



Grana

ISSN: 0017-3134 (Print) 1651-2049 (Online) Journal homepage: <http://www.tandfonline.com/loi/sgra20>


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To cite this article: Benjamin A. Bell & William J. Fletcher (2016): Modern surface pollen assemblages from the Middle and High Atlas, Morocco: insights into pollen representation and transport, Grana, DOI: [10.1080/00173134.2015.1108996](https://doi.org/10.1080/00173134.2015.1108996)

To link to this article: <http://dx.doi.org/10.1080/00173134.2015.1108996>

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

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### Abstract

Thirty-three modern surface samples were collected in the environmentally and climatologically contrasting regions of the Middle and High Atlas Mountains, Morocco. Samples representing forest and steppe montane environments (1935–2760 m above sea level) 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 m<sup>2</sup> 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 to 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*

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 palaeoenvironments and climate (Wright 1967; Jackson & 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; Fægri & Iversen 1950; Davis & 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. 2002; Weng et al. 2004; Canellas-Bolta et al. 2009) and the influence of prevailing winds (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* (Endl.) Manetti ex Carrière across the Middle and High Atlas due to a rain deficit since

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(Received 16 June 2015; accepted 4 September 2015)

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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 & Hicham 2000). Due to these climatic and anthropogenic effects upon the forest, it is important to understand the relationships between the abundance of arboreal pollen (AP) 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, 1991, 1999).

In this paper, we examine the modern pollen assemblages and vegetation relationships at three montane study sites: Lake Tisli 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 (Tisli 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 & 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; (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 Atlantic 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* is observed, alongside the evergreen *Quercus rotundifolia* Lam (syn. *Quercus ilex* subsp. *ballota* [Desf.] Samp.), with deciduous *Q. faginea* Lam. and *Q. 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 (Figure 1B; e.g. Haroni et al. 2009; Navarro et al. 2009).

**High Atlas Mountains: Lake Tisli.** — The High Atlas study site (TIS) is located in the vicinity of Lake Tisli on the Plateau des Lacs, 4 km north of Imichil. Lake Tisli, located at 32° 11' N, 5° 38' W, 2250 m above sea level (a.s.l.), is one of two large lakes of contested karstic/meteor impact origin (Chababout et al. 2013; Ibhi et al. 2013; Akdim 2015) lying west of the larger Lake Isli. It has an area of approximately 0.75 km<sup>2</sup> and a depth of 16 m. Mean annual precipitation recorded at nearby Imilchil is reported to be on the order of 244 to 319 mm 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 in 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. et Reut. and *Prunus prostrata* Labill. develop in rocky crevices and



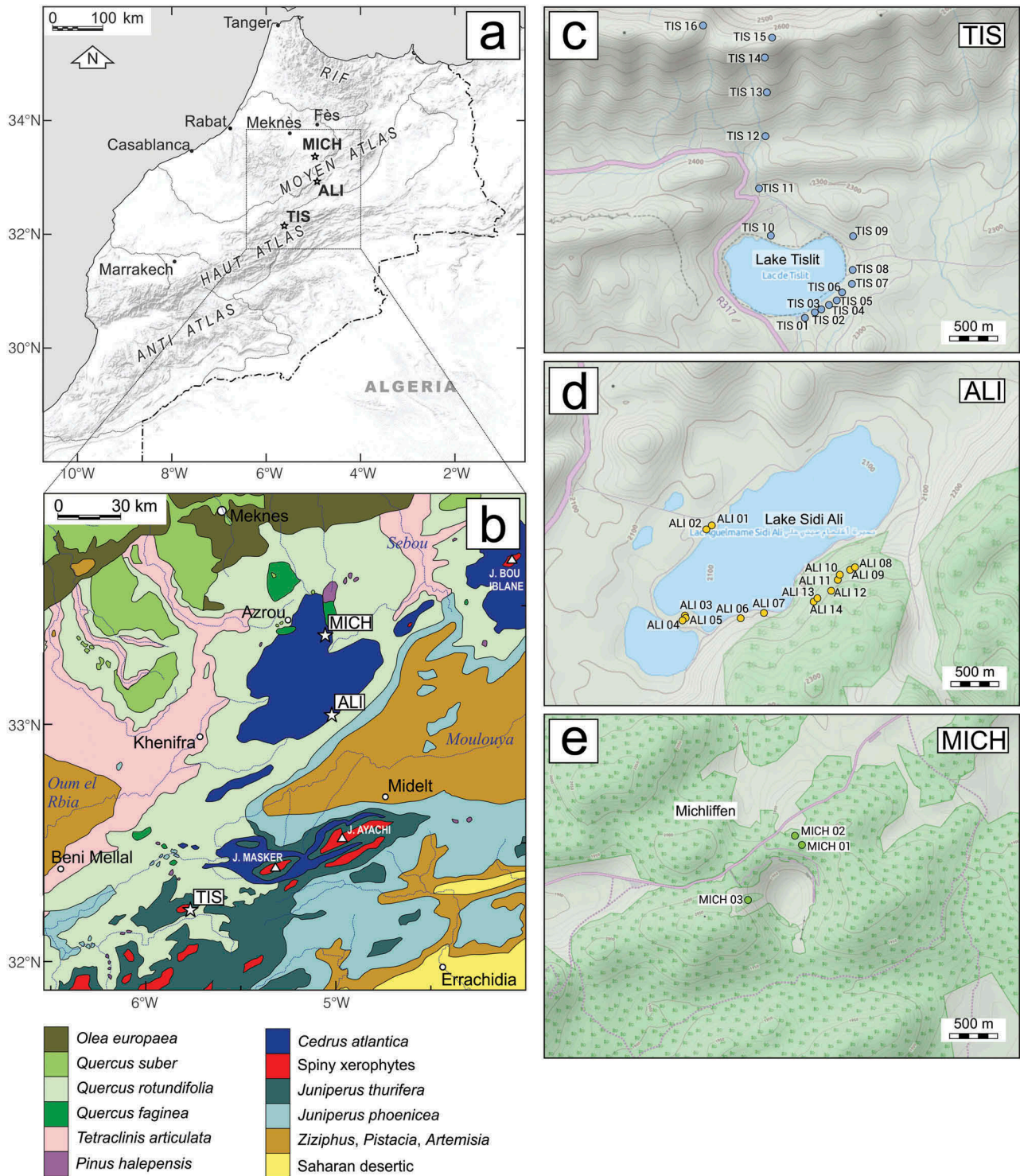


Figure 1. Location of study and sampling sites, and map of vegetation. **A.** Overview map of Morocco showing location of study sites. **B.** Map of dominant vegetation types for the study area based on Emberger (1939). **C.** Map of sample sites around Lake Tislit. **D.** Map of samples sites around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

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 trees

(*Pinus halepensis* Mill. and *Populus* sp.) around the western margin of the lake. Tree cover with *J. thurifera* and *Quercus rotundifolia* is developed at around 20 km distance across the watershed to the





Figure 2. Sample site photographs 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.

northwest on Atlantic (northwest) 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.** — 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 (2080 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 to 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 (January, August) of 2.5 °C and 19.7 °C, respectively (Sayad et al. 2011). Mountain ridges form 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 years 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 yet appear to be widespread establishment of young trees in the area. The surrounding vegetation is a mix of scrub and forest (Figure 2D–F; Morgan 1982; Lecompte 1986). 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.

et Dureiu. The lake is a popular tourist spot and the area is subject to extensive animal grazing.

**Middle Atlas Mountains: 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.), 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 & Melis 2009). 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 macaques (*Macaca sylvanus* L.). 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 *C. atlantica*.

#### Field sampling

Soil surface samples were collected from 33 sites across the study locations in 10 m × 10 m quadrats. Five evenly spaced subsamples (x-pattern) were taken from each quadrat from the top soil (5 mm depth) and leaf litter and combined following Adam and Mehringer (1975) to ensure a well-mixed sample representing an integrated signal of the local pollen rain over the 100 m<sup>2</sup> sampling area and several pollination seasons. Vegetation found in each quadrat was recorded as a presence/absence survey (Table AI), and visual estimates of ground cover and canopy cover recorded (Table I). 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 01–10) at altitudes of 2250 to 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 I). 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 (ALI 01–05) 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 of 2180 to 2200 m a.s.l. on calcareous substrates (Figure 1D). The three MICH sample sites span the lower slopes (MICH 01, 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 three hours and further weighed to calculate organic matter content as a percentage of dry weight.

Pollen samples were prepared from subsamples of 1 cm<sup>3</sup> 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 highly 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× and 1000× magnification. Reference material (Reille 1992a, 1995; Beug 2004) 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 (Table AII). Correspondence analysis (CA) (e.g. Hill 1974), 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 European Modern Pollen Database (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.



Table I. 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 (5 cm) 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           |

## Results

### *Characteristics of the soil surface samples*

Total organic content of the surface samples ranges from < 4% to 22% in the High Atlas, and from 12% to 61% in the Middle Atlas; total pollen content of the surface samples ranges from  $1.1 \times 10^4$  to  $4.7 \times 10^5$  grains per  $\text{cm}^3$  (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 Michlif-fen. 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  $10 \text{ m} \times 10 \text{ m}$  sampling frame ( $R = 0.63$ ,  $p < 0.001$ ).

### *Characteristics of the pollen spectra*

Concerning AP 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. Cupres-saceae (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 (NAP) 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 *Centaurea nigra*-types (equivalent to *Centaurea jaceae*-type; Beug 2004). A number of other pollen types, including Crasulaceae, *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

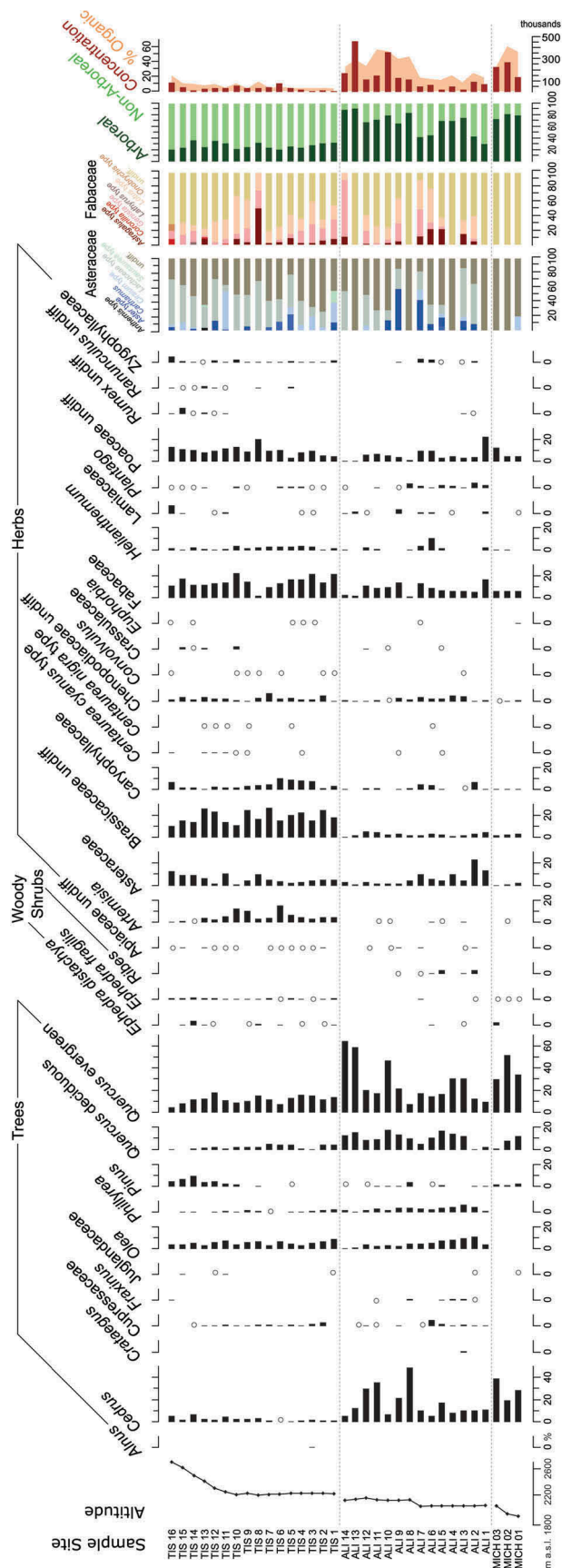


Figure 3. Pollen diagram showing percentage of pollen found for each taxa at each sampling location. Pollen below 0.5% is indicated by an open circle. Total pollen concentration and percentage organic matter is also shown.



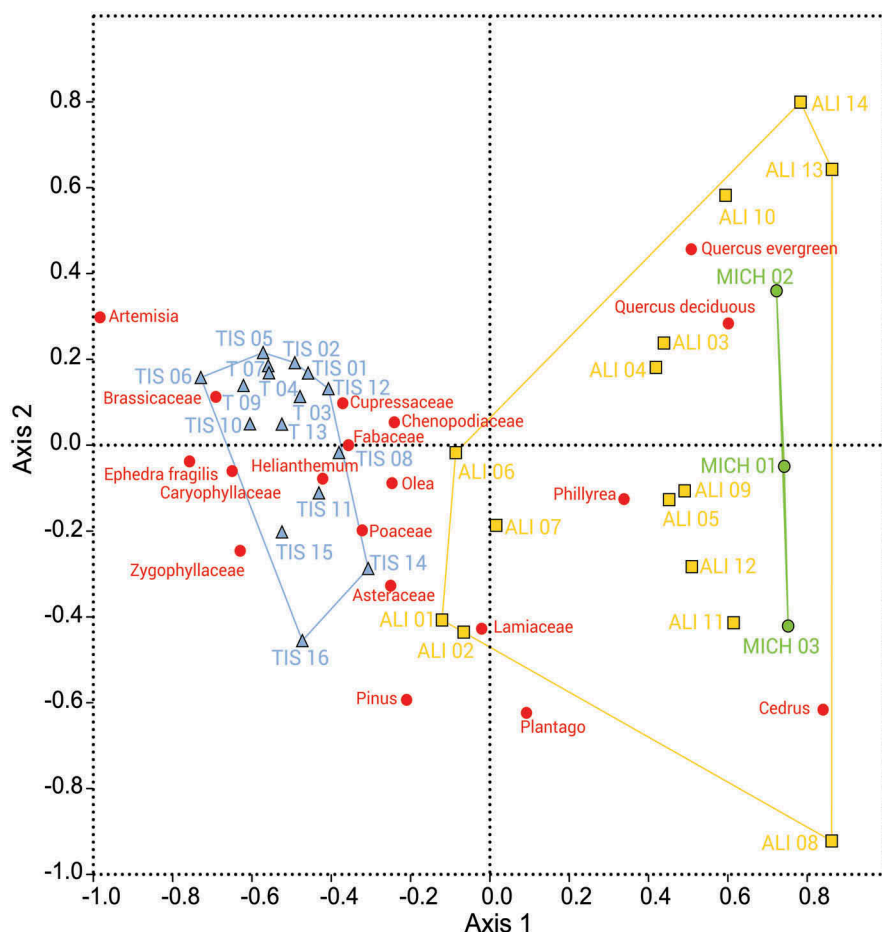


Figure 4. Correspondence analysis (CA) biplot of sample sites and key pollen taxa (those that occurred at 5% or more in at least one sample).

(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 two of the samples. Asteraceae is much more important in the open areas, along with Chenopodiaceae and *Plantago*. There is a large variation in total AP (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% values ( $R = 0.983$ ,  $p < 0.0001$ ) and effectively represent 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 m × 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 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  $> 30$  km 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.

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 versus 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 versus 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 & 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 steppe vegetation of the TIS study area are dominated by NAP types, especially *Artemisia* and other Asteraceae-types, Brassicaceae, Poaceae and Fabaceae, accompanied by Cupressaceae, Caryophyllaceae, *Centaurea cyanus*- and *Centaurea 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 AP abundances across the sites. The main driver for differences reflected in Axis 1 is likely to be macro-climatic 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*

The comparison of the pollen spectra with the basic dataset resulting from the presence/absence survey (Table AI) 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

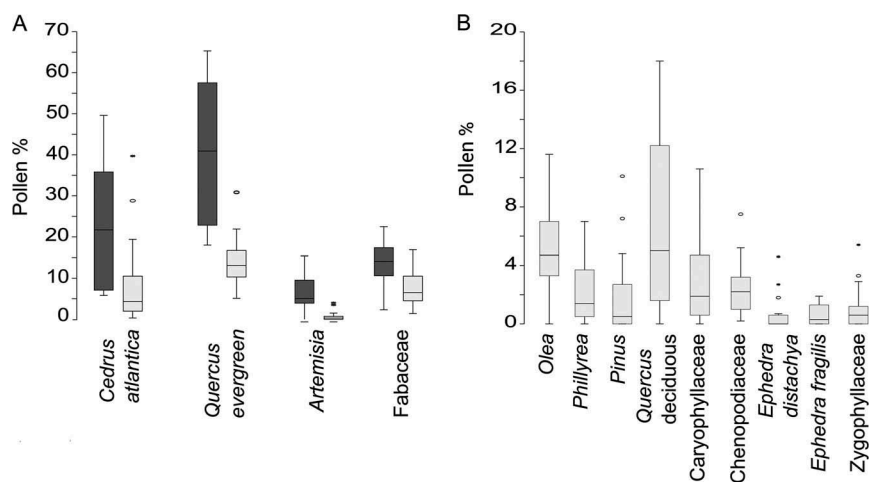


Figure 5. **A.** Box plots showing pollen abundance within a sample where source vegetation was recorded in one or more sampling quadrats (dark grey) versus pollen abundance found in samples where vegetation was not present (light grey) for indicated taxa. **B.** Box plots showing pollen abundance within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

taxa (Figure 5) between the pollen abundance observed where the source vegetation was locally present in the quadrat, compared to pollen abundance where source 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, 2009; Terrab et al. 2006; Fletcher & Sánchez Goñi 2008; 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 5A). 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 *C. 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 5A), 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* versus 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 Late Glacial 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



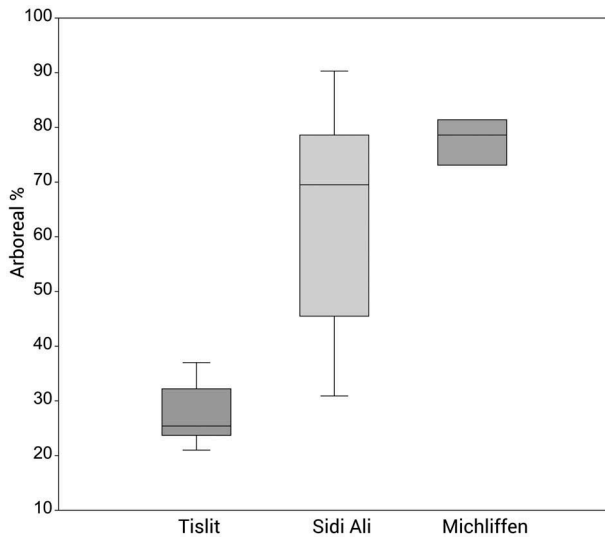


Figure 6. Box plot showing total arboreal pollen percentage at the sample sites grouped by sample location.

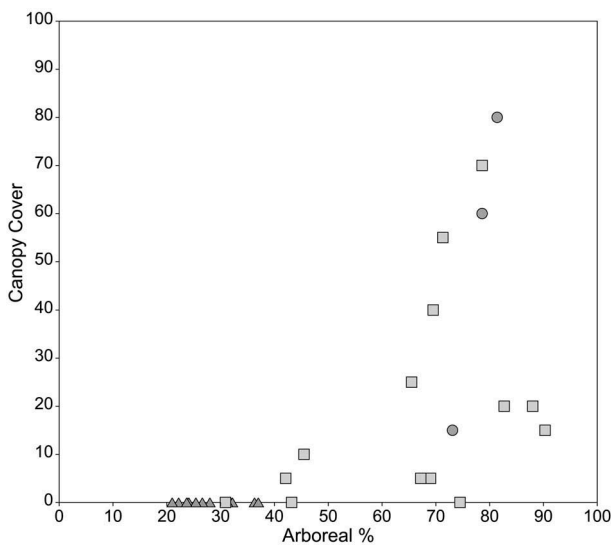


Figure 7. Plot of total arboreal pollen percentage versus canopy cover at the sample sites. Triangles represent Lake Tislit samples, squares represent Lake Sidi Ali samples, circles represent Michliffen samples ( $R = 0.68$ ,  $p < 0.001$ ).

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 *Q. 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  $\sim 12\%$  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 west or northwest. A similar long distance 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 Tisli (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 Tisli. The absence of *Pinus* pollen in samples (TIS 01–07) suggests a complex local pattern with preferential pollen deposition to the north and northeast of the source trees but not towards the east or southeast 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 AP in these samples. Reille (1992b) found *Pinus* was 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, Solomon and 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*

Strong differentiation between the Tisli and Middle Atlas (ALI, MICH) spectra in terms of AP abundance is evident, with values typically below 30% in the Tisli spectra [average = 27.6%, standard deviation (SD) = 5.2] and reaching up to 60–90% in the Sidi Ali (average = 65.6%, SD = 18.3) and Michliffen (average = 77.7%, SD = 4.2) spectra (Figure 6). CA also confirms the importance of AP 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 ( $R = 0.682$ ,  $p < 0.0001$ ) between AP% and canopy cover estimates within the 10 m × 10 m quadrats (i.e. 100 m<sup>2</sup> scale; Figure 7).

Observation of the associated scatterplot highlights several points. AP abundance attains values of 20 to 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), AP 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)] 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 to 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 & Woldring 1990), and remain important for the interpretation of fossil spectra. The positive correlation with canopy cover at the scale of 100 m<sup>2</sup> supports further investigations into relationships between AP and arboreal vegetation cover at a wider range of spatial scales. In the future, this could include regionally-specific calibration of sur-

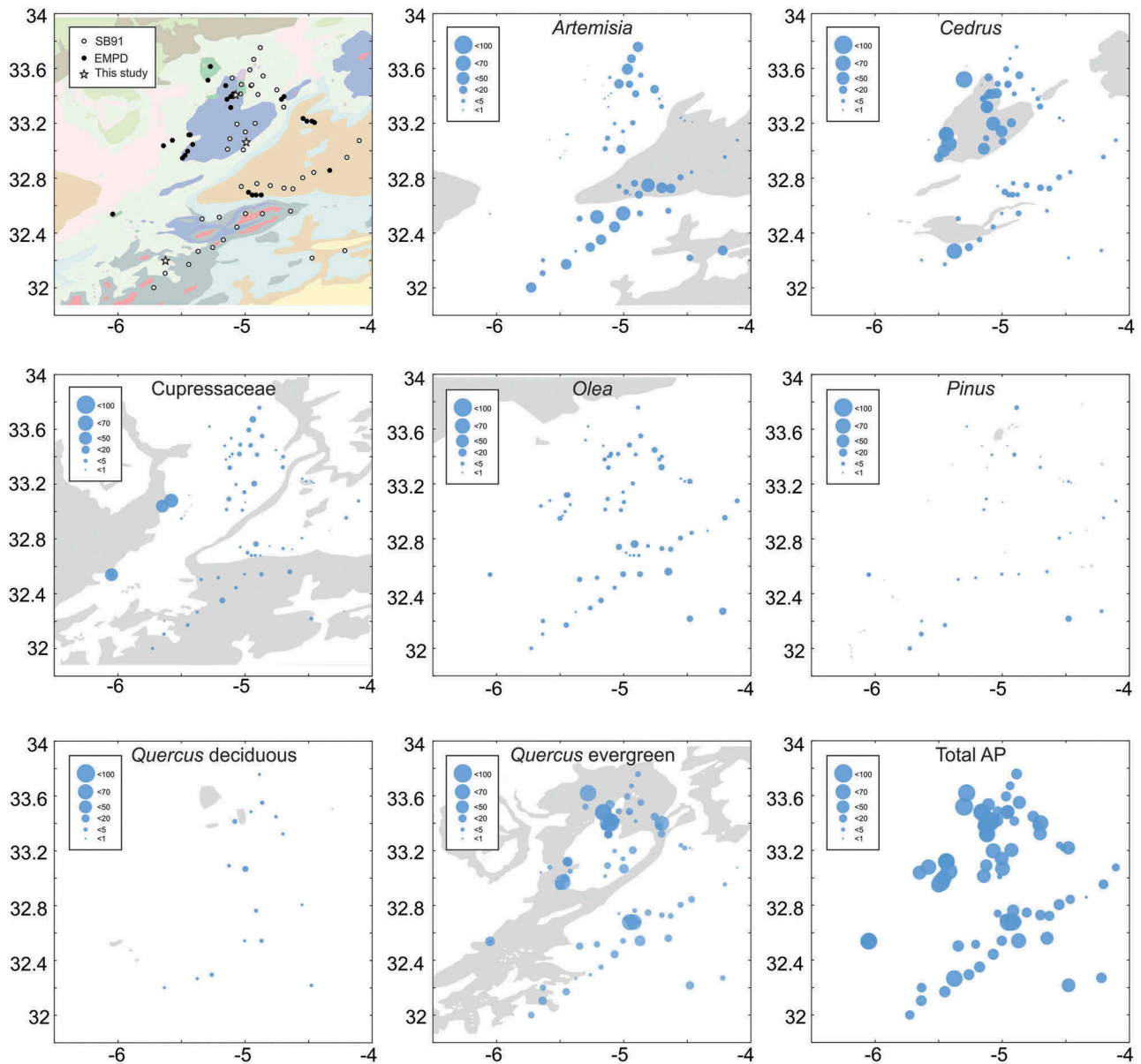


Figure 8. Bubble plots showing percentage of pollen from modern surface samples for indicated species. Location of corresponding vegetation cover shown in grey. EMPD = Data from the European Modern Pollen Database (Davis et al. 2013). SB91 = Data digitised from Saadi and Bernard (1991). Pollen data from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

face pollen spectra versus satellite imagery for reconstruction of arboreal cover (e.g. Jackson & Williams 2004).

#### Comparison with archived surface sample data

The averaged data for TIS, ALI and MICH spectra is placed in the wider geographical context of surface pollen data from the EMPD and SB91 in Figure 8. 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. Cupressaceae, despite the ecological



importance and wide distribution of source taxa [including *Juniperus* spp. and *Tetraclinis articulata* (Vahl) Mast.], 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 twentieth century.

## Conclusion

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 AP abundances, as well as 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 High Atlas (TIS) and Middle Atlas (ALI, MICH) sites is possible (as highlighted, for example, by the CA), 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 *Centaurea nigra*-types, and *Ephedra*-types. Comparing the pollen spec-

tra 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 m × 10 m quadrat. Our results highlight long-distance effects and 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. 2002; 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 (Leipzig University, Leipzig, Germany) and S. Mischke (University of Iceland, Reykjavík, Iceland) with 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). The authors gratefully acknowledge the assistance of Nick Scarle in cartography at the School of Environment, Education and Development, University of Manchester, UK. The authors thank two anonymous reviewers for helpful comments that have improved the final manuscript.

## Supplemental data

Supplemental data for this article can be accessed [here](#).

## Disclosure statement

No potential conflict of interest was reported by the authors.

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## References

- Adam DP, Mehringer Jr PJ. 1975. Modern pollen surface samples – an analysis of subsamples. *Journal of Research of the U.S. Geological Survey* 3: 733–736.
- Akdim B. 2015. Karst landscape and hydrology in Morocco: Research trends and perspectives. *Environmental Earth Sciences* 74: 251–265. doi:10.1007/s12665-015-4254-5.
- Barrow C, Hicham H. 2000. Two complimentary and integrated land uses of the western High Atlas Mountains, Morocco: The potential for sustainable rural livelihoods. *Applied Geography* 20: 369–394. doi:10.1016/S0143-6228(00)00010-2.
- Beug HJ. 2004. Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Munich: Dr Pfeil.
- Bhattacharya T, Beach T, Wahl D. 2011. An analysis of modern pollen rain from the Maya lowlands of northern Belize. *Review of Palaeobotany and Palynology* 164: 109–120. doi:10.1016/j.revpalbo.2010.11.010.
- Birks HJB, Gordon AD. 1985. Numerical methods in Quaternary pollen analysis. San Diego: Academic Press.
- Born K, Fink AH, Paeth H. 2008. Dry and wet periods in the northwestern Maghreb for present day and future climate conditions. *Meteorologische Zeitschrift* 17: 533–551. doi:10.1127/0941-2948/2008/0313.
- Bottema S, Woldring H. 1990. Anthropogenic indicators in the pollen record of the Eastern Mediterranean. In: *Man's Role in the Shaping of the Eastern Mediterranean Landscape: Proceedings of the Symposium on the Impact of Ancient Man on the Landscape of the Eastern Mediterranean Region & the Near East*: Groningen, The Netherlands, 6–9 March 1989. Rotterdam: Balkema.
- Bradshaw RHW. 1981. Modern pollen-representation factors for woods in south-east England. *Journal of Ecology* 69: 45–70. doi:10.2307/2259815.
- Broström A, Nielsen AB, Gaillard M-J, Hjelle K, Mazier F, Binney H, Bunting J, Fyfe R, Meltsov V, Poska A, Räsänen S, Soepboer W, Von Stedingk H, Suutari H, Sugita S. 2008. Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: A review. *Vegetation History and Archaeobotany* 17: 461–478. doi:10.1007/s00334-008-0148-8.
- Canellas-Bolta N, Rull V, Vigo J, Mercader A. 2009. Modern pollen-vegetation relationships along an altitudinal transect in the central Pyrenees (southwestern Europe). *The Holocene* 19: 1185–1200. doi:10.1177/0959683609345082.
- Chaabout S, Chennaoui Aoudjehane H, Reimold WU, Aboulahris M, Aoudjehane M. 2013. Evidence of non-impact cratering origin of Imilchil (Morocco) Lakes (Isli and Tislit). *Proceedings of the Large Meteorite Impacts and Planetary Evolution V Conference*, Sudbury, Canada, 5–8 August 2013, 3074.
- Cheddadi R, Fady B, François L, Hajar L, Suc J-P, Huang K, Demarteau M, Vendramin GG, Ortu E. 2009. Putative glacial refugia of *Cedrus atlantica* deduced from Quaternary pollen records and modern genetic diversity. *Journal of Biogeography* 36: 1361–1371. doi:10.1111/jbi.2009.36.issue-7.
- Cheddadi R, Lamb HF, Guiot J, Van der Kaars S. 1998. Holocene climatic change in Morocco: A quantitative reconstruction from pollen data. *Climate Dynamics* 14: 883–890. doi:10.1007/s003820050262.
- Cheddadi R, Rossignol-Strick M. 1995. Improved preservation of organic matter and pollen in eastern Mediterranean sapropels. *Paleoceanography* 10: 301–309. doi:10.1029/94PA02673.
- Davis BAS, Zanon M, Collins P, Mauri A, Bakker J, Barboni D, Barthelmes A, Beaudouin C, Bjune AE, Bozilova E, Bradshaw RHW, Brayshay BA, Brewer S, Brugiapaglia E, Bunting J, Connor SE, De Beaulieu JL, Edwards K, Ejarque A, Fall P, Florenzano A, Fyfe R, Galop D, Giardini M, Giesecke T, Grant MJ, Guiot J, Jahns S, Jankovská V, Juggins S, Kahrmann M, Karpińska-Kolaczek M, Kolaczek P, Kühl N, Kuneš P, Lapteva EG, Leroy SAG, Leydet M, Guiot J, López Sáez JA, Masi A, Matthias I, Mazier F, Meltsov V, Mercuri AM, Miras Y, Mitchell FJG, Morris JL, Naughton F, Nielsen AB, Novenko E, Odgaard B, Ortu E, Overballe-Petersen MV, Pardoe HS, Peglar SM, Pidek IA, Sadori L, Seppä H, Severova E, Shaw H, Święta-Musznicka J, Theuerkauf M, Tonkov S, Veski S, Van der Knaap SO, Van Leeuwen JFN, Woodbridge J, Zimny M, Kaplan JO. 2013. The European Modern Pollen Database (EMPD) project. *Vegetation History and Archaeobotany* 22: 521–530. doi:10.1007/s00334-012-0388-5.
- Davis MB, Goodlett JC. 1960. Comparison of the present vegetation with pollen-spectra in surface samples from Brownington Pond, Vermont. *Ecology* 41: 346–357. doi:10.2307/1930226.
- Davis OK. 1984. Pollen frequencies reflect vegetation patterns in a great basin (U.S.A.) mountain range. *Review of Palaeobotany and Palynology* 40: 295–315. doi:10.1016/0034-6667(84)90013-7.
- Dean WE. 1974. Determination of carbonate and organic-matter in calcareous sediments and sedimentary rocks by loss on ignition: Comparison with other methods. *Journal of Sedimentary Petrology* 44: 242–248.
- Emberger L. 1939. *Aperçu général sur la végétation du Maroc: Commentaire de la carte phytogéographique du Maroc* 1:1500000. Berne: Huber.
- Erdtman G. 1943. *An Introduction to pollen analysis*. Waltham, MA: Chronica Botanica.
- Erdtman G. 1960. The acetolysis method. A revised description. *Svensk Botanisk Tidskrift* 54: 561–564.
- Fægri K, Iversen J. 1950. *Text-book of modern pollen analysis*. Copenhagen: Munksgaard.
- Fall PL. 2012. Modern vegetation, pollen and climate relationships on the Mediterranean island of Cyprus. *Review of Palaeobotany and Palynology* 185: 79–92. doi:10.1016/j.revpalbo.2012.08.002.
- Fink AH, Born CM, Bruecher T, Piecha K, Pohle S, Schulz O, Ermert V. 2010. Climate. In: Speth P, Christoph M, Dieckruger B, eds. *Impacts of global change on the hydrological cycle in west and northwest Africa*, 54–58. Heidelberg: Springer.
- Fletcher W, Sánchez Goñi MF. 2008. Orbital- and sub-orbital-scale climate impacts on vegetation of the western Mediterranean basin over the last 48,000 yr. *Quaternary Research* 70: 451–464. doi:10.1016/j.yqres.2008.07.002.
- Gaillard M-J, Birks HJB, Emanuelsson U, Karlsson S, Lagerås P, Olausson D. 1994. Application of modern pollen/land-use relationships to the interpretation of pollen diagrams – reconstructions of land-use history in south Sweden, 3000–0 BP. *Review of Palaeobotany and Palynology* 82: 47–73. doi:10.1016/0034-6667(94)90019-1.
- Giorgi F. 2006. Climate change hot-spots. *Geophysical Research Letters* 33: L08707. doi:10.1029/2006GL025734.
- Guimarães JTF, Souza-Filho PWM, Alves R, De Souza EB, Da Costa FR, Reis LS, Prafulla KS, Sahoo PK, De Oliveira Manes C-L, Junior ROS, Oti D, Dall'Agnol R. 2014. Source and distribution of pollen and spores in surface sediments of a plateau lake in southeastern Amazonia. *Quaternary International* 352: 181–196. doi:10.1016/j.quaint.2014.06.004.
- Haroni SA, Alifriqui M, Ouhammou A. 2009. La diversité floristique des pelouses humides d'altitude: Cas de quelques sites du Haut Atlas Marocain. *Acta Botanica Malacitan* 3: 91–106.
- Hicks S. 2001. The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal. *Review of Palaeobotany and Palynology* 117: 1–29. doi:10.1016/S0034-6667(01)00074-4.

- Hill M. 1974. Correspondence analysis: A neglected multivariate method. *Applied statistics* 23: 340–354.
- Ibhi A, Nachit H, Abia EH, Touchnt AA, Vaccaro C. 2013. Isli and Tislit: The first dual impact crater discovered in Morocco. *International Journal of Astronomy and Astrophysics* 3: 1–4. doi:10.4236/ijaa.2013.32A001.
- Jackson ST, Williams JW. 2004. Modern analogs in Quaternary paleoecology: Here today, gone yesterday, gone tomorrow? *Annual Review of Earth and Planetary Sciences* 32: 495–537. doi:10.1146/annurev.earth.32.101802.120435.
- Khanduri VP, Sharma CM. 2009. Cyclic pollen production in *Cedrus deodara*. *Sexual Plant Reproduction* 22: 53–61. doi:10.1007/s00497-008-0091-y.
- Lamb H, Eicher U, Switsur V. 1989. An 18,000-year record of vegetation, lake-level and climatic change from Tigalmamine, Middle Atlas, Morocco. *Journal of Biogeography* 16: 65–74. doi:10.2307/2845311.
- Lamb HF, Damblon F, Maxted W. 1991. Human impact on the vegetation of the Middle Atlas, Morocco, during the last 5000 years. *Journal of Biogeography* 18: 519–532. doi:10.2307/2845688.
- Lamb HF, Duigan CA, Gee JHR, Kelts K, Lister G, Maxted RW, Merzouk A, Niessen F, Tahiri M, Whittington RJ, Zeroual E. 1994. Sedimentation in a high-altitude, semi-arid environment: The palaeolimnological record of Lake Isli, High Atlas, Morocco. In: Millington AC, Pye K, eds. *Environmental change in drylands: Biogeographical and geomorphological perspectives*, 147–161. London: Wiley.
- Lamb HF, Roberts N, Leng M, Barker P, Benkaddour A, Van der Kaars S. 1999. Lake evolution in a semi-arid montane environment: Responses to catchment change and hydroclimatic variation. *Journal of Paleolimnology* 21: 325–343. doi:10.1023/A:1008099602205.
- Lamb HF, Van der Kaars S. 1995. Vegetational response to Holocene climatic change: Pollen and palaeolimnological data from the Middle Atlas, Morocco. *The Holocene* 5: 400–408. doi:10.1177/095968369500500402.
- Lecompte M. 1986. *Biogéographie de la montagne marocaine: Le Moyen-Atlas central*. Paris: Éditions du Centre National de la Recherche Scientifique.
- Markgraf V. 1980. Pollen dispersal in a mountain area. *Grana* 19: 127–146. doi:10.1080/00171318009424995.
- Moore PD, Webb JA, Collison ME. 1991. *Pollen analysis*. Oxford: Blackwell.
- Morgan NC. 1982. An ecological survey of standing waters in North West Africa: II. Site descriptions for Tunisia and Algeria. *Biological Conservation* 24: 83–113. doi:10.1016/0006-3207(82)90062-3.
- Nakagawa T, Brugiapaglia E, Digerfeldt G, Reille M, Beaulieu J-L, Yasuda Y. 2008. Dense-media separation as a more efficient pollen extraction method for use with organic sediment/deposit samples: Comparison with the conventional method. *Boreas* 27: 15–24. doi:10.1111/bor.1998.27.issue-1.
- Navarro T, Oualidi JEL, Taleb M, Pascual V, Cabezu B. 2009. Dispersal traits and dispersal patterns in an oro-Mediterranean thorn cushion plant formation of the eastern High Atlas, Morocco. *Flora* 204: 658–672. doi:10.1016/j.flora.2008.08.005.
- Hammer Ø, Harper D, Ryan P. 2001. *Past: Paleontological Statistics Software Package for education and data analysis*. *Palaeontologia Electronica* 4: 1–9.
- Peyron M. 1980. Les chutes de neige dans l'Atlas marocain. *Revue de Géographie Alpine* 68: 237–254. doi:10.3406/rga.1980.2203.
- Prentice IC. 1985. Pollen representation, source area, and basin size: Toward a unified theory of pollen analysis. *Quaternary Research* 23: 76–86. doi:10.1016/0033-5894(85)90073-0.
- Quezel P. 2002. *Reflexions sur l'évolution de la flore et de la végétation au Maghreb méditerranéen*. Paris: Ibis Press.
- Reille M. 1992a. *Pollen et spores d'Europe et d'Afrique du Nord*. Marseille: Laboratoire de Botanique Historique et Palynologie.
- Reille M. 1992b. New pollen-analytical researches in Corsica: The problem of *Quercus ilex* L. and *Erica arborea* L., the origin of *Pinus halepensis* Miller forests. *New Phytologist* 122: 359–378. doi:10.1111/nph.1992.122.issue-2.
- Reille M. 1995. *Pollen et spores d'Europe et d'Afrique du Nord*, Supplement 1. Marseille: Laboratoire de Botanique Historique et Palynologie.
- Rhanem M. 2011. Aridification du climat régional et remontée de la limite inférieure du cèdre de l'Atlas (*Cedrus atlantica* Manetti) aux confins de la plaine de Midelt (Maroc). *Physio-Géo* 5: 143–165.
- Ritchie JC. 1995. Current trends in studies of long-term plant community dynamics. *New Phytologist* 130: 469–494. doi:10.1111/nph.1995.130.issue-4.
- Rognon P. 1987. Late Quaternary climatic reconstruction for the Maghreb (North Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology* 58: 11–34. doi:10.1016/0031-0182(87)90003-4.
- Saadi F, Bernard J. 1991. Rapport entre la pluie pollinique actuelle, le climat et la végétation dans les steppes à *Artemisia* et les milieux limitrophes au Maroc. *Palaeoecology of Africa and the Surrounding Islands* 22: 67–86.
- Salamani M. 1993. Premières données paléophytogéographiques du cèdre de l'Atlas (*Cedrus atlantica*) dans la région de Grande Kabylie (NE Algérie). *Palynosciences* 2: 123–130.
- Sayad A, Chakiri S, Martin C, Bejjaji Z, Echarfaoui H. 2011. Effet des conditions climatiques sur le niveau du lac Sidi Ali (Moyen Atlas, Maroc). *Physio-Géo* 5: 251–268.
- Solomon AM, Silkworth AB. 1986. Spatial patterns of atmospheric pollen transport in a montane region. *Quaternary Research* 25: 150–162. doi:10.1016/0033-5894(86)90053-0.
- Solomon S, Plattner G-K, Knutti R, Friedlingstein P. 2009. Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences of the United States of America* 106: 1704–1709. doi:10.1073/pnas.0812721106.
- Stockmarr J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores* 13: 615–621.
- Sugita S. 1994. A model of pollen source area for an entire basin. *Review of Palaeobotany and Palynology* 82: 194. doi:10.1016/0034-6667(94)90034-5.
- Tauber H. 1965. *Differential pollen dispersion and the interpretation of pollen diagrams, with a contribution to the interpretation of the elm fall*. Copenhagen: Reitzels Forlag.
- Terrab A, Paun O, Talavera S, Tremetsberger K, Arista M, Stuessy TF. 2006. Genetic diversity and population structure in natural populations of Moroccan Atlas cedar (*Cedrus atlantica*; Pinaceae) determined with *cpSSR* markers. *American Journal of Botany* 93: 1274–1280. doi:10.3732/ajb.93.9.1274.
- Waele J, Melis MT. 2009. Geomorphology and geomorphological heritage of the Ifrane-Azrou region (Middle Atlas, Morocco). *Environmental Geology* 58: 587–599. doi:10.1007/s00254-008-1533-4.
- Weng C, Bush MB, Silman MR. 2004. An analysis of modern pollen rain on an elevational gradient in southern Peru. *Journal of Tropical Ecology* 20: 113–124.
- Wright HE. 1967. The use of surface samples in Quaternary pollen analysis. *Review of Palaeobotany and Palynology* 2: 321–330. doi:10.1016/0034-6667(67)90162-5.
- Wright HE, McAndrews J, Van Zeist W. 1967. Modern pollen rain in western Iran, and its relation to plant geography and Quaternary vegetational history. *The Journal of Ecology* 55: 415–443. doi:10.2307/2257886.
- Yu G, Tang L, Yang X, Ke X, Harrison SP. 2002. Modern pollen samples from alpine vegetation on the Tibetan Plateau. *Global Ecology and Biogeography* 10: 503–519. doi:10.1046/j.1466-822X.2001.00258.x.