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DOI:

[10.1080/00173134.2015.1108996](https://doi.org/10.1080/00173134.2015.1108996)

Document Version

Accepted author manuscript

[Link to publication record in Manchester Research Explorer](#)

Citation for published version (APA):

Bell, B., & Fletcher, W. J. (2016). Modern surface pollen assemblages from the Middle and High Atlas, Morocco: Insights into pollen representation and transport. *Grana*, 55(4), 286-301.
<https://doi.org/10.1080/00173134.2015.1108996>

Published in:

Grana

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Title

Modern surface pollen assemblages from the Middle and High Atlas, Morocco: Insights into pollen representation and transport

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Abstract

33 modern surface samples were collected in the environmentally and climatologically contrasting regions of the Middle and High Atlas Mountains, Morocco. Samples representing forested and steppe montane environments (1935 m to 2760 m a.s.l.) are clustered around study sites at Lake Tislit (High Atlas, semi-arid oro-Mediterranean bioclimate), and Lake Sidi Ali and Michliffen (Middle Atlas, sub-humid montane Mediterranean bioclimate). Good discrimination between regional pollen spectra is evident, with Middle Atlas samples reflecting higher arboreal cover (*Cedrus* and evergreen *Quercus*) and High Atlas samples with high abundances of non-arboreal taxa, including *Artemisia* and Fabaceae. These four taxa (*Cedrus*, evergreen *Quercus*, *Artemisia* and Fabaceae) are furthermore shown to be reliable indicators of local source vegetation within a 100 m² quadrat, taking into account threshold abundances of 7%, 20%, 4% and 10%, respectively. Deciduous *Quercus*, *Olea* and *Phillyrea* show long-distance pollen dispersal across both regions, contributing to non-trivial arboreal pollen (AP) values of up to 35% (typically 20-30%) in the High Atlas spectra. In the Middle Atlas, AP values of 40-50% occur in open sampling locations and >60% under forest canopy cover. These insights should be taken into account when interpreting ancient pollen spectra from regional lakes and bogs for palaeoenvironmental reconstruction.

Keywords

Modern pollen rain, pollen analysis, pollen dispersal, vegetation, montane environments, *Cedrus atlantica*, Correspondence Analysis, European Modern Pollen Database

Introduction

Preservation of pollen and spores in sedimentary records provides a proxy of past environment, vegetation and climate. Challenges arise interpreting the pollen record due to differential pollen preservation, production and dispersal, as well as the physical characteristics of the sampling site making reconstructions difficult (Davis 1984; Birks & Gordon 1985; Prentice 1985; Gaillard et al. 1994; Sugita 1994; Ritchie 1995; Hicks 2001). Understanding the relationships between modern vegetation and pollen assemblages is therefore imperative for the interpretation of fossil pollen and the reconstruction of paleoenvironments and climate (Wright 1967; Jackson and Williams 2004; Fall 2012). The use of modern surface samples can improve the understanding of under- and over-represented taxa and the long-distant transport of pollen (Erdtman 1943; Faegri and Iversen 1950; Davis and Goodlett 1960; Bradshaw 1981; Bhattacharya et al. 2011). For example, in montane environments it is important to understand the altitudinal movement of pollen (Yu et al., 2001; Weng et al., 2004; Canellas-Bolta et al. 2009) and the influence of prevailing (Markgraf, 1980).

Morocco is a crucial area for the reconstruction of palaeoclimate change for the Maghreb (e.g Rognon 1987; Lamb et al. 1989). The region is sensitive to the effects of future climate change with increased temperatures, reduced precipitation and more frequent droughts predicted (Giorgi 2006; Born et al. 2008; Solomon et al. 2009). Climate change in the region has caused dieback of *Cedrus atlantica* across the Middle and High Atlas due to a rain deficit since the 1980s, especially in areas which are not ecologically optimum for the species (Rhanem 2011). Many parts of the Middle and High Atlas ranges are now near the climatological limits of forest development. The areas are also subject to intense anthropogenic activity through agriculture and grazing, causing further degradation to the landscape (Lamb et al. 1994; Barrow and Hicham 2000). Due to these climate and anthropogenic effects upon the forest it is important to understand the relationships between the abundance of arboreal pollen and tree cover in the pollen spectra. Therefore, insights from palaeoecology into the sensitivity and resilience of ecosystems as well as context provided by historical perspectives on environmental change are critical (Lamb et al. 1989; Lamb et al. 1991; Lamb et al. 1999)

In this paper we examine the modern pollen assemblages and vegetation relationships at three montane study sites: Lake Tislit in the High Atlas, and Lake Sidi Ali and Michliffen in the Middle Atlas. This study is based on an opportunistic sampling of surface soils (n=33) undertaken near two lakes and one forest. The lakes (Tislit and Sidi Ali) were investigated in the context of bathymetric, seismic and hydrological surveys in 2012, leading to new multiproxy investigations of lake sediments.

The knowledge of surface sample pollen spectra is therefore of particular interest for the interpretation of emerging new palaeoecological records. We also examine our results in the context of archived surface pollen data for the study region. The European Modern Pollen Database (Davis et al. 2013) contains a large dataset of unpublished surface samples from Morocco (n=284), which has been previously used for quantitative climate reconstruction (e.g. Cheddadi et al. 1998). However, the lack of metadata on site and vegetation characteristics limits the value of this dataset in terms of further detailed evaluation of vegetation-pollen relationships. We also make reference to a published study (Saadi and Bernard 1991, henceforth SB91) of surface pollen spectra from Morocco (n=73) for which geographical coordinates and brief vegetation notes are available.

The aims of the current study are to 1) characterise the typical pollen spectra at the three sites and explore the potential for discrimination of different regional vegetation cover types; 2) examine local variability in pollen spectra over small spatial scales; 3a) identify taxa that are good indicators of local presence and propose approximate threshold values for local presence; 3b) identify those taxa that are poor discriminators of local presence; and 3c) identify taxa that are representative of long-distance transport.

Material and methods

Study areas

The Atlas Mountains comprise the Middle (Moyen) Atlas, High (Haut) Atlas and Anti-Atlas ranges, covering the eastern, central, and southerly areas of the country respectively (Figure 1a). The regional climate alternates between wet and dry seasons influenced by polar air masses and subtropical high-pressure systems, respectively. In winter, North Atlantic westerlies bring cooler air and rain, while in summer the region experiences hotter temperatures and drought due to a combination of Atlantic (Azores) and Saharan high pressure systems (Fink et al. 2010). The climate of the Middle Atlas is relatively cool and humid compared with the High Atlas, and here the most extensive development of *Cedrus atlantica* (Endl.) Manetti ex Carrière is observed, alongside the evergreen *Quercus rotundifolia* Lam (syn. *Quercus ilex* subsp. *ballota* (Desf.) Samp.), with deciduous *Quercus faginea* Lam. and *Quercus pyrenaica* Willd. at lower altitudes (Emberger 1939; Quezel 2002). In the relatively drier and more continental High Atlas, the dominant vegetation cover is composed of *Juniperus thurifera* L. and steppic formations (e.g. Haroni 2009, Navarro et al. 2009) (Figure 1b).

Figure 1. Location of study sites and sampling locations, and map of vegetation. A. Overview map of Morocco showing location of study sites. B. Map of dominant vegetation types for the study area based on Emberger (1939). C. Map of sample sites around Lake Tislit. D. Map of samples sites around Lake Sidi Ali. E. Map of sample sites at Michliffen. Map source: © OpenStreetMap contributors.

High Atlas Mountains: Lake Tislit (TIS). — The High Atlas study site (TIS) is located in the vicinity of Lake Tislit on the Plateau des Lacs, 4 km north of Imichil. Lake Tislit, located at 32° 11'N, 5° 38'W, 2250 m a.s.l., is one of two large lakes of contested karstic/meteor impact origin (Ibhi et al. 2013;

Chaabout et al. 2013; Akdim 2015) lying west of the larger Lake Isli. It has an area of approximately 0.75 km² and a depth of 16 m. Mean annual precipitation recorded at nearby Imilchil is reported to be on the order of 244 mm to 319mm with very high inter-annual variability (Peyron 1980; Lamb et al. 1994). Precipitation is characterised by intense rainstorms in spring and summer which cause flash floods and increase surface erosion in the area. Average maximum summer temperatures reach 30°C, while winter minima average -4°C (Lamb et al. 1994). The vegetation is characteristic of the oro-Mediterranean thorn cushion plant formations of the High Atlas (Navarro et al. 2009) consisting of sparse shrubs and a range of perennial herbs and grasses (Figure 2a-c). These include cushion-form spiny sub-shrubs such as *Bupleurum spinosum* Gouan and members of the Fabaceae family (*Erinacea anthyllis* Link, *Cytisus* spp., *Astragalus* spp.), accompanied by low-growing plants from Crassulaceae, Helianthemum spp. and Lamiaceae (Thymus spp.). *Berberis hispanica* Boiss. & Reut. and *Prunus prostrata* Labill. develop in rocky crevices and gullies. There is considerable grazing pressure from sheep and goats. There is little to no tree cover in the immediate area, excluding occasional junipers (*Juniperus thurifera*) near the lake itself, and a few planted trees (*Pinus halepensis* Mill. and *Populus* sp.) around the western margin of the lake. Tree cover with *Juniperus thurifera* and *Quercus rotundifolia* is developed at around 20 km distance across the watershed to the northwest on Atlantic (north-west) facing slopes, and *Cedrus* forest is located around 40 km distance to the northeast on the slopes of Jbel Masker.

Middle Atlas Mountains: Lake Sidi Ali (ALI). — The first of two Middle Atlas study sites (ALI) is located in the vicinity of Lake Sidi Ali at 33° 03'N, 5° 00'W, 20 km south of Timahdite. It is one of the largest and highest altitude (2,080 m.a.s.l.) lakes in the Middle Atlas, located towards the south-eastern limits of the mountain range (Akdim 2015). Data from the weather station at the site for 1971-2010 indicate a mean annual precipitation of 415 mm and mean annual temperature of 10.4°C, with average temperatures of the coldest and warmest months (Jan, Aug) of 2.5°C and 19.7°C, respectively (Sayad et al. 2011). Mountain ridges forms the south-eastern and northern margins of the lake, with open to semi-dense forest cover. The site lies within the montane-Mediterranean bioclimate, and the dominant arboreal taxa at the site are *Cedrus atlantica*, *Quercus rotundifolia* and *Juniperus thurifera*. The forest cover around Sidi Ali is degraded by commercial logging, cutting for firewood, and grazing pressure. The cedar population at Sidi Ali, which includes individuals of >900 yr in age (Copes-Gerbitz, unpublished dendrochronological data), shows signs of extensive senescence and dieback. Restoration efforts including planting of seedlings are underway, but there does not appear to be widespread success of young trees in the area. The surrounding vegetation is a mix of scrub and forest (Morgan 1982; Lecompte 1986) (Figure 2d-f). A wide range of

woody taxa can be observed around Sidi Ali, including *Ribes uva-crispa* L., *Rosa* spp. and *Berberis hispanica* along the rocky lake margins, spiny cushion-form shrubs in open areas including *Erinacea anthyllis*, and a range of mesic tree taxa in the best preserved forest fragments on the north-facing slopes of the lake's southern margin. These latter include *Acer monspessulanum* L., *Crataegus lacciniata* Steven ex Besser and *Fraxinus dimorpha* Coss. & Dureiu. The lake is a popular tourist spot and the area is subject to extensive animal grazing.

Figure 2. Sample site photos showing typical environmental setting and vegetation. A. TIS 01 B. TIS 07 C. TIS 12 D. ALI 01 E. ALI 07 F. ALI 11 G. MICH 01 H. MICH 02 I. MICH 03.

Middle Atlas: Michliffen. — The second Middle Atlas study site (MICH) is located in the Michliffen caldera at 33° 32'N, 5° 6'W (~2000 m a.s.l.), and 40 km to the north of Sidi Ali. The caldera is one of several extinct Plio-Pleistocene volcanoes in the northern plateaux of the Middle Atlas (Waele and Melis 2008). Climate at Ifrane, located 13 km to the north of Michliffen is characterised by mean annual precipitation of 900 mm, mean annual temperature of 11.4°C, and mean January (August) temperatures of 4°C (21.4°C). Michliffen is a popular touristic destination with a small ski resort, but retains a healthy forest cover (Figure 2g-i), as well as a population of the emblematic Barbary

macacques (*Macaca sylvanus*). The southern-facing caldera slopes are covered by a montane Mediterranean mixed needle leaf-broadleaf forest with *Cedrus atlantica* and *Quercus rotundifolia*, with other taxa including *Acer monspessulanum* and *Juniperus oxycedrus* L.. The northern-facing slopes are dominated by stands of *Cedrus atlantica*.

Field Sampling

Soil surface samples were collected from 33 sites across the study locations in 10 x 10 m quadrats. Five evenly spaced subsamples (x-pattern) were taken from each quadrat from the top soil (5mm depth) and leaf litter and combined following Adam and Mehringer (1975) so as to ensure a well-mixed sample representing an integrated signal of the local pollen rain over the 100m² sampling area and several pollination seasons. Vegetation found in each quadrat was recorded as a presence/absence survey (Supplementary File 1), and visual estimates of ground cover and canopy cover recorded (Table 1). It should be noted that due to sampling in September, many annual species and cryptophytes may not have been visible. Detailed taxonomic identifications were also hindered by the lack of flowering at this time and heavy grazing impact.

In the High Atlas, samples were collected around the margins of Lake Tislit (TIS 1-10) at altitudes between 2250 - 2280 m, and along an altitudinal transect (TIS 11-16) extending towards the north and reaching up to 2670 m (Figure 1c). The sampling locations were generally characterised by low vegetation cover and thin, xeric soils with sparse leaf litter (Table 1). Middle Atlas samples ALI 01-07 are located around the western and southern margins of the Lake Sidi Ali at ~2090 m elevation in areas of open, scrubby vegetation, on basaltic substrates with sandy soils (ALI01-05) or on rocky soils on calcareous substrates (ALI 06-07). Samples ALI 08-14 are located in the forested area to the south of the lake at higher elevations between 2180 - 2200 m a.s.l. on calcareous substrates (Figure 1d). The three MICH sample sites span the lower slopes (MICH01, 1935 m a.s.l.) to ridge summit (MICH 03, 2088 m a.s.l.) (Figure 1e).

Laboratory methods

Organic matter was calculated using loss-on-ignition for each sample following Dean (1974). Pre-weighed samples were dried overnight at 105°C, weighed, then fired at 550°C for 3 hours and further weighed to calculate organic matter content as a percentage of dry weight.

Table 1. Sample site location data including latitude and longitude, altitude, soil substrate, and estimates of ground and canopy cover.

Site	Latitude	Longitude	Altitude	Substrate	Ground Cover	Canopy Cover
TIS 01	32.19253	-5.63389	2275	Hillslope xeric soil on weathered mudstones	5	0
TIS 02	32.19301	-5.6329	2279	Hillslope xeric soil on weathered mudstones	15	0
TIS 03	32.19331	-5.63222	2280	Hillslope xeric soil on weathered mudstones	15	0
TIS 04	32.19367	-5.63142	2282	Hillslope xeric soil on weathered mudstones	10	0
TIS 05	32.19408	-5.63063	2284	Hillslope xeric soil on weathered mudstones	15	0
TIS 06	32.1948	-5.63002	2265	Hillslope xeric soil on weathered mudstones	15	0
TIS 07	32.19553	-5.62895	2268	Hillslope xeric soil on weathered mudstones	20	0
TIS 08	32.19681	-5.6289	2251	Silty soil on lake shore sediments	95	0
TIS 09	32.19977	-5.62894	2282	Hillslope xeric soil on weathered mudstones	15	0
TIS 10	32.19984	-5.63752	2260	Alluvial fan	25	0
TIS 11	32.20404	-5.63877	2305	Alluvial fan	10	0
TIS 12	32.20866	-5.63808	2363	Xeric soil with loose stone cover	40	0
TIS 13	32.21254	-5.63794	2464	Xeric soil with loose stone cover	20	0
TIS 14	32.21563	-5.6382	2561	Xeric soil with loose stone cover	20	0
TIS 15	32.2174	-5.63739	2670	Xeric soil with loose stone cover	10	0
TIS 16	32.2185	-5.64466	2760	Angular rock field	20	0
ALI 01	33.07393	-5.00434	2095	Basalt rocks, fine sands and silts	35	0
ALI 02	33.07358	-5.00493	2089	Basalt boulder field, silty soil	10	0
ALI 03	33.066	-5.00717	2093	Fine sand and silt	20	0
ALI 04	33.06556	-5.00742	2094	Basaltic boulder field with aeolian sands	50	40
ALI 05	33.06579	-5.00715	2092	Basaltic boulder field with aeolian sands	25	5
ALI 06	33.06621	-4.9989	2089	Rocky limestone slope with silty soil	40	10
ALI 07	33.06575	-5.00133	2087	Rocky calcareous slope with silty soil	35	5
ALI 08	33.07024	-4.98935	2180	Calcareous rocky slope with light organic soil	60	20
ALI 09	33.07006	-4.98992	2178	Calcareous rocky slope with light organic soil; disturbed ground	15	25
ALI 10	33.0696	-4.99097	2179	Calcareous rocky slope with organic brown soil and thick (5cm) leaf litter	5	70
ALI 11	33.06909	-4.99119	2184	Calcareous rocky slope with stony cover and gritty soil with leaf litter	20	55
ALI 12	33.06819	-4.99185	2211	Rocky calcareous slope with loose soil and stone cover; abundant dead wood and disturbed ground	20	5
ALI 13	33.0675	-4.99327	2191	Rocky, calcareous slope with light organic soil and woody leaf litter	10	15
ALI 14	33.06724	-4.99372	2179	Rocky, calcareous slope with thin organic soil on weathered bedrock with leaf litter	60	20
MICH 01	33.41566	-5.0792	1935	Calcareous soil on rocky substrate with organic leaf litter	90	60
MICH 02	33.41645	-5.07991	1971	Calcareous soil on outcropping limestone with light, organic rich soil	40	80
MICH 03	33.4108	-5.08487	2088	Fine organic soil, rocky limestone	30	15

Pollen samples were prepared from subsamples of 1 cm³ material following standard acetolysis preparation techniques (Erdtman 1960; Moore et al. 1991). Additionally dense-media-separation using sodium polytungstate (SPT) was used due to the high minerogenic sediments within the samples (Nakagawa et al. 2008). Lycopodium marker tablets were added to each sample to allow for absolute pollen analysis (Stockmarr 1971). Pollen was counted under a high power Zeiss microscope at 400 x and 1000 x magnification. Reference material (Reille 1992a; Reille 1995; Beug 2004; Liu et al. 2007) and sample slides held by The University of Manchester Geography Department were used for identification. Count sizes were between 303 and 643 grains (mean = 356) with 52 taxa identified. Pollen percentages for plotting in the pollen diagram were calculated against a main sum of all taxa excluding degraded and unidentifiable grains (Supplementary File 2). Correspondence Analysis (CA) (e.g. Hill, 1973), a method for indirect gradient analysis suitable for datasets where large environmental gradients are anticipated, was performed on the untransformed pollen percentage dataset for taxa occurring at least once above a 5% threshold. Asteraceae, Fabaceae, Caryophyllaceae and *Plantago* sub-types were grouped for the analysis. Statistics were calculated using PAST (Hammer et al. 2001). Comparative pollen data for the central Moroccan region corresponding to Figure 1b was downloaded from the EMPD (Davis et al., 2013) and digitised from the main pollen diagram of SB91, corresponding to a total of 89 surface samples within the study region. For the purposes of comparison, averages of the assemblages for TIS, ALI and MICH samples, respectively, were calculated.

Results

Characteristics of the soil surface samples

Total organic content of the surface samples ranges from <4% to 22% in the High Atlas, and 12% to 61% in the Middle Atlas; total pollen content of the surface samples ranges from 1.1×10^4 - 4.7×10^5 grains per cm³ (Figure 3). The surface samples are highly minerogenic with low concentrations of pollen in the Tislit area and in open areas near Sidi Ali, and are richer in organic content with higher pollen concentrations in wooded areas of Sidi Ali and Michliffen. Overall, pollen concentration is positively correlated ($R=0.76$, $p<0.001$) with the total organic matter content of the samples, as well as with canopy cover in the 10x10 m sampling frame ($R=0.63$, $p<0.001$).

Figure 3. Pollen diagram showing percentage of pollen found for each taxa at each sampling location. Pollen below 0.5% is indicated by an open circle. Total pollen concentration and percentage organic matter is also shown.

Characteristics of the pollen spectra

Concerning arboreal pollen types, *Cedrus* pollen is detected in almost all samples at abundances >1%. Abundances are higher in ALI and MICH samples, reaching up to 50% under *Cedrus* canopy cover at ALI, while values do not exceed 7% in any TIS sample. Cupressaceae (including *Juniperus* pollen) appears poorly represented in the pollen spectra at both locations (typically ~1%), despite being locally present and regionally significant at all sites. *Olea* is noteworthy for being detected in virtually all TIS and ALI samples (values up to 12%), despite not growing locally and being typical of lower altitude bioclimatic stages. Similarly, *Phillyrea* is present in most ALI samples, but not TIS or MICH. *Pinus* is not well represented in the pollen spectra, with the exception of TIS samples from the slopes above Lake Tislit, where abundances up to 10% are detected. The deciduous *Quercus* type is documented in almost all samples, with higher (>10%) values in ALI samples. The evergreen *Quercus* type is detected in all samples, with TIS values less than 20% and ranging up to 40-60% in the ALI and MICH spectra. *Ephedra* types, typical of rocky terrain, are generally represented in low abundances, with more in the TIS spectra (up to 5%) as compared to the ALI (<1%) and MICH (<3%) spectra. *Ribes*, typical of the rocky margins of Lake Sidi Ali, is detected in low abundances in the ALI spectra (<4%). Among other rare arboreal taxa, occasional grains of Juglandaceae are recorded across the sites (TIS 01, 11, 12, 16 and ALI 20, 14), and *Alnus* and *Crataegus* occur in one sample each (TIS 03 and ALI 03, respectively).

Concerning non-arboreal pollen types, *Artemisia* occurs in values up to ~15%, with the higher abundances characteristic of the TIS spectra. Brassicaceae, Caryophyllaceae and Poaceae pollen types are virtually ubiquitous, but generally occur in higher abundances (up to ~25%, 10%, ~20% respectively) in the TIS spectra. Chenopodiaceae pollen is detected in almost all spectra, but at consistently low abundances (<8%). Fabaceae pollen is well represented in most of the spectra, reaching values up to ~20%, with higher abundances in the TIS spectra, generally. While many of the Fabaceae grains were only identified to family level, *Astragalus*, *Coronilla* and *Genista* types (following Beug 2004) are well represented (Figure 2). *Helianthemum* pollen is generally detected in low abundances only, but is more common in the TIS spectra than in the ALI or MICH spectra; similar patterns are observed for *Centaurea cyanus* and *C. nigra* types. A number of other pollen types, including *Crassulaceae*, *Rumex* and Zygophyllaceae are detected sporadically in low abundances in the spectra.

Local variability in pollen spectra

While the TIS spectra are broadly homogeneous, there are subtle contrasts between the near-lake (low elevation) samples (TIS 01-10) and the higher slope samples (TIS 11-16). *Artemisia* and Caryophyllaceae are better represented in the near-lake samples, along with grazing-indicators *Helianthemum* and *Plantago*. There are also minor abundances of Cupressaceae consistent with local presence of junipers. In contrast, Asteraceae and, to a lesser extent, Poaceae are more abundant on the higher altitude slopes, along with higher abundances of extralocal to regional arboreal taxa (*Cedrus* and *Pinus*).

ALI samples display stronger contrasts between open, scrub and wooded areas with higher abundances of the dominant arboreal taxa *Cedrus* and *Quercus* evergreen in the wooded areas. Cupressaceae, although well represented in the local vegetation is poorly represented in the pollen spectra reaching only 6% in sample ALI 06. *Olea* and *Phillyrea* both non-local taxa reach highest abundances in the open areas. *Ribes* is distinctive to the open areas, but is poorly represented overall with ~4% in only 2 of the samples. Asteraceae is much more important in the open areas, along with Chenopodiaceae and *Plantago*. There is a large variation in total arboreal pollen (30-85%) from scrub to closed canopy areas. MICH samples are dominated by arboreal types *Cedrus* and *Quercus* with some NAP (Fabaceae and Poaceae); however, clear patterns regarding spatial variability are not evident due to the smaller number of samples at this location.

Discrimination between the study sites

Sample and taxon scores on the first and second CA axes are shown in Figure 4. The combined axes account for 56% of the variance (Axis 1, eigenvalue = 0.2998, 40.4%; Axis 2, eigenvalue = 0.1194, 16.1%). Sample scores on Axis 1 are strongly correlated with AP% ($R=0.983$, $p<0.0001$) and effectively represents arboreal vegetation development, with positive scores for samples with higher AP. Axis 1 discriminates clearly between the TIS (oro-Mediterranean steppe) and Middle Atlas samples (ALI and MICH, montane Mediterranean forest), with an intermediate cluster reflecting ALI sample sites with open vegetation characteristics. Sample scores on Axis 1 are also positively correlated with local canopy cover within the 10 x 10 m quadrats ($R=0.667$, $p<0.0001$) and organic content of the surface soils ($R=0.862$, $p<0.0001$).

Axis 2 discriminates primarily between *Quercus*- and *Cedrus*-rich samples from the Middle Atlas with positive scores for *Quercus*-rich samples, suggesting an influence of localised soil moisture availability, with positive scores for more drought tolerant and deeply rooted *Quercus* and negative

scores for more moisture sensitive, shallow-rooting *Cedrus* species. However, environmental data to confirm this interpretation is not available. Axis 2 also reveals a significant altitudinal pattern, with more negative scores for higher altitude sites within the TIS cluster ($R=-0.86$, $p<0.0001$), but not for the other study sites. Overall, this altitudinal pattern at TIS can be linked to higher abundances of *Cedrus* in the higher altitude TIS locations (especially TIS 11, 14-16). Overall, sample scores on Axis 2 appear unlikely to reflect a common environmental gradient, as the key taxon (*Cedrus*) is locally present at the Middle Atlas sites, but only present at part of a regional pollen rain at the TIS study site with source vegetation located >30km distant. The altitudinal discrimination of TIS sites on axis 2 therefore appears to reflect subtle contrasts in the relative contribution of local to regional pollen sources, perhaps linked to local productivity decreases with increasing altitude and a relatively greater contribution of pollen from distant sources.

Figure 4. CA biplot of sample sites and key pollen taxa (those that occurred at 5% or more in at least one sample). Axis 1 accounts for 40.4% of the variance, effectively representing arboreal pollen abundance. Axis 2 accounts for 16.1% of the variance which has positive correlation with soil organic matter.

The CA (Figure 4) shows High Atlas samples more closely grouped indicating less variability in the pollen spectra compared to the Middle Atlas samples. Species scores highlight the importance of non-arboreal taxa including *Artemisia*, Brassicaceae, Caryophyllaceae, Poaceae and *Helianthemum* in the TIS spectra, along with Cupressaceae. The Middle Atlas spectra (ALI and MICH) are distinguished by high abundances of *Quercus* (evergreen and deciduous type), *Cedrus* and *Phillyrea*. Sidi Ali samples are the most varied due to the more varied landscape (open scrub, forest) and indicate higher local-scale pollen variability. Michliffen spectra, which are dominated by AP, are separated by the dominance of either *Quercus* or *Cedrus* pollen, but fall within the range of ALI samples and are not clearly discriminated in the CA biplot.

Discussion

Regional characterisation of the modern pollen rain

Significant relationships between soil organic content, local canopy cover and pollen concentration point to a general linkage between vegetation cover type (open vs. wooded), soil and leaf litter organic content, and pollen concentration. These relationships may be linked to vegetation source effects, e.g. higher biomass, productivity and pollen production in forested environments vs. open environments, and/or to preservation factors associated with the more organic-rich surface soils and leaf litter layer (e.g. shading, moisture levels) developing under forest canopy. These latter factors are consistent with findings in other sedimentary contexts linking improved pollen preservation with higher organic content, e.g. marine sediments (Cheddadi and Rossignol-Strick, 1995).

The composition of the pollen samples shows meaningful differences across the different sampled environments, suggesting excellent potential for discrimination between different regional vegetation types from pollen spectra, either modern or ancient. In particular, the pollen spectra associated with the oro-Mediterranean steppic vegetation of the TIS study area are dominated by non-arboreal pollen types, especially *Artemisia* and other Asteraceae types, Brassicaceae, Poaceae, and Fabaceae, accompanied by Cupressaceae, Caryophyllaceae, *Centaurea cyanus* and *nigra* types, *Convolvulus* and *Ephedra* types. The pollen spectra of the montane Mediterranean Middle Atlas sites (ALI, MICH) in contrast are generally dominated by arboreal taxa (*Cedrus* and *Quercus* types) accompanied by *Fraxinus* and *Ribes* near Lake Sidi Ali. The first axis of the CA discriminates clearly between the High Atlas and Middle Atlas samples, reflecting primarily the contrasting importance of arboreal pollen type abundances across the sites. The main driver for differences reflected in axis 1 is likely to be macroclimatic contrasts between the study areas, in particular the combined influence on growing season moisture availability of higher precipitation and cooler summer temperatures in

the Middle Atlas. Within the Middle Atlas samples, MICH samples and forested ALI samples are distinguished from more open, scrubby ALI sampling sites, partly reflecting higher precipitation at the MICH sites but also reflecting supplementary influences on arboreal cover at more localised scales (e.g. between ALI samples) of substrate type and/or grazing intensity.

Insights into pollen dispersal and long-distance transport

Figure 5. A: Box plots showing pollen abundance within a sample where source vegetation was recorded in one or more sampling quadrats (dark grey) versus pollen abundance found in samples where vegetation was not present (light grey) for indicated taxa. **B:** Box plots showing pollen abundance within a sample for indicated taxa where vegetation was not present in any sampling quadrats.

The comparison of the pollen spectra with the basic dataset resulting from the presence/absence survey (Appendix 1) highlights several taxon-specific patterns that may be important for the interpretation of regional ancient spectra. Here, we propose several taxon-specific hypotheses that are supported by our exploratory dataset and should be further tested using pollen traps and more extensive botanical surveys. Mann-Whitney tests showed that there was a significant difference ($P < 0.05$) for the indicated taxa (Figure 5) between the pollen abundance observed where the vegetation was locally present in the quadrat, compared to pollen abundance where vegetation was absent. This comparison is of particular interest for large, woody taxa for which there is no uncertainty about their presence/absence within the quadrat (due to seasonal changes, grazing losses, etc.).

Cedrus atlantica, a key forest taxon of considerable biogeographical and palaeoecological interest (Lamb et al. 1991; Cheddadi et al. 1998; Terrab et al. 2006; Fletcher and Goñi 2008; Cheddadi et al. 2009; Rhanem 2011) displays minor long-distance transport, being found as part of a regional pollen rain in the TIS samples in low abundances (typically 2.5%). In the Middle Atlas, pollen abundances reach up to 50% (mean=19.2%) in spectra from within pure or mixed *Cedrus* stands (ALI 08-14, MICH 01-03). Abundances in samples which lie only a few hundred metres from *Cedrus* trees (e.g. ALI 01-07) are considerably lower (typically 11%). Overall, *Cedrus* pollen does not appear to be strongly dispersed, and our data suggests a threshold value of ~7% as indicative of local presence (Figure 4a). SB91 document similar low levels of *Cedrus* pollen outside the source regions, for example in the Mouloya Basin and pre-Saharan steppes. Our findings support their perspective and that of Salamani (1993), and Lamb and van der Kaars (1995), that *Cedrus* pollen is not well dispersed in the environment.

In areas near *Cedrus* stands (ALI 08-14, MICH 01-03) the average abundance of *Cedrus* is 25%, but slightly higher in MICH samples (29.3%) compared with the forested ALI samples (23.3%). Although the difference is modest, other factors beside the abundance of *Cedrus* trees, such as pollen-production in response to moisture availability, may be affecting pollen abundance. Khanduri and Sharma (2009), for example, found a significant positive correlation between the number of pollen-producing strobili per branch of *Cedrus deodara* (Roxb. ex D.Don) G.Don and annual rainfall ($r = 0.739$, $P < 0.01$) in the Himalayas, and similar patterns may be anticipated for *C. atlantica* between the relatively humid MICH and dry ALI sites. It may also be a result of human caused degradation to the forest (stripping of branches for firewood) with qualitative observations suggesting this to be a more significant factor at the more degraded ALI sites compared to the relatively intact MICH sites.

Quercus evergreen pollen displays more important levels of long-distance transport, as it occurs in moderate abundances (average 14%, up to 31%) even where not locally present. The findings confirm that evergreen *Quercus* pollen is generally well dispersed in the study region (Lamb et al. 1989), including in the treeless TIS sector. Nevertheless, we observe that values greater than 20% predominantly occur in those samples where evergreen *Quercus* trees were recorded in the quadrat (Figure 4a), and therefore propose a threshold value for local presence for *Quercus* evergreen. This finding suggests that percentages below ~20% must be interpreted with caution in vegetation reconstructions from ancient pollen spectra in the study regions.

Artemisia emerges as regionally distinctive taxon. Comparing spectra from sites with *Artemisia* vs sites without, an approximate threshold value of ~4% for local presence is evident. It is

noteworthy that total values for *Artemisia* are not especially high at any site in the present study, suggesting that regional analogues may not exist for the *Artemisia* rich assemblages of the Lateglacial and early Holocene in the Middle Atlas (e.g. Lamb et al. 1989). It is interesting to note that values of *Artemisia* in this study are much lower than those recorded by SB91; this difference may be due to a botanical focus in that study on areas with abundant *Artemisia*.

For Fabaceae pollen, a threshold for local presence of 10% is suggested by the data. Considering that this pollen type represents an entomophilous group of plants for which pollen dispersal may be poor, pollen abundances in both High and Middle Atlas locations are quite high (reaching >20%). However, the relatively high values and relationship with local presence highlight the significance of a local, gravity component near the source plants in the surface soil spectra that may not be as well-represented in other site/samples types (e.g. lake sediments, peat bogs). In contrast with the findings of Canellas-Bolta et al. (2009), who found Fabaceae to be a poor indicator of local presence in the Pyrenees, our findings suggest that variability in Fabaceae pollen may be significant in fossil spectra, with important implications for the detection of thorn-cushion vegetation cover and associated grazing pressures.

Several pollen types do not display significant differences associated with presence/absence in the quadrats, including Brassicaceae, Asteraceae (excluding *Artemisia*), *Helianthemum*, Poaceae, Lamiaceae and *Plantago*. These taxa do display inter-sample variability that may be related to local environmental factors (e.g. grazing pressure, soil moisture, etc.) for which data is not available. Detection of local presence may also be hindered by low visibility and representation of annual species in the survey.

Several key taxa were not recorded in the vegetation survey, but were documented in the pollen spectra (Figure 5b). Obviously, this can be due in part to issues of seasonal visibility, and that the sampling design will not account for taxa that may have been growing in close proximity to the quadrats but did not happen to fall with the sampling frame. However, some important insights emerge nevertheless. *Quercus* deciduous type pollen occurs in values up to 18%. This pollen type most likely derives from deciduous and semi-deciduous oaks such as *Quercus faginea* and *Q. pyrenaica* growing at lower altitudes in the humid, supra-Mediterranean bioclimatic stage. For example, *Q. faginea* flourishes near Azrou at around 1600 m a.s.l.. *Olea* (and the closely related *Phillyrea*) is also widely detected in the spectra at values up to ~12% and 7% respectively, despite not growing in the study regions. *Olea* is widespread in the thermo- and meso-Mediterranean stages, with extensive plantations around Meknes and Volubilis at 600 m elevation, for example.

Both *Quercus* deciduous type, *Olea* and *Phillyrea* appear to be widely dispersed beyond the source areas and over-represented at both the Middle Atlas locations and (excluding *Phillyrea*) in the High Atlas study site. In these cases, and in light of the broad distribution of vegetation formations at the wider regional scale, pollen transport would appear to derive from lower altitude zones to the W or NW. A similar upwind transport has been reported for *Olea* pollen in the Pyrenees, where it occurs consistently at low abundances in the sub-alpine and alpine zones (Canellas-Bolta et al. 2009).

Pinus is a well-known widely dispersed pollen producer (Erdtman 1943), and is found across the Middle and High Atlas, but does not form the dominant vegetation cover in any area near the study sites. Overall, *Pinus* pollen does not appear to be significantly over-represented at the study sites, in contrast with patterns in temperate or boreal latitudes. *Pinus* pollen deposition is principally detected on the southward-facing slopes above Lake Tislit (samples TIS 10-16) and at the eastern end of the lake (TIS 08, 09) average 2.8%, with highest value of 10.1% and TIS 14. This pollen may be derived from the pine trees growing along the western shore of Lake Tislit. The absence of *Pinus* pollen in samples (TIS 01-07) suggests a complex local pattern with preferential pollen deposition to the N and NE of the source trees but not towards the E or SE possibly associated with local air currents. *Pinus* pollen is poorly represented in the Middle Atlas samples (average 0.9%) and suggests a regional signal. The lower percentage may be a result of under-representation caused by the higher abundance of other arboreal pollen in these samples. Reille (1992b) found *Pinus* was to be under-represented in areas with mixed vegetation forests despite a wide distribution in Corsica, which would correspond with our findings.

Caryophyllaceae and Chenopodiaceae were not recorded at the sample locations, but are widely represented by many species in the study regions, including annual species that may not have been observed in the September field season. Similarly, *Ephedra* types were not locally present in the quadrats, but occur across the study regions. Zygophyllaceae pollen, possibly representing *Zygophyllum* and *Fagonia* spp., is more common in the TIS samples and is likely to reflect long-distance transport from low elevation desert regions.

Markgraf (1980), in a study of alpine vegetation in Switzerland, found that pollen productivity decreases as elevation increases, independent from plant density, such that higher elevation pollen spectra are more likely to reflect a regional signal carried from lowlands by prevailing wind conditions. In California, Soloman & Silkworth (1986), found pollen deposition values to be high and variable near source plants, while lower, more uniform values were found at great distance from source. These observations are generally consistent with our findings. TIS samples

have low pollen values with less variability, across the sampling locations for many of the non-present taxa (e.g. *Cedrus*, *Quercus*, *Ephedra*), while ALI samples show higher values with greater variability between sample locations where vegetation is present. This suggests that in the High Atlas, pollen abundance values in excess of the threshold values inferred in this study would be required to support local presence of anemophilous plants in the fossil record.

Relationships between vegetation cover and arboreal pollen abundance

Figure 6. Box plot showing total arboreal pollen percentage at the sample sites grouped by sample location.

Figure 7. Plot of total arboreal pollen percentage versus canopy cover at the sample sites. Blue (online version) triangles represent Lake Tisli samples, yellow squares = Lake Sidi Ali samples, and green circles = Michliffen samples. ($r = 0.68$, $P < 0.001$).

Strong differentiation between the Tisli and Middle Atlas (ALI, MICH) spectra in terms of arboreal pollen abundance is evident, with values typically below 30% in the Tisli spectra (average=27.6%, s.d.=5.2) and reaching up to 60-90% in the Sidi Ali (a=65.6% s.d.=18.3) and Michliffen (a=77.7% s.d.=4.2) spectra (Figure 6). CA also confirms the importance of arboreal pollen abundance as the primary distinguishing characteristic of the pollen spectra across the study locations (Figure 3). In terms of potential for reconstruction of arboreal cover from AP% values, we note a significant correlation between ($R=0.682$, $p<0.0001$) between AP% and canopy cover estimates within the 10x10 m quadrats (i.e. 100 m² scale) (Figure 7). Observation of the associated scatterplot highlights several points. Arboreal pollen abundance attains values of 20-35% at TIS sites in the absence of

significant local or landscape-scale tree cover. These values, reflecting primarily *Quercus* types and *Olea*, highlight a significant regional to extra-regional airborne rain component, and reinforce the caution required for inferences regarding local presence of taxa in the open vegetation communities of the High Atlas. For sample locations with canopy cover greater than ~20% (i.e. forested ALI and MICH locations), arboreal pollen abundances increase in an approximately linear fashion with canopy cover. This suggests a close control on local soil pollen assemblages by the immediately surrounding vegetation, and dominance of gravity and trunk space pollen components (*sensu* Tauber 1965). At more open sampling locations at ALI and MICH with canopy cover up to 20%, a very wide range of AP values are recorded (30-90%). This suggests greater influence of wind-borne pollen (canopy and rain components (*sensu* Tauber 1965) from the surroundings in these more open sampling locations, consistent with higher abundances of extra-regional pollen (e.g. *Olea* and *Phillyrea*).

In summary, AP values of up to 35% are typical of open vegetation settings (TIS), values of 40-50% occur in open sampling locations in the vicinity of forested areas (ALI 08-14), and values >60% occur in forested areas (ALI, MICH). These values are consistent with previous observations in other Mediterranean settings (Wright et al. 1967; Bottema and Woldring 1990), and remain important for the interpretation of fossil spectra. The positive correlation between canopy cover at the scale of 100 m² supports further investigations into relationships between arboreal pollen and arboreal vegetation cover at a wider range of spatial scales. In the future, this could include regionally-specific calibration of surface pollen spectra vs satellite imagery for reconstruction of arboreal cover (e.g. Jackson and Williams 2004).

Comparison with archived surface sample data

Figure 8 places the averaged data for TIS, ALI and MICH spectra in the wider geographical context of surface pollen data from the EMPD and SB91. This comparison reinforces many of the key observations made at the small spatial scale of intensive analysis at the TIS, ALI and MICH sites. For example, high values for *Cedrus* show a good match to proximity to the main vegetation source areas, reinforcing the inference of high values for this taxon being a reliable indicator for local proximity of source plants. *Olea* shows consistent abundances throughout the region regardless of distance to the main source areas to the northwest, confirming the extensive long-distance transport of this pollen-type. *Pinus* displays low values, highlighting that *Pinus* is not strongly over-represented in regional pollen spectra, but rather reflects dispersal and mixing from small, localised pockets of vegetation cover scattered throughout the study region.

Figure 8. Bubble plots showing percentage of pollen from modern surface samples for indicated species. Location of corresponding vegetation cover shown in grey. EMPD = Data from the European Pollen Database (Davis et al. 2013). SB91 = Data digitised from Saadi and Bernard, (1991). Pollen data from this study shown here was averaged for each study area (TIS, ALI, MICH).

Cupressaceae, despite the ecological importance and wide distribution of source taxa (including *Juniperus* spp. and *Tetraclinis articulata*), are generally poorly represented in the regional spectra, with the exception of three samples in the western part of the study region, possibly indicating greater pollen productivity or dispersal from *Tetraclinis*. *Quercus* evergreen pollen occurs across all locations, but with highest values in the Middle Atlas near the dominant vegetation source areas. This pattern is consistent with the inference that this pollen type is widely dispersed but nevertheless may provide a reliable indicator of local presence when recorded at high abundances.

The deciduous *Quercus* pollen type is infrequently recorded in the archived datasets, but appears in low frequencies across the study region. *Artemisia* is generally recorded at higher values in the High Atlas and lower values in the *Cedrus*-dominated regions of the Middle Atlas, consistent with differences between the TIS, ALI and MICH samples. We note that the SB91 spectra generally record higher *Artemisia* abundances which may reflect a sampling strategy in that study focused on *Artemisia* communities. While the analysis supports many of the observations from the new datasets, we note a caveat that the dominant vegetation cover types derived from Emberger (1939) shown in Figure 8 do not represent species distribution ranges, and that the vegetation may have been significantly influenced by anthropogenic modification and climatic change during the 20th century.

Conclusions

Modern surface pollen assemblages can provide important insights into pollen production and dispersal at a range of spatial scales. In dry Mediterranean and semi-arid areas near the climatological limits of forest development, it is especially interesting to understand the relationships between tree cover and arboreal pollen abundances, as well as upwind altitudinal movement of pollen. In this study 33 new pollen spectra are reported from three oro-Mediterranean montane sites located between 1935 and 2760 m a.s.l. in the Middle and High Atlas, Morocco. As the study reflects an opportunistic/exploratory sampling strategy, key patterns emerging from the dataset should be considered as hypotheses meriting further testing. Discrimination between vegetation covers of the the High Atlas (TIS) and Middle Atlas (ALI, MICH) sites is possible (as highlighted, for example, by the Correspondence Analysis), primarily reflecting contrasting development of arboreal cover (especially *Cedrus* and evergreen *Quercus*). The High Atlas spectra are furthermore rich in non-arboreal taxa such as *Artemisia*, Brassicaceae, Caryophyllaceae and Fabaceae, and distinguished by noteworthy occurrences of *Helianthemum*, *Centaurea cyanus* and *nigra* types, and *Ephedra* types. Comparing the pollen spectra with presence/absence information from vegetation survey highlights taxa that can be considered as good indicators of local presence (*Cedrus*, evergreen *Quercus*, *Artemisia*, Fabaceae), taking into account threshold values of around 7%, 20%, 4% and 10%, respectively, as indicative of local occurrence within the 10 x 10 m quadrat. Our results highlight long-distance effects and upwind altitudinal transport of three taxa (deciduous *Quercus*, *Olea*, *Phillyrea*). Overall, the findings from this new data at the small spatial scale of the three study sites are supported at the wider regional scale by comparison with existing data from the EMPD and SB91. The insights from this study should be taken into account in the interpretation of ancient pollen spectra from lakes and bogs in the region. For improving the understanding of

pollen production and transport vectors in Moroccan montane environments, several lines of investigation should prove fruitful, including additional surface studies across larger altitudinal ranges (e.g. Yu et al., 2001; Canellas-Bolta et al., 2009), nested botanical survey at varied spatial scales leading to quantitative determination of species-specific pollen production values (e.g. Broström et al. 2008), and evaluation of pollen spectra in lake surface sediments (e.g. Guimarães et al. 2014).

Acknowledgements

WF kindly acknowledges C. Zielhofer and S. Mischke Field and field support provided by German Science Foundation Pilot Research Grant “Late Quaternary geomorphological and environmental response to rapid hydrological cycles in the Atlas Mountains, Morocco” (DFG ZI 721/9-1). We gratefully acknowledge the assistance of Nick Scarle in Cartography at the School of Environment, Education and Development, (University of Manchester). We thank two anonymous reviewers for helpful comments that have improved the final manuscript.

Supplementary Files

Supplementary data mentioned in this manuscript (pollen assemblage data) can be downloaded from Mendeley Data, available at: <http://dx.doi.org/10.17632/48ygt7bx7f.2>

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