressaceae, *Olea*, *Cerealia*-type, Liguliflorae, Chenopodiaceae, Asteraceae, *Plantago* and Poaceae are found associated with higher temperatures. The climatic implications of these results provide useful insights for paleoenvironmental interpretations. However, caution should be used when applying any direct pollen–climate transfer functions in this moderately humanized Cypriot landscape.

Acknowledgements

This research was funded by the National Science Foundation (Grant # 1031527) as part of an archaeological and paleoenvironmental project directed by the author and Steve Falconer. Liz Ridder, Mariela Soto-Berelov and Tracy Schirmang helped collect the vegetation data and the modern pollen samples. Lisa Lavold-Foote prepared the pollen samples. Mariela Soto-Berelov modeled climate data. Steve Falconer assisted with the numerical analyses; Liz Ridder made the map and Barbara Trapido-Lurie prepared the other figures. Two anonymous reviewers provided productive comments to improve the manuscript. An American Center of Oriental Research/Council of American Overseas Research Centers Research Fellowship provided the opportunity to complete this analysis and manuscript preparation.

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