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Pollen–vegetation–rainfall relationships in the Gebel al-Akhdar, Northeast Libya

Chris O. Hunt [a,*], Lisa Coyle McClung [b], Laura Edwards [a], Hwedi el-Rishi [c], Graeme Barker [d]

[a] School of Biological & Environmental Sciences, Liverpool John Moores University, Liverpool L3 3AF, UK
[b] School of Natural & Built Environment, Queen's University Belfast, Belfast BT7 1NN, UK
[c] Department of Geography, Benghazi University, Benghazi, Libya
[d] McDonald Institute for Archaeological Research, University of Cambridge, Cambridge CB2 3ER, UK

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ABSTRACT

Very little work has been done on vegetation–pollen relationships in Northeast Africa, which presents barriers for interpreting pollen diagrams in this region. This paper therefore investigates rainfall-vegetation–pollen relationships in the Gebel al-Akhdar in Northeast Libya. The Gebel al-Akhdar is an unique upland habitat island, isolated between the Mediterranean Sea and the Sahara Desert, characterised by a high degree of endemicity amongst its flora and invertebrate fauna, and with an extremely long history of human activity. Orographically-driven rainfall supports dry Mediterranean woodland and maquis on the northern slopes of the Gebel, with scrub-steppe passing into steppe and then pre-desert on the dryer southern slopes. Here we document rainfall/vegetational/pollen relationships along North–South transects across the Gebel al-Akhdar. Vegetation around pollen sample sites was recorded. Precipitation was interpolated from ERA5 satellite data, and from the local meteorological network. Surface pollen assemblages allow us to distinguish habitats with higher effective moisture on the northern slopes of the Gebel from those with lower effective moisture on the southern slopes. Coastal garrigue is characterised by high *Pinus* pollen, reflecting the very low pollen productivity of this habitat. Despite complexities in the relationship between vegetation and surface pollen, most parts of the rainfall distribution in the Gebel al-Akhdar can be characterised palynologically, giving confidence in the use of palynology to characterise past rainfall regimes in the region.

1. Introduction

Understanding taphonomic relationships and patterns is fundamental to pollen-based palaeoecology and palaeoclimate work, but very little work of this type has been carried out in Northern Africa. There is early work in the Sahara by Cour et al. (1971), Maley (1972), Schulz (1976) and Ritchie (1986). On the North African littoral, there is work on the Nile Delta in Egypt by Ayyad et al. (1992), in Tunisia by Jaouadi et al. (2015), in Atlantic Morocco by Amami et al. (2010) and in the High Atlas by Bell and Fletcher (2016). This sparsity of research, relative to the rest of the continent, is evident in the synthesis of modern pollen deposition in Africa by Gajewski et al. (2002). Pollen taphonomic work has been carried out in Libya (Simpson and Hunt, 2009) but this was restricted to a sticky slide study of short-term pollen deposition patterns in the Haua Fteah cave. Interpretation of stratigraphic pollen investigations has up to this point had to depend on an understanding of the ecology of the plants identified (Adams et al., 2013; Barker and Hunt, 2024; Hunt et al., 2002, 2011).

In this study we investigate pollen in surface samples in the region and compare assemblages with vegetation around the sample sites. We map precipitation from ERA5 satellite data and from local rainfall records. This provides the opportunity to explore relationships between rainfall, vegetation and pollen deposition in the region.

2. The Gebel al-Akhdar

The Gebel al-Akhdar (Green Mountain: Fig. 1) is an inverted Mesozoic and Tertiary basin in Northeast Libya, with a stratigraphy largely comprised of platform carbonates. It rises to an altitude of ∼876 m (Buru, 1960) in a wide ridge, trending East–West for about 350 km between the Gulf of Bomba and the Gulf of Sirte. Along the Mediterranean coast, a coastal plain, known locally as the *Sahel,* varies in width

* Corresponding author.
E-mail address: C.O.Hunt@ljmu.ac.uk (C.O. Hunt).

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from a few hundred metres to about 8 km. South of the coastal plain the land rises through two great escarpments to the broad crest of the Gebel, then falls gently to close to sea level on the margins of the Sahara Desert. The northward-facing escarpments of the Gebel are dissected by deep, gorge-like wadis, the most notable of which is Wadi Kouf.

Climatically, the Gebel al-Akhdar has a Mediterranean, summer-dry climate with the main growing season in the Spring. Rainfall as registered by local meteorological stations increases with altitude and is greater on the north side of the Gebel (Fig. 1; Fig. S1; Table 1). It varies spatially in any given year because most heavy rain is of convective origin and this is very localised, with a generally-lesser but more widespread contribution from winter frontal systems in most years. It also varies considerably from year to year (Sen and Eljadid, 1999; Ageena, 2013) as exemplified by the catastrophic Storm Daniel, where over 400 mm of rain (~80% of annual average rainfall) fell at Al Bayda between 8–10th September 2023.

Biogeographically, the Gebel al-Akhdar is an unique habitat island, isolated between the Mediterranean Sea and the Sahara Desert (Fig. 1). In the western-central part of the Gebel, orographically-driven rainfall, concentrated on the windward (northern) face of the upland, supports coastal garrigue with *Sarcopoterium spinosum*, *Phlomis*, *Thymus*, Chenopodiaceae, ephemeral grasses and various spiky Asteraceae passing within a few hundred metres of the coast into dense *Juniperus phoenecia*-dominated krummholz-like low scrub at low altitude, passing above ~100 m into dry Mediterranean woodland of *Pinus halepensis*, *Juniperus phoenecia*, *Pistacia*, *Olea*, *Cercis*, *Quercus coccifera*, *Arbutus* and *Salvia*, with remnant *Cupressus*-dominated woodland, now mostly degraded to maquis, at higher altitudes, generally above 300 m, as far east as Lamludah and as far west as Qasr Libya. Deeply-incised wadis in this central zone are characterised by diverse dry woodland with *Cupressus* and minor *Quercus coccifera,* a very rare deciduous *Quercus* sp., *Olea* and other species. The woodland formations are often degraded by fire and grazing to maquis with *Juniperus*, *Olea*, *Cistus*, *Arbutus*, *Cytisus*, *Salvia*, *Sarcopoterium spinosum*, annual grasses, geophytes and herbs and sometimes relict *Cupressus* of great size. On the dryer southern slopes there is a progression from scrub-steppe near the crest of the Gebel, passing into steppe, then Chenopod-dominated dwarf shrub-steppe and finally pre-desert on the margins of the Sahara. The pre-desert is characterised by unvegetated interfluves with vegetation of *Retama*, *Ephedra, Pistacia* and ephemeral grasses and herbs only in the watercourses. It is evident that grazing pressure has had significant impacts on vegetation throughout the region. Vegetation is distinctly more diverse, denser and taller in fenced compounds where grazing animals are excluded than it is in immediately adjacent grazed areas.

Rainfall levels decline eastward and near el-Athrun the coastal *Juniperus* scrub and dry woodland is replaced by sparse scrub-steppe of dwarf *Pinus* and some *Juniperus*. East of Derna, arboreal vegetation is virtually absent and there is dry steppe on the northern slopes of the Gebel.

This isolated area of vegetation is characterised by a high degree of endemicity amongst its flora and invertebrate fauna. The vegetation of the Gebel al-Akhdar contains at least 43 endemic species (El-Barasi and Saaed, 2013) and more than three quarters of terrestrial molluscs are endemic (e.g. Brandt, 1959). Currently, the vegetation history of the

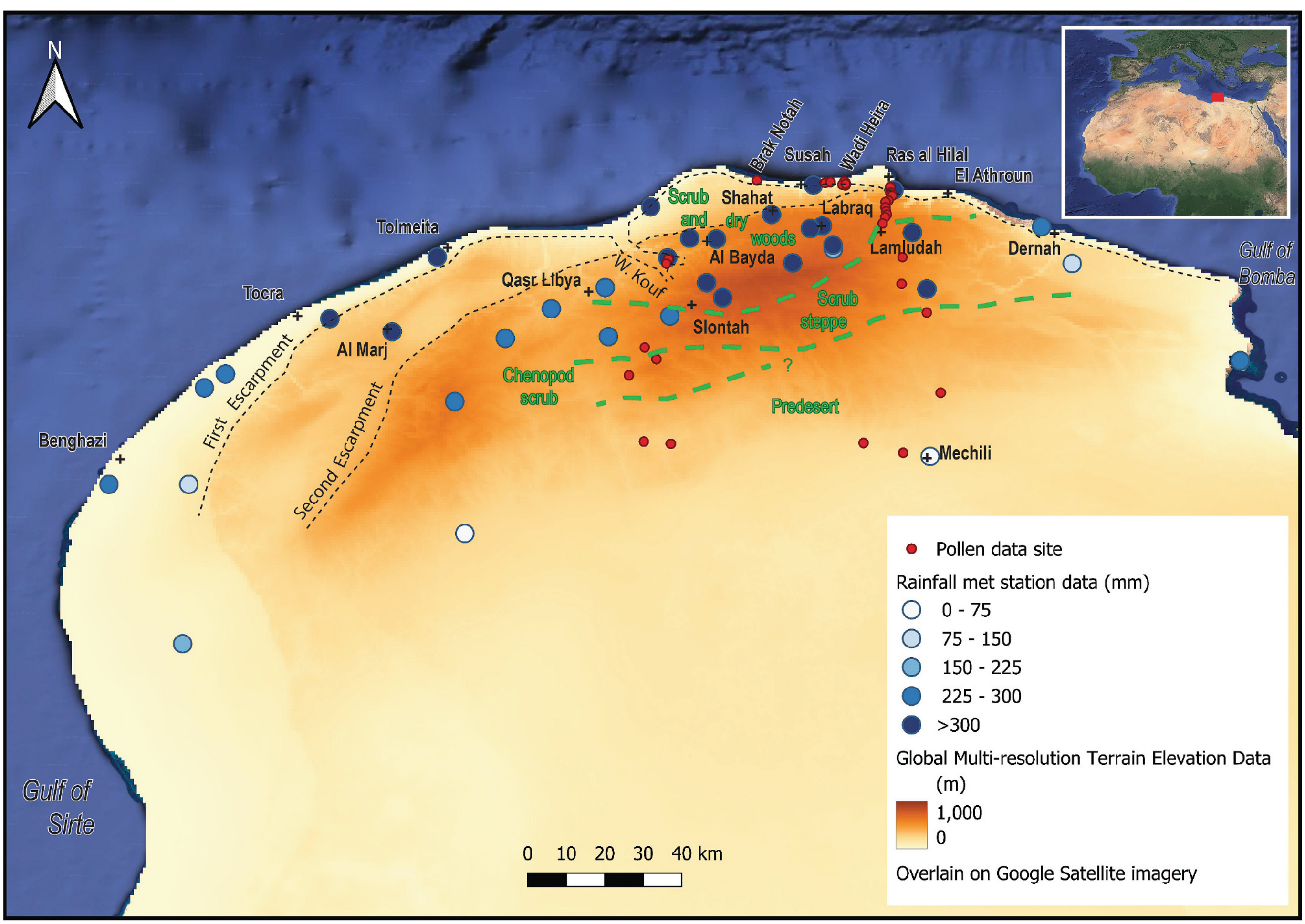

Fig. 1. Location of the Study area showing sample sites, meteorological stations, locations mentioned in the text and observed vegetation (Drawn by LE, COH).

Table 1
Mean annual rainfall in millimetres per year for stations around the Gebel al-Akhdar (data from Sen and Eljadid, 1999; Ageena, 2013; National Meteorological Centre, 2021, see also SI Fig. 1). Locations in decimal degrees; m asl – metres above sea level.

Station	Northing	Easting	Altitude (m asl)	Annual average rainfall (mma^{-1})
Masah	32.75218	21.62732	510	573.5
Shahat	32.81667	21.85000	621	563.6
Al Bayda	32.75000	21.70000	537	518.0
Al Faydiyah	32.68517	21.90754	764	451.5
Safsaf	32.77859	21.95527	661	446.8
Slontah	32.59077	21.71675	767	433.0
Al Marj	32.49822	20.81923	331	415.4
Al Kouf	32.69903	21.56800	426	413.5
Al Abraq	32.78587	21.98802	675	392.9
Quba	32.76749	22.23244	591	378.8
Ras el Hilal	32.88333	22.18250	45	362.9
Susah	32.89701	21.96355	35	360.1
Umar al Mukhtar	32.63139	21.67333	762	356.0
Tolmeita	32.70129	20.94172	26	346.2
Al Fataiyah	32.61430	22.27200	251	343.6
Qaygab	32.73333	22.01667	714	336.8
Al Hania	32.83798	21.52149	19	335.3
Tocra	32.53330	20.65000	14	319.1
Al Bayyadah	32.56064	21.25171	363	299.7
Qasr Libya	32.61835	21.39778	447	293.0
Beninah	32.08333	20.26667	129	292.9
Dernah	32.78333	22.58333	26	292.5
Marawah	32.48464	21.40672	485	281.6
A'ilat Lammis	32.34556	20.30889	8	281.0
Tanslukka	32.38333	20.36667	5	281.0
Taknis	32.48005	21.12652	434	278.1
Qandulah	32.54113	21.57366	624	275.5
Zawayit al Argoub	30.31559	19.68017	4	271.4
Benghazi	32.08333	20.05000	25	270.0
Jardis al Ahrar	32.30830	20.98941	628	258.0
Umm Hafein	32.41917	23.12333	6	242.0
Ahqaf Al Jabbaret	32.72306	22.01778	722	196.0
Sirt	31.18917	16.57000	19	193.0
Slouq	31.65000	20.25000	56	167.0
Agadabia	30.22917	19.95060	31	163.0
Tobruq	31.96667	24.01667	50	160.0
al-Fatayah	32.68333	22.66667	312	112.0
Qaroubah	32.08333	20.26667	126	97.2
Mechili	32.15917	22.28056	196	55.3
Aujilah	29.09167	21.33278	66	52.0
Ash Sawashiah	29.17000	21.29417	29	24.0
Jalo	31.95000	21.01667	37	18.5
al-Jaghbub	29.75000	24.96667	10	6.0

region is poorly known, with no published work dealing with periods before the Late Holocene (Adams et al., 2013; Barker and Hunt, 2024; Hunt et al., 2002, 2011).

3. Materials and methods

Sampling traverses were made using traverses along public roads and on foot. Where possible, we sampled at least 1 km from the road in relatively less-degraded areas of vegetation. Spot samples were also picked up during archaeological survey. Sites were located using handheld GPS (Table 2; SI Fig. 2).

To negate biases caused by the pollen production of individual plants, samples were taken using a variant of the pinch-sampling technique. Soil or surface sediment gathered in a series of small surface scrapes was taken where possible from areas of about 4–10 m^2 and the resulting material was combined and homogenised by shaking into a single sample, following Adams and Mehringer (1975). In the laboratory, large plant debris and rocks were removed by passing the samples through a clean 2 mm sieve and the resulting fine fraction was homogenised before subsampling for analysis. Samples were disaggregated in boiling sodium pyrophosphate 5% solution, then sieved through 120 μm and on nominal 6 μm nylon mesh to remove solutes, fines and coarse particles. An acid wash with 5% HCl removed carbonates and the resulting suspension was swirled on a clock-glass to remove silt and fine sand. The resulting concentrates were stained using safranin and mounted in Aquatex. Counts of more than 300 pollen and spores were made wherever possible, using the QUB pollen reference collection and reference to Reille (1992, 1995, 1998). The pollen sum included all pollen and all spores of ferns and fern-allies.

Total precipitation data at a resolution of 0.25 degrees for a forty year period (1981–2020) were obtained from the ECMWF Reanalysis v5 (ERA5) monthly averaged data on single levels from 1940 to present dataset from the Copernicus Climate Change Service (Hersbach et al., 2023). From these data, a long term (40 year) average value for annual precipitation was calculated and the gridded data were resampled to 0.1 degree using the bicubic sampling method in the GRASS r.resamp.interp tool within QGIS (Fig. 2).

The inverse distance weighted (IDW) tool in QGIS was used to produce a 0.1 degree IDW gridded rainfall dataset from the rainfall meteorological station site data using a distance coefficient of 2 (SI Fig. 3). The Ordinary kriging SAGA tool within QGIS was used to produce a 0.1 degree kriged gridded rainfall data from rainfall meteorological station site data with a search distance of 0.5 degrees (SI Fig. 4). Values of the ERA5, IDW and krig 0.1 degree gridded data were extracted at the locations of the pollen sites in QGIS for further analysis.

Digital elevation model (DEM) data at a resolution of 30 arc seconds were obtained from the Global Multi-resolution Terrain Elevation Data (GMTED2010) developed by the US Geological Survey and National

Table 2
Sampling locations and vegetation on these sites.

Site no.	UTM (34S)	Latitude (°N)	Longitude (°E)	Altitude (m)	Geomorphology	Vegetation physiognomy	Key taxa
1000 (BN4)	0575785 3641558	32.909614	21.810429	0	Water-filled doline on north-facing coastal slope	Coastal garrigue, reeds around sampling site	Poaceae, *Asphodelus, Artemisia,* Asteroidae, *Juniperus phoenecia, Pistacia, Phlomis, Olea, Pinus halepensis, Phragmites*
1503	0598237 3641064	32.903371	22.050442	~160	Northward-facing hillslope	Juniper-broadleaved-pine maquis, openings with grasses and asphodels	*Juniperus phoenecia* (70%), *Ceratonia, Quercus coccifera, Pistacia, Pinus halepensis,* Poaceae, *Asphodelus, Helianthemum, Phlomis,* Labiatae
1504	0598234 3640266	32.896175	22.050325	~150	Northward-facing coastal escarpment	Juniper scrub woodland with grassy understorey	*Juniperus phoenecia, Allium* cf. *ursinum,* Poaceae, *Phlomis,* Labiatae
1530	0597930 3641354	32.906015	22.04719	14	Coastal slope, north-facing	Open coastal garrigue	*Pistacia, Sarcopoterium spinosum,* Poaceae, Labiatae, *Phlomis, Thymus, Plantago,* Asteroidae
1584	0593081 3640948	32.902776	21.995305	20	Coastal plain	Coastal garrigue	*Pistacia, Sarcopoterium spinosum, Artemisia, Cichorium, Geranium, Crepis*-type, *Silene, Bellis, Sedum,* Carduoidae, Poaceae
1590	0594442 3641200	32.904932	22.009882	2	Coastal plain	Sparse coastal garrigue on limestone pavement	*Silene,* Poaceae, *Phlomis, Senecio,* Carduoidae, *Erica, Sideritis*
1600	0609647 3639857	32.891402	22.172284	33	Alluvial fan on coastal plain	Open juniper scrub/maquis, ephemeral grasses	*Juniperus phoenecia* (80%), Poaceae, *Pistacia, Sarcopoterium spinosum, Ceratonia, Pinus halepensis, Phlomis*
1601	0609799 3638255	32.876938	22.173718	158	North-facing hillslope on escarpment overlooking the Mediterranean	Open juniper scrub/maquis	*Juniperus phoenecia* (60%) Poaceae, *Pistacia, Salvia, Phlomis, Pinus halepensis, Olea, Berberis, Arbutus, Cistus*
1602	0609930 3637792	32.87275	22.175063	249	Northeast-facing hillslope in coastal valley	Open maquis	*Juniperus phoenecia* (20%), *Ceratonia* (10%), *Olea* (10%), *Arbutus* (10%), Poaceae, *Sarcopoterium spinosum, Pistacia, Genista, Cistus, Phlomis, Artemisia, Allium, Salvia, Phlomis, Berberis, Origanum*
1604	0610181 3637265	32.867972	22.177683	336	Northeast-facing hillslope in coastal valley	Scrubby open pine-juniper woodland	*Pinus halepensis* (60%), *Juniperus phoenecia* (20%), *Salvia, Genista, Artemisia,* Poaceae, *Pistacia, Arbutus, Sarcopoterium spinosum, Cistus*
1605	06092503635782	32.85469	22.167558	467	South-facing hillslope	Woodland with regenerating burnt patches	*Ceratonia, Juniperus phoenecia, Olea, Cretaegus, Cistus, Lonicera.* Regenerating patches with *Pistacia,* Poaceae, *Phlomis*
1606	0608508 3635366	32.850922	22.15958	504	Plateau	Limestone pavement with juniper maquis with grazed grassy patches	*Juniperus phoenecia* (40%), Poaceae, *Pistacia, Phlomis, Arbutus, Cistus, Olea, Sarcopoterium spinosum, Thymus, Crepis-type,* Carduoideae
1607	0608508 3633724	32.836203	22.159389	522	Interfluve with valley to east	Juniper maquis woodland, patches of barley cultivation	*Juniperus phoenecia* (30%), *Arbutus* (20%), *Ceratonia,* Scrophulariaceae, Poaceae, *Valeriana*
1608	0608669 3632570	32.82578	22.160973	544	North facing low-angle slope	Garrigue and scrub-steppe	*Sarcopoterium spinosum* (20%), *Cistus* (10%), *Juniperus phoenecia* (20%), *Arbutus* (10%), Poaceae, *Borago, Artemisia*
1609	0608894 3631572	32.816757	22.163259	619	High plateau, gently north-sloping	Dense maquis	*Genista* (40%), *Arbutus, Cistus, Pistacia, Olea, Juniperus phoenecia, Lonicera,* Labiatae, Scrophulariaceae, Poaceae
1610	0608457 3630781	32.8096695	22.1585005	655	High plateau	Maquis with steppe and bare ground	*Arbutus* (20%), *Juniperus phoenecia* (20%), *Cistus,* Poaceae, *Ulex, Salvia, Anagalis, Olea*
1611	0607845 3628880	32.792582	22.151742	652	High plateau	Garrigue and scrub-steppe, rather degraded on edge of town	*Sarcopoterium spinosum, Salvia, Arbutus,* Carduoideae, Poaceae, *Anagalis, Geranium, Euphorbia, Crepis-type, Urginea, Thymus, Foeniculum, Cytisus, Pistacia, Arenaria, Iberis*
1612	0613001 3618771	32.700893	22.205567	579	Low-angle Interfluve	Low scrub-steppe	*Sarcopoterium spinosum, Salvia, Artemisia, Thymus, Echium, Crepis-type,* Poaceae, Labiatae, Carduoideae, *Veronica, Anagalis, Helianthemum, Glaucium, Iris, Foeniculum, Sinapis,*
1613	0612879 3610709	32.628195	22.203291	563	Low-angle valley side	Steppe with much bare ground and shrubs in nearby watercourse	*Thymus, Plantago, Iris, Foeniculum,* Carduoideae, *Urginea,* Chenopodiaceae, Poaceae, *Crepis*-type
1614	0619386 3602163	32.550437	22.271552	449	Low-angle Interfluve	Dwarf scrub steppe with grassy area in minor watercourse	Chenopodiaceae, Poaceae, *Lathyrus, Crepis*-type, *Malva, Plantago, Echium*
1615	0623228 3578012	32.332203	22.30931	327	Low-angle interfluve	Dwarf shrub steppe with 98% bare ground	Chenopodiaceae, Poaceae, *Crepis*-type, *Sinapis*
1616	0613847 3559817	32.169089	22.207482	192	Low-angle plateau with stony interfluves and silty depressions	Dwarf-shrub steppe, bare ground with annual grasses, barley cultivation and broom in depressions	Chenopodiaceae, Poaceae, *Retama*
1617	0603660 3562650	32.195628	22.099762	216	Wadi floor, with flanking stony interfluves	Shrub-steppe in wadi floors. Interfluves with very sparse Chenopod dwarf scrub	Poaceae, *Retama, Artemisia, Tuberaria, Crepis*-type, *Iberis,* Carduoideae, Chenopodiaceae, *Thymus*
1618	0554335 3562032	32.193521	21.576455	290	Wadi floor with flanking stony interfluves	Depression with shrub-steppe and barley cultivation, interfluves with very sparse dwarf scrub	Carduoidae, *Foeniculum, Crepis*-type, *Echium, Sinapis,* Chenopodiaceae, Labiatae, Poaceae, *Hordeum, Avena fatua*

(*continued on next page*)

Table 2 (*continued*)

Site no.	UTM (34S)	Latitude (°N)	Longitude (°E)	Altitude (m)	Geomorphology	Vegetation physiognomy	Key taxa
1619	0547399 3573318	32.19941	21.502903	392	Low-angle backslope of Gebel	Sparse chenopod scrub-steppe, occasional acacias	Chenopodiaceae, *Crepis*-type, Poaceae, *Sinapis, Artemisia, Acacia*
1620	0543483 3582616	32.379684	21.462268	505	Low-angle backslope of Gebel	Steppe	Poaceae, *Senecio*, Chenopods, *Crepis*-type, Carduoidae, *Vicia*
1621	0550500 3587500	32.423446	21.537124	600	Low-angle interfluve	Steppe	*Artemisia*, Chenopods, Carduoidae, Poaceae, *Echium, Hordeum spontaneum, Senecio*, Scrophulariaceae, *Crepis*-type, *Acacia*
1622	0547500 3591000	32.455151	21.505393	380	Low-angle interfluve	Scrub-steppe	*Juniperus phoenecia* (20%), Poaceae, Carduoidae, – *Crepis* type, *Asphodelus, Urginea, Senecio, Plantago, Arabis, Matricaria*
1624	0598402 3640650	32.899623	22.052162	90	Steep north-facing escarpment	Juniper scrub	*Juniperus phoenecia* (60%), Poaceae, *Phlomis*
1627	0597452 3640442	32.897832	22.041983	105	Steep east-facing valley side	Juniper scrub, Mediterranean woodland; steppe on steep slopes	Poaceae, *Juniperus phoenecia, Olea, Quercus coccifera, Arbutus, Phlomis, Sedum*, Carduoidae
1638	0553386 3617805	32.69668	21.569543	293	Wadi floor	Cupressus woodland, with some understorey	*Cupressus, Quercus coccifera* and a deciduous *Quercus* sp., *Arbutus, Olea, Pistacia, Ceratonia, Pinus halepensis*, Poaceae, Carduoidae
1648	0552872 3616332	32.683418	21.563976	342	Wadi side, east-facing	Cypress-dominated woodland with grassy patches and maquis on steep slopes	*Cupressus, Pistacia, Olea, Quercus coccifera, Ceratonia*, Poaceae, *Crepis*-type
1752	0598283 3640678	32.89989	22.050903	73	Shallow doline	Cereal field in midst of juniper-scrub-steppe	*Hordeum*, Carduoidae, with at a distance *Juniperus phoenecia*, Poaceae, *Pistacia, Rhus, Olea*, herbaceous species

Geospatial Intelligence Agency from a variety of satellite data products (Danielson and Gesch, 2011).

The relationship between ERA5 rainfall and pollen taxa was explored using non-parametric Spearman's rs. Relationships between taxa were explored using Cluster Analysis with Ward's Method and Euclidean distance (SI Figs. 4, 5). All statistical work was done in PAST software (Hammer et al., 2001).

4. Results

The distribution of pollen is shown on transects from the coast into the interior (Figs. 3,4). Most taxa, especially the trees, shrubs and grasses, are widely distributed across all vegetation types. Poaceae are well-represented in all samples and *Pinus* is ever-present, while Lactuceae, Cistaceae, Chenopodiaceae and Caryophyllaceae are sometimes very well-represented. In Table 3, the range of percentages for each vegetation-type is shown. This enables well-represented and under-represented taxa to be identified.

Some trends are apparent. Coastal garrigue assemblages are characterised by *Sideritis*, *Ophioglossum*, *Trifolium*, Cyperaceae, and high Lactuceae and Poaceae. Coastal juniper scrub samples do not always have *Juniperus* pollen, and have generally very variable assemblages, but always seem to contain pollen of Cistaceae and Cyperaceae, always have high Poaceae and often have high *Pinus*. Woodland assemblages often have very high *Pinus* and always have high Poaceae and some *Quercus*. Upland maquis habitats have Cistaceae, Poaceae and Cyperaceae. Scrub-steppe on the upper part of the South-facing slopes of the Gebel has high Caryophyllaceae, Lactuceae and Poaceae. Chenopod steppe, at lower altitude on the South-facing slopes of the eastern North–South transect from Brak Notah, is characterised by high Chenopodiaceae and Poaceae, and also contains *Bidens*-type, Brassicaceae, Caryophyllaceae and Lactuceae. Finally, the pre-desert wadi floor sediments (the stony interfluves carry little vegetation other than ephemeral plants – mostly grasses and Asteraceae) are scrub-steppe characterised by *Tamarix*, *Bidens*-type, Caryophyllaceae, with high Poaceae and Lactuceae.

In the correlation matrix (SI Fig. 4), there are statistically significant ($p = < 0.05$) positive correlations between ERA 40 rainfall and *Pinus, Fraxinus, Ostrya, Sideritis, Thymus* type*, Sedum, Botrychium* and *Ophioglossum*. There are statistically significant negative correlations between ERA 40 rainfall and *Tamarix*, Lactuceae, *Artemisia* and Caryophyllaceae.

5. Discussion

Table 3 might be used to suggest that some taxa are characteristic of certain vegetation physiognomies: for example, *Sideritis* is present in all samples in garrigue vegetation. However, it is present intermittently in all other vegetation-physiognomies except scrub-steppe. The same applies to most other potential ecological indicator-taxa. It is also noteworthy that tree taxa which produce considerable pollen, such as *Pinus* and *Quercus*, are extremely widely-distributed, despite distributions of the parent plants being rather local in the study area.

Further, cluster analysis of pollen sites does not mirror vegetation physiognomy (Table 4). The ranges of ERA5 40-year rainfall for some cluster groups are also very large (Table 4), consistent with rainfall not being the sole controller of vegetation physiognomy. Almost certainly, modification of vegetation by other pressures – exposure to salt-laden winds in the case of coastal garrigue and severe but uneven grazing pressure throughout the region – is also significant.

The GIS interpolations of rainfall data used in this paper provide approximations of reality. This is because the algorithms used (although the best currently available) are not well-suited to the rather sparse regional rainfall data. The ERA5 40-year rainfall figures broadly mirror the meteorological station data, although it seems to underestimate rainfall relative to stations on the northern escarpments and crest of the Gebel (Fig. 2). The IDW and kriging seem to overestimate rainfall significantly to the south of the crest of the Gebel (SI Figs. 3, 4), almost

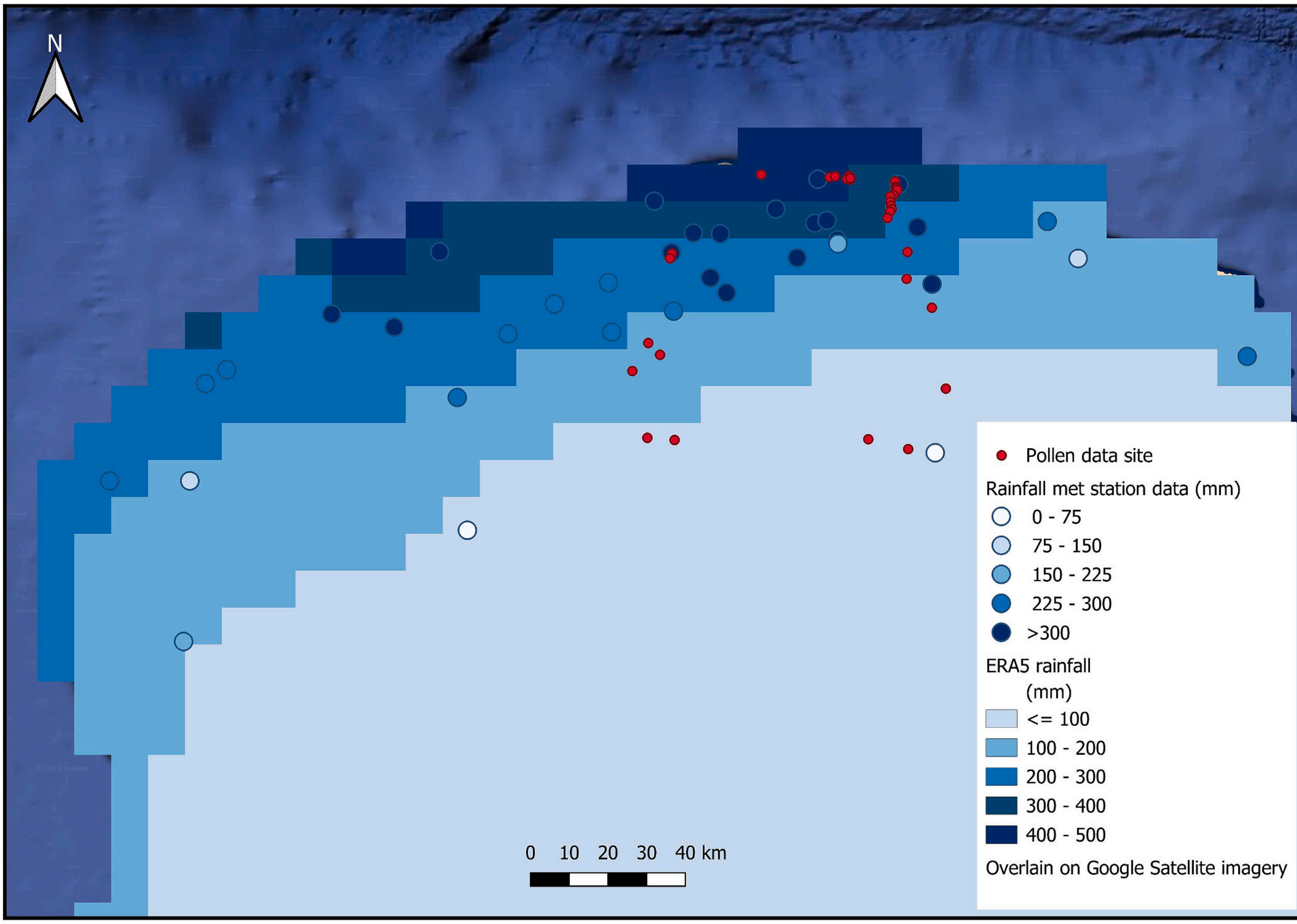

Fig. 2. The study area, showing the 40 year average value for annual precipitation with gridded data resampled to 0.1 degree using the bicubic sampling method in the GRASS r.resamp.interp tool within QGIS. (Analysed and drawn by LE).

certainly because meteorological station density is too low to allow the algorithms to work properly, and for this reason these are not further discussed.

Considering the relationship between the ERA5 40-year rainfall figures and vegetation, there are broad correspondences between rainfall calculated this way and vegetation type. Thus ERA5 40-year rainfall of 60.6–284.4 mm is associated with scrub-steppe, 143.4–158.3 mm with steppe, 364.0–368.4 mm with maquis, 282.0–379.2 with woodland and 379.2–424.5 mm with coastal garrigue. Almost certainly, the maquis sites would, in the past, have been woodland that has been degraded by generations of grazing and fire (Alesmari, 2019).

Excluding the coastal garrigue habitats, where the impact of high rainfall on vegetation is confounded by exposure to salt spray, individual taxa show considerable ranges against ERA5 40-year rainfall. There are, however, a number of taxa which have distributions in a part of the ERA5 40-year rainfall range, or are recorded in higher percentages in part of that range (Fig. 5). Thus, *Ostrya* is limited to sites with rainfall over 284.4 mm. Several other taxa such as *Fraxinus*, *Lycopodium*, Pteropsida, *Thymus*-type, *Bellardia*-type, *Lamium*, *Galium*, *Spergula*, *Acacia*-type, *Bellis*-type, *Sedum*, *Botrychium* and *Ophioglossum* are also found only in the wetter part of the rainfall range and several of these (*Fraxinus, Ostrya, Botrychium, Ophioglossum*) also show a statistically significant positive relationship with ERA 40 rainfall (SI Fig. 4), but none are frequently occurring, and it is thus not certain whether their absence in the drier part of the rainfall range is controlled by moisture relationships.

Regarding the generally-distributed taxa, *Pinus* is best represented (1.3–51.9%, mean 14.5%) where rainfall is 285–380 mm and shows a statistically significant positive relationship with ERA 40 rainfall. Cistaceae are best represented (0.9–45.9%, mean 7.5%) in sites with mid-range to high rainfall (222–353 mm). Cyperaceae are best represented (0.9–8.4%, mean 4.2%) where rainfall is 285–353 mm.

Some steppe habitats with 143–144 mm rainfall have high Chenopodiaceae (6.1–32.6%). Sites with low to very low rainfall (<187 mm) tend to be characterised by generally relatively high Lactuceae (4.8–43.7%, mean 20.7%) and Caryophyllaceae (0.9–27.1%, mean 7.8%). The lowest rainfall sites (< 82 mm) in the pre-desert wadis are often marked by *Tamarix* (3–7.9%, mean 5.3%). Lactuceae, Caryophyllaceae, *Tamarix* and *Artemisia* show a statistically significant negative correlation with ERA 40 rainfall.

It is worth emphasising that the current vegetation distributions are influenced by the prevailing summer-dry rainfall regime with the growing season in the spring. It seems likely from dendrochronological data (D. Brown pers. comm. 2014) that the current rainfall seasonality

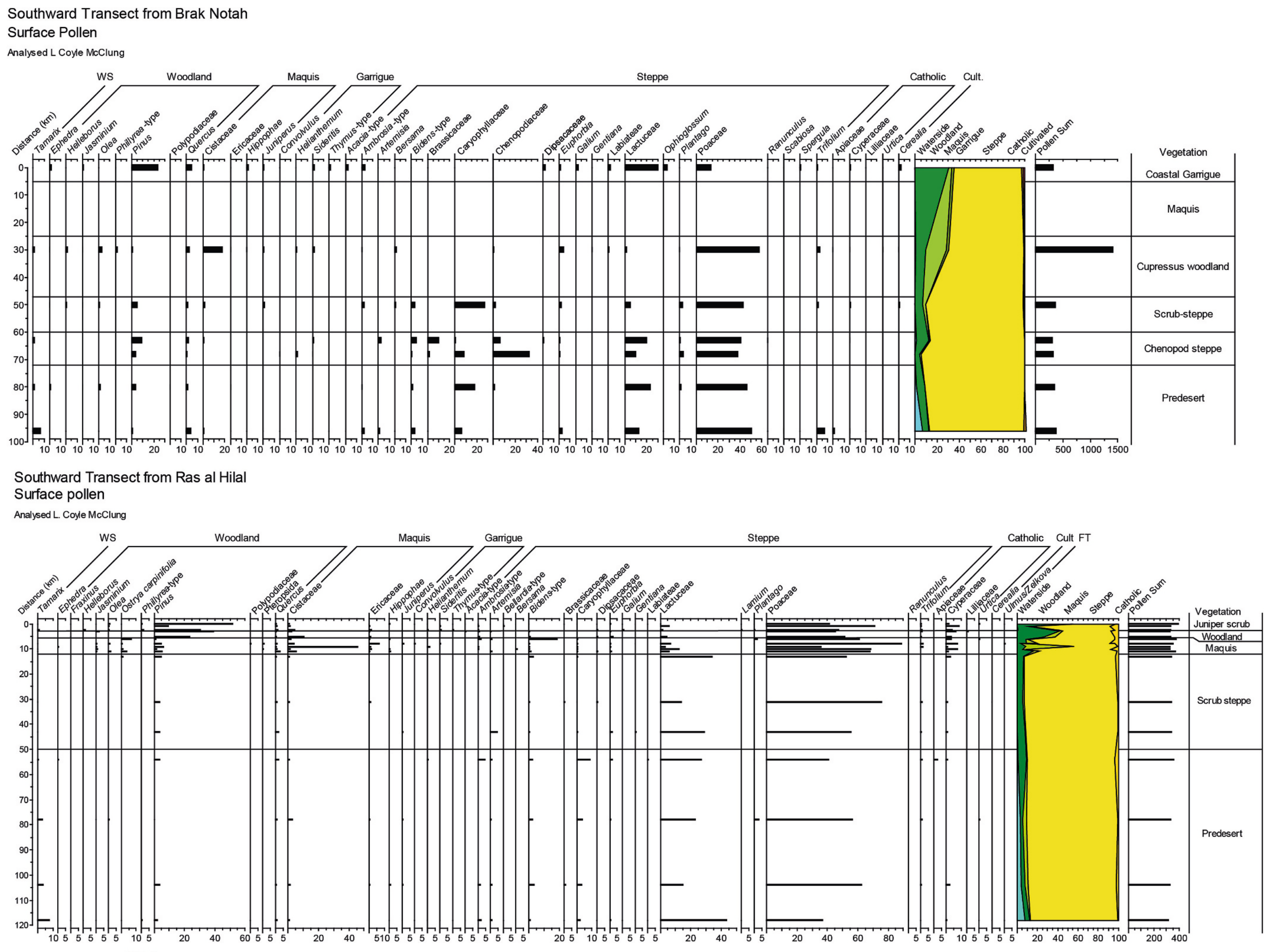

Fig. 3. Surface transects southward from Brak Notah and from Ras al Hillal. (Analysed LCMcC, drawn COH).

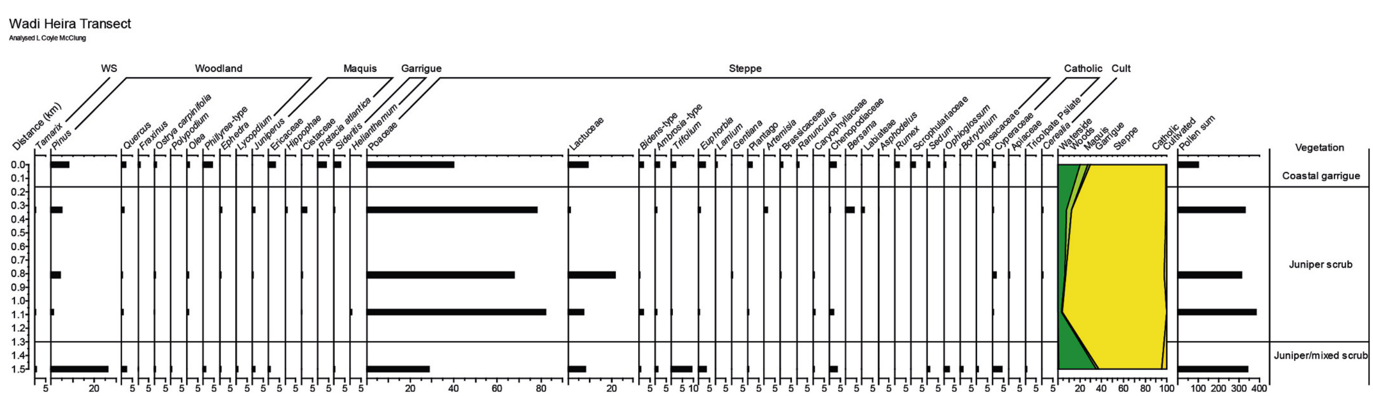

Fig. 4. Surface transect southward from near the mouth of Wadi Heira. Analysed LCMcC, drawn COH).

extends back to the Little Ice Age, but we have no hard information about seasonality before this. It is difficult to predict the impact of different rainfall seasonality on the regional vegetation, given the lack of comparatives with different rainfall regimes in the southeast Mediterranean coastlands.

Other factors are also very significant in controlling the physiognomy of vegetation, notably exposure to salt-laden spray in the case of coastal garrigue, and grazing pressure in the case of all vegetation-types and especially maquis and scrub-steppe. In the early years of the 21st Century when we sampled, the vegetation of the Gebel al-Akhdar was degrading rapidly, mostly as a response to fire and overgrazing (Alesmari, 2019; Suleiman et al., 2016), impacting the distribution of semi-natural vegetation and especially of trees and shrubs on the Gebel. For this reason, we hypothesise that the original rainfall–vegetation relationships are no longer as clear as has been seen in other broadly similar landscapes (e.g. Bottema and Barkoudah, 1979; Davies and Fall,

Table 3
Range of pollen percentages in each physiognomic vegetation-type for each pollen-based taxon. Numbers in **bold** indicate a taxon was present in all samples in the vegetation-type, numbers in *Italics* indicate a taxon was present in >75% of samples in the vegetation-type (except Steppe where italics indicate >66.7%).

	Garrigue	Juniper scrub	Woodland	Maquis	Scrub steppe	Steppe
ERA5 40-year rainfall (mma^{-1})	379.2–424.5	282.1–400.9	282.0–379.1	284.4–379.2	61.7–284.4	143.4–158.3
Tamarix	0.0–0.5	0.0–0.7	0.0–0.9	0–0.9	*0.0–7.9*	0.0–1.3
Pinus	**2.0–24.8**	**1.0–51.9**	**1.5–39.1**	**1.8–30.5**	**0.8–6.3**	**3.4–9.1**
Quercus	**1.8–4.5**	**0.3–1.5**	**0.3–2.7**	*0.0–3.2*	**0.3–3.7**	**0.3–2.0**
Ostrya carpinifolia	0.0	0.0–0.6	0.0–0.3	*0–6.9*	0.0–1.2	0.0
Fraxinus	0.0–1.0	0.0	0.0–0.3	0.0	0.0	0.0
Jasminium	0.0–0.6	0.0	0.0–2.1	0.0–0.9	0.0–0.6	0.0
Olea	0.0–2.0	0.0–0.8	0.0–0.7	0.0–1.6	0.0–1.5	0.0
Pteropsida	0.0	0.0	0.0	0.0–0.9	0.0	0.0
Phillyrea-type	*0.0–4.0*	0.0–1.5	0.0–0.9	0.0–1.5	0.0–0.3	0.0
Helleborus	0.0–0.3	0.0–1.2	0.0–1.1	0.0–1.2	0.0	0.0
Ephedra	*0.0–1.6*	0.0–0.9	0.0–0.6	0.0–0.6	0.0–0.9	0.0
Polypodiaceae	0.0	0.0	0.0–0.3	0.0–0.3	0.0–0.3	0.0
Cistaceae	0.0–1.3	*0.0–17.7*	*0.0–10.1*	**0.3–5.4**	0.0–1.7	0.0–1.0
Pistacia	0.0–4.0	0.0	0.0	0.0	*0.0–45.9*	0.0
Ericaceae	0.0–3.0	0.0–1.5	0.3–1.2	*0.0–6.2*	0.0–1.2	0.0
Hippophae	0.0–2.5	0.0–0.9	0.0	0.0–0.8	0.0–0.6	0.0
Juniperus	*0.0–0.8*	0.0–1.2	0.0–1.2	0.0–0.9	0.0–0.8	0.0–0.3
Convolvulus	0.0	0.0	0.0	0.0–0.3	0.0	0.0–0.3
Helianthemum	0.0–0.8	0.0–0.5	0.0–0.3	0.0–0.3	0.0–1.5	0.0–0.9
Sideritis	**1.3–3.9**	0.0–0.9	0.0–0.3	0.0–0.9	0.0	0.0–0.7
Thymus	0.0–1.0	0.0–0.3	0.0	0.0–0.3	0.0	0.0
Acacia-type	0.0	0.0	0.0–0.3	0.0	0.0	0.0
Ambrosia-type	*0–2.0*	*0.0–0.8*	*0.0–1.2*	0.0–2.1	0.0–4.8	0.0
Artemisia	0.0–0.3	0.0–1.5	0.0–0.3	0.0–0.5	0.0–1.3	*0.0–4.4*
Asphodelus	0.0	0.0–0.3	0.0	0.0	0.0	0.0
Bersama	0.0–0.3	0.0–4.0	0.0–1.1	0.0–0.9	0.0–0.8	0.0
Bidens-type	*0.0–2.0*	0.0–2.1	*0.0–1.2*	*0.0–18.8*	**0.3–3.4**	**0.6–4.4**
Botrychium	0.0–0.3	0.0	0.0–1.2	0.0	0.0	0.0
Brassicaceae	0.0–1.0	0.0–0.3	0.0	0.0–0.3	0.0–0.9	*0.0–10.1*
Caryophyllaceae	0.0	0.0–1.0	0.0–0.3	*0.0–0.8*	**0.3–27.1**	**0.7–8.1**
Chenopodiaceae	0.0–3.0	0.0–2.1	0.0–3.5	0.0	0.0–1.7	*0.0–32.6*
Dipsacaceae	0.0–2.6	0.0–0.6	0.0–0.9	0.0–0.3	0.0–0.3	0.0–0.7
Euphorbia	**1.1–14.1**	0.0–0.6	0.0–3.2	0.0–1.1	0.0–2.6	**0.3–1.7**
Galium	0.0–2.3	0.0–0.9	0.0	0.0–0.9	0.0	0.0
Gentiana	0.0	0.0	0.0–0.1	0.0–0.3	0.0	0.0
Labiateae	0.0–1.6	0.0–0.9	0.0–0.1	0.0	0.0–0.6	0.0
Lamium	0.0–1.0	0.0–0.3	0.0	0.0–0.3	0.0	0.0
Lactuceae	**2.5–30.9**	**0.3–21.5**	**0.3–7.9**	*0.0–21.5*	**3.0–43.7**	**9.9–28.9**
Ophioglossum	0–3.5	0.0	0.0–2.3	0.0	0.0	0.0
Plantago	0.0–2.0	0.0–0.6	0.0–0.3	0.0–2.1	0.0–2.5	*0.0–3.4*
Poaceae	**14.1–51.3**	**41.5–82.3**	**28.7–84.5**	**47.3–68.6**	**35.6–75.5**	**37.9–55.7**
Ranunculus	0.0–1.0	0.0	0.0	0.0–0.3	0.0	0.0–0.3
Rumex	0.0–2.0	0.0	0.0	0.0	0.0	0.0
Scabiosa	0.0	0.0	0.0	0.0	0.0–0.3	0.0
Scrophulariaceae	0.0–2.0	0.0	0.0	0.0	0.0	0.0
Sedum	0.0–2.2	0.0	0.0–1.2	0.0	0.0	0.0
Spergula	0.0	0.0	0.0	0.0–0.3	0.0	0.0
Trifolium	**0.5–2.5**	*0.0–3.3*	**0.3–9.4**	0.0–1.2	0.0–6.9	0.0–0.3
Apiaceae	0.0	0.0–0.3	0.0–0.1	0.0–0.3	0.0–2.8	0.0
Cyperaceae	**0.6–1.3**	*0.3–8.4*	**0.6–6.4**	**1.1–7.4**	*0.0–2.6*	*0.0–0.9*
Liliaceae	0.0	0.0	0.0–0.9	0.0	0.0	0.0
Urtica	0.0	0.0–0.5	0.0–0.1	0.0–0.3	0.0–0.3	0.0
Cerealia	0.0–1.9	0.0–0.3	0.0–0.1	0.0–0.3	0.0–0.8	0.0

2001; Jaouadi et al., 2015; Wright et al., 1967)

It is also apparent that pollen productivity and/or survival was low in many of the sampled sites. *Juniperus* and *Cupressus*, two of the most frequently-recorded arboreal species in the Gebel (Table 2), are known to be low producers of relatively fragile pollen grains. On the other hand, *Pinus*, which is known to produce very abundant pollen (Heim, 1970) and to have very resistant pollen grains (Havinga, 1971), was not noted around many of the sample sites - it was absent at nearly all sites with garrigue, maquis, scrub-steppe and pre-desert vegetation: Table 2 - but is a consistent and often abundant component in all pollen assemblages (Figs. 3–5).

The pre-desert areas in the transects are characterised by unvegetated interfluves, with vegetation only in the wadi floors, where runoff concentrates and moisture is retained in the often-silty wadi sediments. Vegetation is responding to runoff concentration and retained moisture, rather than to actual rainfall, and species such as *Tuberaria*, *Retama* and

Table 4
Characteristic taxa and vegetation of the cluster groups, with ERA5 rainfall ranges.

Cluster	Sample	Vegetation type	Characteristic species	ERA5 40-year (mm)
1a	1752 1590 1504 1638 1627	Juniper scrub Garrigue Juniper scrub Woodland Juniper scrub	*Pinus* (1.5–5.2%) *Quercus* (0.5–3.9%) Poaceae (71.0–84.5%)	282.0–400.9
1b	1607 1610 1601 1612 1609 1616 1624	Maquis Maquis Juniper scrub Scrub-steppe Maquis Scrub-steppe Maquis	*Pinus* (1.8–9.3%) *Quercus* (0.3–3.2%) *Ligustrum* (0.3–4.0%) Cistaceae (0.3–5.4%) Poaceae (60.8–75.5%) Lactuceae (5.6–21.5%) Cyperaceae (0.6–8.4%)	51.4–294.6
1c	1606 1648	Maquis Juniper scrub	*Pinus* (1.0–1.3%) Cistaceae (1.9–17.7%) Poaceae (57.3–61.1%) *Ambrosia*-type (0.1–2.1%) *Plantago* (0.1–2.1%) Cyperaceae (0.6–3.2%) Apiaceae (0.1–0.3%) *Urtica* (0.1–0.3%)	188.7–241.5
2a	1620	Steppe	*Pinus* (6.3%) *Quercus* (0.6%) *Ligustrum* (0.3%) *Sideritis* (0.3%) *Helianthemum* (0.9%) *Convolvulus* (0.3%) Poaceae (37.9%) Lactuceae (9.9%) *Bidens*-type (0.6%) *Plantago* (3.4%) Brassicaceae (1.6%) Caryophyllaceae (8.1%) Chenopodiaceae (32.6%)	143.3
2b	1618 1584 1621 1530 1622	Scrub-steppe Garrigue Steppe Garrigue Scrub-steppe	*Pinus* (0.8–9.1%) *Quercus* (0.8–3.7%) *Ligustrum* (0.7–14.1%) Poaceae (40.0–51.3%) Lactuceae (4.8–19.5%) *Bidens*-type (0.8–4.4%) Cyperaceae (0.3–1.0%)	77.4–400.9
2c	1617 1615 1613 1611 1619 1614	Scrub-steppe Scrub-steppe Steppe Scrub-steppe Scrub-steppe Scrub-steppe	*Pinus* (0.3–4.7%) *Quercus* (0.8–3.7%) Poaceae (36.8–56.7%) Lactuceae (23.1–43.7%) *Bidens*-type (0.3–2.9%) Caryophyllaceae (0.9–17.5%)	60.6–284.4
3a	1608	Scrub-steppe	*Pinus* (6.3%) *Quercus* (0.6%) *Jasminium* (0.6%) *Ligustrum* (0.9%) *Ephedra* (0.3%) Ericaceae (1.2%) Cistaceae 45.9%) *Helianthemum* (1.5%) Poaceae (35.6%) Lactuceae (3.0%) *Bidens*-type (0.3%) *Ambrosia*-type (0.6%) *Trifolium* (1.2%) Caryophyllaceae (0.9%) Cyperaceae (0.9%)	248.4
3b	1503 1000	Woodland Garrigue	*Pinus* (24.8–26.0%) *Quercus* (2.0–4.5%) *Ligustrum* (1.3–3.2%) *Ephedra* (0.6–1.6%) *Juniperus* (0.6–1.2%) *Sideritis* (0.3–1.3%) Poaceae (14.1–28.7%) Lactuceae (7.9–30.9%) *Ambrosia*-type (1.2–2.9%) *Trifolium* (1.0–9.4%) Dipsacaceae (0.9–2.6%) *Ophioglossum* (2.3–3.5%) Cyperaceae (1.3–4.4%)	379.2–424.5
3c	1600 1605 1602 1604	Juniper scrub Woodland Maquis Woodland	*Pinus* (23.2–51.9%) *Quercus* (0.3–1.5%) Cistaceae (0.8–10.1%) Poaceae (41.5–51.5%) Lactuceae (0.3–4.2%) Cyperaceae (2.0–6.4%)	352.3

Tamarix are thus able to flourish in spite of the low rainfall.

6. Conclusions

In this paper we have explored the relationship between rainfall, vegetation physiognomy and surface pollen assemblages in and around the Gebel Al-Akhdar massif of Cyrenaica, Northeast Libya. The relationship between rainfall and vegetation is partly confounded by several factors: exposure of plants to salt spray seems to be a dominant influence shaping coastal garrigue, while in pre-desert wadis the concentration of runoff enables a suite of relatively moisture-requiring taxa to survive. The most important confounding factor, however, seems to be grazing pressure. Much of the northern, windward, slope of the Gebel has high-enough rainfall to support woodland vegetation, but this has been reduced in many places to scrubby maquis, and the surviving woodland is often not dense or continuous enough to exclude a herb layer.

The relationship between vegetation and surface pollen is primarily complicated by the long-distance dispersal of tree pollen, especially *Quercus* and *Pinus*, the pollen of which is very widely distributed. It is suspected that pollen of corrosion-resistant taxa, such as *Pinus* and the various Asteraceae, may preferentially survive in the strongly oxidising, calcareous and biologically active soils of the region, so their representation is likely to be greater in the soils than it would be in the pollen rain. These issues introduce a further layer of complexity into the rainfall–pollen relationship.

In spite of these issues, there are however statistically significant correlations between ERA 40 rainfall and some pollen taxa. Most parts of the rainfall distribution in the Gebel al-Akhdar can be characterised palynologically. We can thus infer that palynology can be used with confidence to characterise past rainfall regimes in the region.

Contributions

COH: research design, field work, statistical analysis, writing, supervision.

LCMcC: pollen analysis, data entry.

LE: GIS analysis and mapping, writing.

He-R: field work, met data collection, writing.

GB: writing, supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal

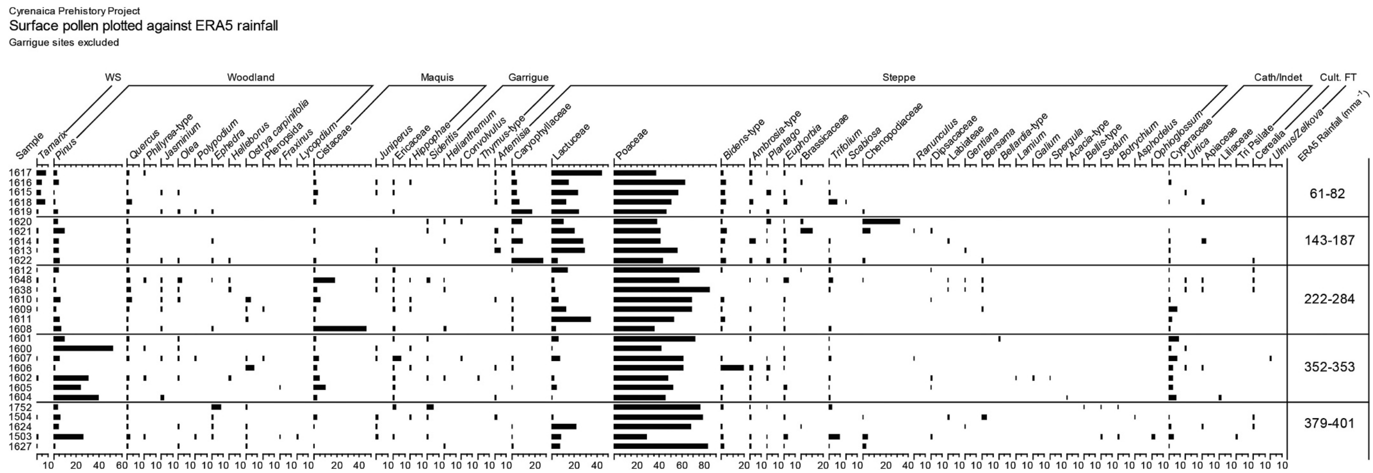

Fig. 5. Percentage surface pollen distributions plotted against ERA5 40-year rainfall. (Analysed LCMcC, statistical work and drawing COH).

relationships which may be considered as potential competing interests:

C. O. Hunt reports administrative support was provided by Directorate of Antiquities, Libya. Prof G. Barker reports a relationship with Directorate of Antiquities, Libya that includes: non-financial support. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data included as SI in paper

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2024.105272.

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