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## Holocene history of peatland communities of central Rif (Northern Morocco)

Serge D. Muller <sup>a,\*</sup>, Amina Daoud-Bouattour <sup>b,c</sup>, Séverine Fauquette <sup>a</sup>, Marion Bottollier-Curtet <sup>d</sup>, Nabil Rifai <sup>e</sup>, Mary Robles <sup>a</sup>, Er-Riyahi Saber <sup>f</sup>, Mohammed El Madihi <sup>g,h</sup>, Saïd Moukrim <sup>g</sup>, Laila Rhazi <sup>g</sup>

<sup>a</sup> Institut des Sciences de l'Évolution (ISEM), Univ. Montpellier, CNRS, IRD, EPHE, 34095 Montpellier cedex 05, France

<sup>b</sup> Département de Biologie, Faculté des Sciences de Tunis, Université Tunis El-Manar, 2092 Tunis, Tunisia

<sup>c</sup> LR18ES13 Biogéographie, Climatologie appliquée et Dynamiques environnementales, Faculté des Lettres, des Arts et des Humanités de Manouba, Université de la Manouba, 2010 Manouba, Tunisia

<sup>d</sup> Les Écologistes de l'Euzière, Domaine de Restinclières, 34730 Prades-le-Lez, France

<sup>e</sup> Département des Eaux et Forêts, 3 rue Harroun Errachid–Agdal, Rabat, Morocco

<sup>f</sup> Département de Géographie, Faculté des Lettres et Sciences Humaines, Université Moulay Ismail, BP 11202, Zitoune Meknès, Morocco

<sup>g</sup> Université Mohammed V de Rabat, Faculté des Sciences, Centre de Recherche Biotechnologies Végétale et Microbienne, Biodiversité et Environnement, 4 avenue Ibn Battouta BP 1014 RP, Rabat, Morocco

<sup>h</sup> Institut de recherche pour la conservation des zones humides méditerranéennes, Tour du Valat, Le Sambuc, 13 200 Arles, France

\* *Corresponding author. E-mail address: [serge.muller@umontpellier.fr](mailto:serge.muller@umontpellier.fr) (S.D. Muller).*

### Abstract

The Maghreb's Mediterranean coastal edge is home to many peatlands with boreal floristic affinities and high conservation value. The work aims at investigating the Holocene developmental history of these wetlands in Northern Morocco, based on pollen record, loss-on-ignition and radiocarbon dating. First, the comparison between modern pollen spectra and present-day hydrophytic vegetation makes it possible to identify the local pollen signal. Second, while peatlands have existed in the Rif for at least 13,000 years, their initiation mostly by paludification extends throughout the Holocene. Their plant composition remains relatively unchanged for millennia, but swamp undergrowth could locally experience changes in taxa dominance. Mid- to late-Holocene sedimentation changes appear to result from the human-induced regional decline of cedar. The major changes experienced by wetlands occurred recently, due to clearing, burning and overgrazing. Effective conservation policies should be urgently implemented in order to save the last relict peatlands of Northern Morocco.

**Keywords:** Late Quaternary – Pollen – Maghreb – Mediterranean Wetland – Anthropisation - Conservation

## 1. Introduction

The Mediterranean coastal fringe of the Maghreb is home to peatlands with boreal vegetation affinities, located at the rear edge of their main distribution area, which extends from Mediterranean mountains to Scandinavia (Joosten et al., 2017). These peat-forming wetlands are located in the wettest northern regions of the Maghreb (Fig. 1(A)): (1) in Morocco, the Loukkos Valley close to Larache and the Jebala Range of the Rif; (2) in Algeria, the high coastal reliefs from Edough to Akfadou, and the sandy coastal complexes of El Kala National Park and Guerbès-Senhadja; and (3) in Tunisia, the Kroumiria mountain range and the hill region of Mogods. These regions are all included in biodiversity hotspots: the Betic-Rifan complex in the west (Médail and Quézel, 1999) and the Kabylies-Numidia-Kroumiria complex in the east (Véla and Benhouhou, 2007).

North African peatland habitats include alder swamps that occur in the three countries of the Maghreb (Meddour and Laribi, 1999), *Sphagnum* fens that are particularly developed in Northern Morocco (Dahlgren and Lassen, 1972; Muller et al., 2010, 2011), and peaty heathlands of *Erica scoparia* that are known in Northern Tunisia (Ferchichi-Ben Jamaa et al., 2010) and were recently identified as an ancient, long-living community in Northeastern Algeria (Ghit et al., 2018). Despite the unquestionable ecological, biogeographical and economic values of these habitats (e.g. Bragg and Lindsay, 2003; Andersen et al., 2016), very few dedicated palaeoecological studies focus on the Mediterranean region. Whereas North African peatlands have long been studied in order to reconstruct past regional vegetation dynamics (Reille, 1977; Ben Tiba and Reille, 1982; Damblon, 1991; Salamani, 1991, 1993; Stambouli-Essassi et al., 2007; Benslama et al., 2010; Muller et al., 2015), their own vegetation and sedimentation dynamics have only been investigated in Northeastern Algeria (Ghit et al., 2018). As a result, the Holocene origin and history of North African peatlands and swamps are virtually entirely unknown.

The study of Reille (1977) provides a number of pollen diagrams for the Jebala Range (Rif, Morocco). These diagrams, while poorly dated, contain valuable information about the past local vegetation of the studied wetlands, and raises some questions. In particular, one intriguing feature of these diagrams is the heterogeneous record of cereal-type pollen that is high (5-10%) and almost continuous in some sites, but not in others. While noting that this pollen type includes also wild taxa, Reille (1977) interpreted the high percentages found at the base of the pollen diagram of Bartete (initially named Arbatète), as translating an ancient cultural episode. This interpretation agrees with recent findings (Ballouche and Marinval, 2003; Zielhofer and Linstädter, 2006; Zapata et al., 2013), but poses a problem with respect to another record in a site located 1200 m away, on the same aspect (Muller et al., 2015).

The present study aims at (1) characterising the pollen record of wetland plant communities of the Jebala Range and (2) reconstructing the origin and past history of the peat-forming wetlands of Rif. First, we established a model of pollen representation of peat-forming plant communities based on surface pollen data and associated phytosociological relevés, both collected in various regional wetlands representing all the regional wetland habitats. In addition, a biometric study of selected Poaceae pollen was undertaken in order to resolve the problem of the long-term cereal-type pollen record of Reille (1977). Second, this present-day model was used to interpret past local pollen records from Reille (1977) and from two new cores taken from Jbel Bou Hachem, the main relief of Jebala Range.

## 2. Material and methods

### 2.1. Geographical, geological and biogeographical setting

The Rif mountain range, which forms the Gibraltar Arc with the Betic Range, began to rise during the Oligocene from the convergence of Africa and Europe (Chalouan et al., 2008). From the northeast to the southwest (Romagny et al., 2014), it includes the following:

- an internal zone along the Mediterranean coast consisting essentially of more or less metamorphosed continental basement (Sebtides and Ghomarides nappes) and sedimentary covers composed of limestone rock (the so-called Rif Dorsal);
- the Maghrebien Flysch Basin Units comprising a nappe stack of predominantly turbiditic deposits that constitute the Jebala Range;
- an external zone corresponding to Triassic to Miocene formations of the African palaeomargin that was folded and thrust up during the Miocene collision.

Our samples come from the Jebala Range, where Jbel Bou Hachem, located northwest of Chefchaouen, constitutes the highest relief (1602 m asl; Fig. 1(B)). The major phytogeographic interest of this massif (Sauvage, 1958) in terms of forest diversity and wetland abundance, including remarkable *Sphagnum* fens (Dahlgren and Lassen, 1972; Muller et al., 2011), led to it being named a Site of Biological and Ecological Interest (SBEI) in 1996 and an Important Plant Area (IPA) in 2004, and its inclusion in the Intercontinental Mediterranean Biosphere Reserve (IMBR) in 2006 (Benabid, 2000; Taleb and Fennane, 2011).

Characterised by a humid to sub-humid bioclimate, the Rif harbours a variety of fragmentary forest ecosystems (Sauvage, 1958; Benabid, 2000; Ajbilou et al., 2006), organised in mosaic with deforested zones mainly occupied by Mediterranean scrublands (matorrals), degraded therophytic meadows and cultivated lands, including the production of kif (*Cannabis sativa*), whose expansion is provoking an on-going forest decline (Quézel and Barbero, 1990; Taiqui, 1997).

### 2.2. Study sites and fieldwork

Vegetation surveys, systematically associated with surface sediment sampling, were conducted in May 2010 and June 2012 on 13 wetlands located on 4 reliefs of the Jebala Range (Fig. 1(B); Table 1). All sites lay on sandstone with the exception of DAY2, which sits on limestone at the boundary between the Jebala Range and the Rif Dorsal. The botanical nomenclature follows Fennane et al. (1999, 2007, 2014), Dobignard and Chatelain (2010-2013) and Le Floc'h et al. (2010).

New sediment cores (Fig. 1(B)) were taken from three wetlands (BAR, 248 cm; MF1b, 132 cm; MF3, 530 cm) with a 50 x 5 cm Russian sampler, and conserved in plastic film until sampling in the laboratory. BAR (*Bartete*) is a cultivated peaty meadow on a flat, gently sloping surface at the head of a watershed. The site was previously studied as '*Daya Arbatète*' by Reille (1977), who postulated a pollen-based Early Holocene age for basal sediment layers and found high Cereal-type pollen percentages that he interpreted as ancient cultural episodes. MF1 (*Maison Forestière-1*) is a roughly circular fen of 0.2 ha, located 300 m below the Bou Hachem forest house and covered by a continuous *Sphagnum* carpet. MF3 (*Maison Forestière-3*), located 1200 m north of MF1, includes a highly degraded alder swamp and a pond covered by aquatic floating plants. Both sites are neither cultivated nor

drained, but they are overgrazed by cows and sheeps. This site was previously studied under the name ‘*Mare à sphaignes du jbel Bou Hachem*’ by Reille (1977). MF1 and MF3 surroundings are currently dominated by bracken (*Pteridium aquilinum*), the zeen oak (*Quercus canariensis*) forest having been cut down in the early 2000s.

### 2.3. Laboratory work and data analysis

**Modern samples study.** After chemical treatment (Berglund and Ralska-Jasiewiczowa, 1986) including a 36-hour digestion with 70% hydrofluoric acid, the 13 surface sediments were used to identify the local pollen signal and the local pollen indicators, based on a comparison with floristic relevés. Pollen slides were mounted in glycerol. Ascendant hierarchical classifications (AHC) were carried out on phytosociological relevés comprising 13 sites and 149 taxa, using the Paired Group Clustering (UPGMA) and the Chord distance with Past 4.03 (Hammer et al., 2001).

**Palaeoecological study.** First, we took 1-cm<sup>3</sup> samples every 2 cm for loss-on-ignition (LOI) on the three studied cores (BAR, MF1b and MF3). LOI measurements were made by re-weighing the samples after five hours at 550°C in an oven (Heiri et al., 2001). Second, we took 1-cm<sup>3</sup> samples every 2 cm for pollen analysis on MF1b and MF3 cores. Palynological analyses of sediments were completed after chemical treatments (see above). Pollen percentages were based on sums excluding Pteridophyte spores and the most over-represented tree taxa (*Alnus*, *Quercus canariensis*-type) to reveal local plant dynamics. Total pollen sums exceed 500 grains, except for some poor levels. Pollen nomenclature follows Birks and Birks (1980) and Faegri and Iversen (1989). Pollen diagrams were constructed with R-Rioja package 0.9-26 (Juggins, 2020), and zonation was realised with the program Coniss (Grimm, 1987).

In order to compare our new palynological data with the ones of Reille (1977), we homogenized the pollen nomenclature, and calculated the percentages on the same basis. We also realized and radiocarbon-dated a new core in the Bartete peatland in order to provide a chronological framework to the undated Reille (1977)’s diagram. The new core was collected in the same area than the Reille (1977)’s one, according to the provided map: both cores measure the same length and their composition are very similar.

**Representation indices.** Indices of association (A), under-representation (U) and over-representation (O) were calculated using presence/absence data from the vegetation survey (Davis, 1984; Hjelle, 1997; Bunting, 2003). These indices (here given as percentages) are defined as follows:

- $A = B0 * 100 / (P0 + P1 + B0)$
- $U = P1 * 100 / (P1 + B0)$
- $O = P0 * 100 / (P0 + B0)$

where B0 is the number of samples in which both the pollen type and its associated plant are present; P0 is the number of samples in which the pollen type is present in the surface sample but not the plant taxa; and P1 is the number of samples in which the pollen type is not present in the surface sample but the plant is present in the vegetation. The representation indices are used for determining the association and representation of each taxon, as follows:

- Strongly associated taxa:  $A > 65\%$ ;

- Associated taxa:  $50\% < A < 65\%$ ;
- Weakly associated taxa: low A values and relatively high values for both U and O;
- Not-associated taxa:  $A = 0$ , and high O and U values;
- Over-represented taxa: low A values, high O values and  $U = 0$ .

Suchéras-Marx et al. (2019) note the recurrent lack of confidence intervals associated with empirical proportions or percentages in micropaleontological studies. Representation indices are effectively usually given without confidence intervals (e.g. Mazier et al., 2006; Brun et al., 2007; Amami et al., 2010). As Davis indices are, up to a factor 100, binomial proportions with, in our case, denominator consistently less than 40, we followed guidelines from Brown et al. (2001) and computed Wilson confidence intervals at level  $\alpha=0.1$ ,  $CI_A$ ,  $CI_U$ , and  $CI_O$  for A, U, and O respectively:

$$CI_A = \frac{B_0 + \kappa^2/2 \pm \kappa \sqrt{B_0 \left(1 - \frac{B_0}{B_0 + P_0 + P_1}\right) + \frac{\kappa^2}{4}}}{B_0 + P_0 + P_1 + \kappa^2}$$

$$CI_U = \frac{P_1 + \kappa^2/2 \pm \kappa \sqrt{P_1 \left(1 - \frac{P_1}{B_0 + P_1}\right) + \frac{\kappa^2}{4}}}{B_0 + P_1 + \kappa^2}$$

$$CI_O = \frac{P_0 + \kappa^2/2 \pm \kappa \sqrt{P_0 \left(1 - \frac{P_0}{B_0 + P_0}\right) + \frac{\kappa^2}{4}}}{B_0 + P_0 + \kappa^2}$$

where  $\kappa = z_{\alpha/2}$ , the  $100(1 - \alpha/2)^{th}$  percentile of the standard normal distribution.

**Dating.** Unfortunately, the sediments contain no macrofossils except some wood charcoals, two of which being identified and radiocarbon-dated. Consequently, the chronology of the three studied cores is based on radiocarbon dating obtained from bulk sediment and macrocharcoal. Calibrated ages (cal. BP, i.e. calendar years before the present) were computed with Calib 8.1.0 (Stuiver and Reimer, 1993) using the calibration dataset IntCal20 (Reimer et al., 2020).

**Habitat typology.** The typology of wetland habitats was based on an ascendant hierarchical classification (paired group clustering, Chord similarity measure) carried out with Past 4.03 (Hammer et al., 2001) and performed on phytosociological relevés (13 sites) comprising only the species encountered at least three times (80 species).

**Biometric data.** Biometric measurements were made on Poaceae pollen slides from the pollen collection of the *Institut des Sciences de l'Evolution, Université de Montpellier*. As noted by Faegri and Iversen (1989), the medium used to mount the observation slides (glycerol or silicone oil) influences grain size. They also note that conversion factors vary between 1.1 and 1.3 for grain size and between 1.1 and 1.5 for pore size (pollen mounted in glycerol being larger than pollen mounted in silicone oil). The pollen collection that was used and all previous published keys except Andersen's (1979) refer to pollen mounted in glycerol. The studied pollen slides are (the number of slides, the collect location and the plant name (when different from the accepted name) are given into square brackets): *Avena barbata* Pott ex Link subsp. *wiestii* (Steud.) Mansf. [20938, Sahara, *A. alba* var. *wiestii*]; *Avena sativa* L. subsp. *sativa* [4502, North America]; *Bromopsis inermis* (Leyss.) Holub subsp. *inermis* [4420, America, *Bromus inermis*]; *Dactylis glomerata* L. [23545, India]; *Elytrigia campestris* (God.



& Gren.) Carreras Martinez [28391, France, *Elymus pungens*]; *Glyceria fluitans* (L.) R.Br. [9092, India; 43407, Corsica]; *Glyceria notata* Chevall. [42804, 42807, Corsica]; *Hordeum brevisubulatum* (Trin.) Link [18973, Iran, *H. turkestanicum*]; *Hordeum vulgare* L. subsp. *distichon* (L.) Körn [42870, 42898, France]; *Leymus condensatus* (J.Presl.) Á.Löve [4504, loc. n.a., *Elymus condensatus*]; *Phragmites australis* (Cav.) Steud. [20828, Portugal, *P. communis*]; *Schedonorus arundinaceus* (Schreb.) Dumort. [30932, France, *Festuca arundinacea*]; *Secale cereale* L. [4164, Poland]; *Thinopyrum elongatum* (Host) D.R.Dewey [28390, Europe, *Elymus elongatus*]; *Triticum aestivum* L. subsp. *aestivum* [33268, France]; *Triticum aestivum* L. subsp. *spelta* (L.) Thell. [23311, France, *T. spelta* var. *arduini*; 23320, Europe, *T. spelta*; 31135, France, *T. spelta*; 31305, France, *T. spelta* var. *coeruleum*]; *Triticum compactum* Host [34465, Europe]; *Triticum turgidum* L. subsp. *dicoccum* (Schrank) Thell. [31130, France, *T. dicoccum*]; *Triticum turgidum* L. subsp. *durum* (Desf.) Husn. [22973, Algeria, *T. durum*; 31313, loc. n.a., *T. durum*; 46850, France, *T. durum* var. *primadur*; 46851, France, *T. durum* var. *arcour*]; *Triticum turgidum* L. subsp. *turgidum* [43408, France]; *Zea mays* L. [46478, USA].

### 3. Results

#### 3.1. Richness and typology of wetland habitats

The vegetation surveys carried out in 13 wetlands of the Jebala Range led to the identification of 148 species, 64 of which encountered only once (Table 2). Floristic richness ranges from 22 to 52; the maximum corresponds to the site MF3 that includes two contiguous habitats (a swamp and a pond). Our data make it possible to distinguish 3 main types of habitats (fen, temporary pond, alder swamp), and 2 less common ones (*Sphagnum* pond, alkaline lake) (Fig. 2):

- **Fens.** The most abundant habitat is represented by fens that accumulate organic clay and occur throughout the Jebala Range: Jbel Bou Hachem (MF1, MF2), Jbel Khezana (ABF, BAR, BAZ) and Jbel Sougna (TANT). These all harbour dense lawns of herbaceous hydrophytic plants (*Baldellia repens*, *Carex distans*, *C. echinata*, *Dactylorhiza maurusia*, *Eleocharis multicaulis*, *Juncus bulbosus*, *Lotus pedunculatus*, *Lysimachia tyrrenia* (= *Anagallis crassifolia*), *Lythrum junceum*, *Myosotis welwitschii*, *Potamogeton polygonifolius*, *Potentilla erecta*, *Silene laeta*), often integrating *Aulacomnium palustre* and *Sphagnum auriculatum* carpets. When present, margins are covered by low scrubs of *Calluna vulgaris*, *Erica ciliaris*, *Genista ancistrocarpa* and *Myrtus communis*.
- **Temporary ponds.** The Mediterranean temporary habitats also occur on the Jebala's three main reliefs: Jbel Bou Hachem (MF3, TAY1), Jbel Khezana (BOU) and Jbel Sougna (MAR), which harbour *Eleocharis palustris*, *Glyceria spicata*, *Isoetes velata* and *Juncus heterophyllus* accompanied by a therophytic community including *Baldellia ranunculoides*, *Callitriche* spp., *Cicendia filiformis*, *Galium palustre* subsp. *elongatum*, *Gratiola mauretanica*, *Helosciadium inundatum*, *Illecebrum verticillatum*, *Juncus bufonius*, *J. pygmaeus*, *Lotus hispidus*, *Lythrum borysthenticum*, *Poa annua*, *Radiola linoides*, *Ranunculus* spp., *Serapias* spp. and *Trifolium* spp.
- **Alder swamps.** Only two relictual alder swamps were found, both of which are located on Jbel Bou Hachem: one is healthy (MF5), while the second is strongly degraded (MF3). *Alnus glutinosa* is associated with *Frangula alnus* subsp. *baetica*, *Hedera helix* subsp.

*maroccana*, *Ilex aquifolium*, *Prunus lusitanica* subsp. *lusitanica*, *Rubus ulmifolius*, *Salix atrocinerea* and *S. pedicellata*, which dominate an undergrowth composed of *Athyrium filix-femina*, *Blechnum spicant*, *Carex remota*, *Lobelia urens*, *Ludwigia palustris*, *Lysimachia tyrrrhenia*, *Potamogeton polygonifolius* and *Potentilla erecta*.

- **Sphagnum pond.** This wetland type is found in only one site, which is located on Jbel Bou Hachem: MF4 lies in a small depression inundated in winter and spring. Carpets of *Sphagnum auriculatum*, which are submerged during part of the year, virtually cover the thin clayey soil. The site also includes *Baldellia ranunculoides*, *Danthonia decumbens*, *Eleocharis* spp., *Exaculum pusillum*, *Gratiola mauretana*, *Juncus bulbosus* and *Potentilla erecta*.
- **Alkaline lake.** The lake of Dayla-2 (DAY2), variously named Anasser (Reille, 1977) and Aanasser (Cheddadi et al., 2015) is located on the southern slope of the Jbel Tizirene, a limestone relief that belongs to the limestone Rifan Dorsal. It harbours a floating mat of high helophytes, including *Phragmites australis*, *Sparganium erectum* and *Typha latifolia*. The associated vegetation is quite different from that encountered in the Jebala Range because of the lack of the strictly calcifuge taxa and the presence of some species not found in the sandstone reliefs (*Carex pseudocyperus*, *Dorycnium rectum*, *Lemna minor*, *Lycopus europaeus*, *Sparganium erectum*, *Typha latifolia*, *Verbena supina*, *Veronica anagalloides*). The lake of Dayla-2 is very close to the lake of Dayla-1 (DAY1) that was studied by Reille (1977) but not sampled here for surface pollen.

### 3.2. Poaceae pollen measurements

The results of the pollen measurements of selected Poaceae species (Table 3) allow distinguishing the following groups (the studied taxa are given into brackets):

- *Zea* (*Zea mays*): grain > 100  $\mu\text{m}$
- *Secale* (*Secale cereale*): grain 60-100  $\mu\text{m}$ , P/E > 1.2, lateral pore
- *Triticum* (*Triticum aestivum* subsp. *aestivum*, *T. aestivum* subsp. *spelta*, *T. turgidum* subsp. *dicoccum*, *T. turgidum* subsp. *durum*, *T. turgidum* subsp. *turgidum*): grain 60-100  $\mu\text{m}$ , P/E < 1.2, (sub)apical pore
- *Glyceria*-type (*Avena sativa* subsp. *sativa*, *Glyceria fluitans*, *G. notata*, *Hordeum vulgare* subsp. *distichon*): grain 40-60  $\mu\text{m}$ , A = 9-18  $\mu\text{m}$
- Poaceae = wild grass-type (*Avena barbata* subsp. *wiestii*, *Bromopsis inermis* subsp. *inermis*, *Dactylis glomerata*, *Elytrigia campestris*, *Hordeum brevisubulatum*, *Leymus condensatus*, *Phragmites australis*, *Schedonorus arundinaceus*, *Thinopyrum elongatum*): grain < 50  $\mu\text{m}$ , A < 12  $\mu\text{m}$ .

with A, Annulus width; P/E, Polar diameter/Equatorial diameter.

### 3.3. Present-day hydrophytic pollen record

The local pollen richness (60 pollen and spore taxa) represents 40.5 % of the hydrophytic species richness (148 species belonging to 97 genera and 53 families) of the wetlands of the Jebala Range. Representation indices based on presence-absence data (Davis, 1984; Hjelle, 1997; Bunting, 2003; Amami et al., 2010) help to characterise the association between pollen and vegetation for 45 taxa present in both plant and pollen datasets: 27 taxa are weakly to strongly associated and 18 are overrepresented (Table 4). Both vegetation



surveys (Table 2) and the diagram based on modern pollen data (Fig. 3) are likely to provide complementary clues for discriminating good indicators of their local occurrence or of the local presence of their community. Indeed, they allow identifying good plant indicators (plants more or less restricted to a particular community) and comparing the respective values of vegetation and plant abundances (the representation indices only take in account the presence-absence). On the basis of this dataset, we identify the following taxa that can be used to reconstruct the different communities in the fossil record (strongly associated taxa and associated taxa noted in bold):

- Swamps: *Alnus* (*A. glutinosa*), *Frangula* (*F. alnus*), ***Ilex*** (*I. aquifolium*), *Prunus*-type (*P. lusitanica*), *Salix* (*S. atrocinnerea*, *S. pedicellata*), *Dryopteris*-type (*Athyrium filix-femina*, *Blechnum spicant*)
- Fens: *Erica*-type (*E. ciliaris*), *Genista*-type (*G. ancistrocarpa*), ***Alisma*-type** (*Baldellia repens*), **Cyperaceae** (*Carex* spp., *Eleocharis multicaulis*), ***Lobelia*** (*L. urens*), ***Lysimachia tenella*-type** (*L. tenella*, *L. tyrrhenia*), ***Sphagnum*** (*S. auriculatum*)
- Temporary ponds: ***Alisma*-type** (*Baldellia ranunculoides*), ***Cicendia/Exaculum*** (*C. filiformis*, *E. pusillum*), *Glyceria*-type (*G. spicata*), *Lythrum borysthenticum*-type (*L. borysthenticum*, *L. junceum*, *L. portula*), *Gratiola*-type (*G. mauretana*), ***Ranunculus*-type** (*R. baudotii*, *R. ophioglossifolius*), *Isoetes* (*I. velata*)
- Alkaline lake: ***Alisma*-type** (*A. lanceolatum*), *Callitriche* (*C. stagnalis*), **Cyperaceae** (*Carex pseudocyperus*), *Montia* (*M. minor*), ***Potamogeton*-type** (*P. polygonifolius*), *Sparganium/Typha* (*S. erectum*)
- *Sphagnum* pond: *Genista*-type (*G. ancistrocarpa*), ***Alisma*-type** (*Baldellia ranunculoides*), ***Cicendia/Exaculum*** (*C. filiformis*, *E. pusillum*), **Cyperaceae** (*Carex distans*, *Eleocharis multicaulis*, *E. palustris*, *Isolepis cernua*), ***Sphagnum*** (*S. auriculatum*)

#### 3.4. Radiocarbon dating and sediment composition

The studied wetlands of Northern Morocco are called “peatlands”, especially because of their vegetation typical of European peatlands (Dahlgren and Lassen, 1972; Muller et al., 2010, 2011). However, they generally do not accumulate a true peat, which should essentially be constituted of partially degraded plant remains. As shown by the Figure 4, the organic-matter content of the three studied cores is mainly less than 10% and never exceeds 50%. The sediment accumulated should then be called organic or peaty clay. The weak organic content probably results from the Mediterranean climate that induced both a strong decomposition during the summer months and detritic inputs of mineral particles in autumn and spring. Moreover, the three studied sequences are highly heterogeneous and include intercalated layers of sand, suggesting past changes in the watershed vegetation cover.

The radiocarbon dates available for the Jebala Range are synthesized in Table 5. They reveal several periods of wetland initiation: ca. 13000 cal. BP (BAR, degraded alder swamp (Reille, 1977)), ca. 9000 cal. BP (BOU-BEK, pond (Cheddadi et al., 2016), ca. 5500-5000 cal. BP (MF1b, fen (Muller et al., 2015); MF3, alder swamp and pond) and ca. 2000-1000 cal. BP (DAY2, lake; MAR (Reille, 1977), pond; RHE1, swamp (Reille, 1977); TAN, lake (Reille, 1977)). Alder swamps and fens (BAR, MF1b, MF3) are globally older than ponds and lakes (DAY2, MAR, TAN) that only initiated in the last 2 millennia, but there is no absolute

rule: the swamp RHE1 initiated around 1600 cal. BP, while the pond BOU/BEK initiated in the early Holocene at *ca.* 9000 cal. BP. Sediment accumulation rates (SAR) are also very different between both types of wetlands: with the exception of the swamp RHE1, fens and alder swamps present significantly lower SAR (*ca.* 0.2 mm.yr<sup>-1</sup>) than ponds and lakes, which SAR is generally near 1 mm.yr<sup>-1</sup> and reaches 5.5 mm.yr<sup>-1</sup> in the central part of the alkaline lake DAY-2 (Table 1). Despite the heterogeneous sediment content of cores, the age-depth models (Fig. 4) reveal few changes of SAR, with the exception of the severe lowering of apparent SAR around 60 cm depth at BAR. This could result from a hiatus of sedimentation or more probably from human-triggered disturbances of the upper part of the sediment column. In the Bartete site, the Reille (1977)'s age was realised on a different core (Lv-635; BAR3) than ours (BAR). However, our chronology suggests that this age is too young, as is the one obtained in our sequence from a wood charcoal (Poz-51919; Muller et al., 2015).

The three sites show a decrease in organic matter (OM) content with depth due both to the process of decomposition and to the deposition of sand in the lower part of the sequences (below 114 cm at BAR, below 104 cm at MF1b and below 200 cm at MF3). Some sharp changes can be observed in relation with the nature of the sediment that primarily correspond to a transition from mineral (sand and clay) to more organic sediments (peaty clay or decomposed peat) that occur at *ca.* 780 cal. BP (78 cm) at MF3, and later, around 440 cal. BP at MF1b (36 cm) and at BAR (55 cm). A detritic event is recorded by an abrupt lowering of OM content at a depth of 28 cm (*ca.* 310 cal. BP) in the MF3 sequence.

### 3.5. Hydrophytic pollen data

The local pollen diagrams of MF1b, MF3 and BAR are presented Figs. 5, 6 and 7, respectively.

#### 3.5.1. Maison forestière-1, core MF1b

MF1b-Z1 (128-66 cm; 4900-1970 cal. BP). The lowest part of the sequence (Fig. 5) shows high percentages of unidentified pollen, which indicate poor preservation conditions possibly due to running water in an (open?) depression. The surprising association between aquatic taxa (*Callitriche*, *Glyceria*-type, *Ranunculus*-type) and *Sphagnum* suggests a waterlogged habitat resembling the *Sphagnum* pond MF4.

MF1b-Z2 (66-34 cm; 1970-390 cal. BP). The increase in pollen percentages of Cyperaceae, *Potentilla*, *Salix* and *Sphagnum*, coupled with a progressive increase in OM content, attests to the onset of a fen plant community that probably limited the water runoff.

MF1b-Z3 (34-0 cm; 390-0 cal. BP). The abrupt increase in Cyperaceae linked with the appearance of *Alisma*-type, Juncaceae, *Lysimachia tenella*-type and *Lythrum borysthenicum*-type reflects the recent constitution of the site's present-day plant cover.

#### 3.5.2. Maison forestière-3, core MF3

MF3-Z1 (512-328 cm; 5300-3800 cal. BP). *Alnus* dominates the swamp surrounding the pond (Fig. 6). The undergrowth is mainly constituted by *Ilex*, associated with *Frangula*. The occurrences of Apiaceae, Cyperaceae, *Glyceria*-type and *Ranunculus*-type translate the aquatic community inhabiting the waterhole.

MF3-Z2 (328-184 cm; 3800-2220 cal. BP). The increases of Cyperaceae and *Sphagnum* may reveal internal modifications in swamp structure, also revealed by the replacement of *Ilex* by *Frangula* at the end of the zone. Apiaceae and *Callitriche* could translate either the pond's aquatic vegetation or the swamp's herbaceous undergrowth.

MF3-Z3 (184-88 cm; 2220-890 cal. BP). The ongoing swamp transformation is marked by the lowering of *Alnus* and *Frangula* percentages associated with the expansion of *Salix*. Conversely, the aquatic vegetation underwent some changes: Cyperaceae probably constituted a riparian belt encircling the pond, while *Glyceria*-type and *Ranunculus*-type developed in the open-water zone. The alder swamp was probably less closed than in the past, but remains home to a rich flora including *Frangula*, *Ilex*, *Prunus*-type, *Dryopteris*-type, *Osmunda* and *Sphagnum*.

MF3-Z4 (88-0 cm; 890-0 cal. BP). The decrease in *Salix* attests the local decline of willow groves, just before the definitive opening of the alder swamp. The more regular pollen record of aquatic plants (*Alisma*-type, *Glyceria*-type, Juncaceae, *Ranunculus*-type, other aquatics) could translate either the diversification of pond vegetation or to it being better recorded in less degraded sediments.

### 3.5.3. Bartete, BAR

The ages proposed below for the sequence of Reille (1977) are inferred from our core taken in 2012 at the same location (Fig. 7). Because they have not been made on the same sediment sequence, we only give putative ages rounded per 500 years.

BAR-Z1 (240-145 cm; ca. 12500-6500 cal. BP). The basal high percentage of *Alnus* suggests that the sediment-accumulating swamp initiated within a pre-existing alder riparian forest. The lack of details of Reille (1977)'s diagram concerning hydrophytic taxa makes it difficult to specify the composition of this habitat, but the occurrence of Apiaceae and Ranunculaceae could reflect the presence of waterlogged places inside the swamp or on its edge.

BAR-Z2 (145-35 cm; ca. 6500-50 cal. BP). *Cedrus* increase reveals the development of a cedar forest around the swamp. The dense canopies of both cedar forest and alder swamp probably filtered between 6500 and 3000 cal. BP the regional pollen input (Tauber, 1965), here characterised by the curve *Other taxa*, modifying swamp composition (more *Salix*, less Ranunculaceae).

BAR-Z3 (35-0 cm; ca. 50-0 cal. BP). The abrupt decrease of *Alnus* at 35 cm deep reflects the disappearance of the local alder swamp and the constitution of the present-day cultivated peat meadow. The two modern radiocarbon ages obtained from two different core segments just above and below 50 cm in depth, and the one of  $1010 \pm 50$  cal. BP obtained by Reille (1977) on the BAR3-1977 core (Table 5) largely below the fall of the *Alnus* curve, make it possible that the swamp was cleared and the site cultivated only recently, perhaps even in the 20<sup>th</sup> century. The recent increase in Cyperaceae, *Lysimachia* and *Lythrum* reveals the constitution of the modern plant community and the rise in *Plantago* probably indicates that surrounding shrublands were grazed.

## 4. Discussion

### 4.1. Unravelling *Glyceria* from other Poaceae pollen types

Despite the very homogenous monoporate pollen morphology of the Poaceae family, a number of keys have been proposed, with different appreciations of the few available diagnostic features (e.g., [Firbas, 1937](#); [Erdtman, 1943](#); [Grohne, 1957](#); [Beug, 1961, 2004](#); [Andersen, 1979](#); [Küster, 1988](#); [Faegri and Iversen, 1989](#); see [Tweddle et al., 2005](#) for a detailed review of these works). Most of the recent studies have attempted to discriminate cereals from wild grasses taking morphometric and statistical approaches, but they have failed to give univocal diagnostic characters ([Tweddle et al., 2005](#); [Joly et al., 2007](#)). Nevertheless, [Tweddle et al. \(2005\)](#) show that a more reliable identification can be achieved by combining the approaches of [Andersen \(1979\)](#) and [Küster \(1988\)](#), and [Joly et al. \(2007\)](#) provide a practical key for discriminating cereals from wild grasses, with very useful indications of the degree of confidence of the attribution of some taxa to each group.

Our results confirm the distinction of *Zea* with a lower threshold of 100  $\mu\text{m}$ , of *Secale* based on its large size (60-100  $\mu\text{m}$ ) and its specific morphology, and of *Cerealia*-type (cereal-type) that is comprised between 60 and 100  $\mu\text{m}$ . They moreover suggest that *Cerealia*-type is restricted to the genus *Triticum*, since *Avena* and *Hordeum* present smaller pollen grains.

The large size of *Glyceria* pollen leads to it being generally included in the “cereal-type”. [Erdtman \(1943\)](#) incorporated it in its “intermediate group” (grain 32-35  $\mu\text{m}$ ), defined by the shape of cereals and by the size of wild grasses, but the dimensions given are not consistent with our measurements ([Table 3](#)). [Andersen \(1979\)](#) included *Glyceria* in its “*Hordeum* group” (grain 38-54  $\mu\text{m}$ , annulus 10-13  $\mu\text{m}$ ), and [Joly et al. \(2007\)](#) in its “wild grass-type” (grain < 47  $\mu\text{m}$ , annulus < 11  $\mu\text{m}$ ). Those two conceptions are more or less consistent with [Küster \(1988\)](#), who defined a “*Glyceria*-type” (grain 40-80  $\mu\text{m}$ , annulus diameter lower than twice the pore diameter, with a diffuse outer boundary) including several wild grasses (*Anthoxanthum*, *Elymus*, *Holcus*, *Hordelymus*, *Phragmites*, *Setaria*, *Spartina*). Our results support the definition of the “*Glyceria*-type”, but with some discrepancies with the [Küster \(1988\)](#)’s conception: the type, which includes the cultivated *Avena sativa* and *Hordeum vulgare* subsp. *distichon*, is characterised by a ratio annulus/pore > 2 and an annulus width of (7)9-18  $\mu\text{m}$  ([Table 3](#)). Surprisingly, our measurements are not consistent with the annulus size given by [Andersen \(1979\)](#) (10-13  $\mu\text{m}$ ) and [Joly et al. \(2007\)](#) (< 11  $\mu\text{m}$ ).

The Poaceae pollen type, which corresponds to wild grass-type, includes all Poaceae species that cannot be classified in a specific group. It is generally defined first by a grain size of less than 30(40)  $\mu\text{m}$  ([Erdtman, 1943](#)), 40  $\mu\text{m}$  ([Küster, 1988](#); [Faegri and Iversen, 1989](#)), 44  $\mu\text{m}$  ([Andersen, 1979](#)) or 47  $\mu\text{m}$  ([Joly et al., 2007](#)). With the exception of [Erdtman \(1943\)](#) who notes a pore < 2  $\mu\text{m}$  with no annulus, most published keys give an upper threshold value of 10-11  $\mu\text{m}$  for annulus ([Andersen, 1979](#); [Faegri and Iversen, 1989](#); [Joly et al., 2007](#)). Our biometric data, while concerning few wild species, suggest raising the upper threshold values of annulus to 12  $\mu\text{m}$  and of the grain size to 50  $\mu\text{m}$ . This type consequently includes a significant part (24%) of the taxa included in *Glyceria*-type, implying its probable systematic underestimation in pollen counts.

This calls into question the reliability of the past pollen record of cereals. For example, the *Cerealia*-type pollen (ca. 50  $\mu\text{m}$ ) record from Lake Acıgöl in southwestern Turkey has recently been interpreted as reflecting the appearance of proto-cereals over the past 2.3 million years ([Andrieu-Ponel et al., 2021](#)). According to our results, only pollen grains larger than 60  $\mu\text{m}$  can be attributed with certainty to *Cerealia*-type, and probably even to *Triticum*.

This suggests that such a record in a lacustrine environment could well have come from riparian populations of aquatic wild Poaceae like *Glyceria* spp., known to tolerate brackish water (e.g., [Fennane et al., 2014](#)), and that the decreasing trend of *Cerealia*-type percentages at Lake Acigöl could translate the progressive salinization of the lake.

#### 4.2. Pollen representation of peat-forming plant communities of Northern Morocco

The plant and pollen richness are evaluated in the wetlands of the Jebala Range at 148 species and 60 taxa, respectively, which allows calculating a loss of information of *ca.* 60%. Despite this well-known bias concerning species diversity in pollen records ([Odgaard, 1999](#)), most of the keystone species of the main wetland plant communities are well recorded, making it possible to discern them in pollen spectra.

The swamps of the Rif are structured mainly by *Alnus glutinosa*, the most often associated with *Frangula alnus*, *Ilex aquifolium* and, locally, *Osmunda regalis*. Alder pollen percentages exceed 10% in only four sites: two of which (MF3 and MF5) house it, the two others (BAR and BAZ) do not ([Fig. 3](#)). BAR and BAZ, currently cultivated, are close together and located at the top of a watershed where *Alnus* is abundant in riparian situation. Its important pollen record in the pollen sequence of BAR ([Fig. 7](#)) ([Reille, 1977](#)) indicates that alder reached the site during the Holocene and disappeared from it, only some decades ago. The pollen surface assemblage then probably records the last local alder trees before clearing. The *Alnus* pollen record thus appears as a reliable indicator of its past local presence. The pollen records of *Frangula*, *Ilex* and *Osmunda*, while weak, are associated with high pollen percentages of *Alnus*, and are thus supplementary indicators of alder swamps.

Fens and the alkaline lake house numerous Cyperaceae, whose most abundant species belong to the genera *Carex* and *Eleocharis*, locally mixed with *Cyperus longus*, *Isolepis* spp. and *Pycreus flavescens*. They also include some aquatic Apiaceae (*Helosciadium inundatum*, *H. nodiflorum*, *Oenanthe lachenalii*). Both families, when associated in pollen records, appear to be good markers of these two habitats ([Fig. 3](#)). The pollen record of ligneous plants, which appear to be more diversified in fens than in the alkaline lake, makes it possible to distinguish them. Indeed, *Calluna*, *Erica*-type, *Genista*-type, *Prunus*-type and *Salix* are commonly recorded in surface pollen spectra from fens, whereas only *Erica*-type is present in DAY2 pollen record ([Fig. 3](#)). Since *Sphagnum* is a regular component of fens, its spore record is also useful for recognising this habitat.

Open water holes, such as ponds (BOU, MF3, TAY1) and alkaline lakes (DAY1, DAY2), house the aquatic herb *Glyceria spicata*, which could be locally abundant. Based on the diagnostic features discussed above, we identified a *Glyceria*-type pollen morphology that was recorded in small proportions in all the analysed surface spectra, making it difficult to perceive the local presence of the plant. This widespread pollen signal could be attributed to the generally anemophilous (while sometimes ambophilous; [Schulze-Albuquerque et al., 2020](#)) pollination of Poaceae species. However, the complete pollen diagrams of BAR, MF1b and MF3 ([Figs. 5 to 7](#)) unambiguously reveal the long-term presence of this species at MF3 (continuous curve; average  $4.1 \pm 1.1$  %) and its long-term absence or rarity at BAR (discontinuous curve of *Cerealia*-type; average  $0.6 \pm 0.3$  %) and MF1b (discontinuous curve; average  $0.6 \pm 0.1$  %). Furthermore, ponds and lakes could be distinguished on the basis of the pollen record of characteristic plants, such as components of *Isoetion* (*Cicendia-Exaculum*,



*Gratiola*-type, *Isoetes*, *Lythrum*, *Ranunculus*-type) in ponds, and perennial hydrophytes (*Potamogeton*-type, *Sparganium*/*Typha*) in lakes.

#### 4.3. Initiation of peat-forming wetlands in the Rif

The palaeoecological data available in the Rif provide some clues that can be used to reconstruct the past origin of the present-day peat-forming wetlands. The Bartete sequence (Reille, 1977) (Fig. 7) proves that sediment-accumulating wetlands have existed in the Rif for at least 13,000 years. Although few radiocarbon-based chronologies are available for this mountain range, those that do exist (Reille, 1977; Cheddadi et al., 2015, 2016; Muller et al., 2015) (Table 5) show unambiguously that sediment accumulation began at different periods from the end of the Lateglacial to the late Holocene. Among the investigated lakes (DAY1, DAY2, TAN) or ponds (BOU, MAR, MF3, MF4, TAY1), only MF4 harbours a significant community of peatland plant species (including *Aulacomnium palustre*, *Carex distans*, *Danthonia decumbens*, *Eleocharis multicaulis*, *Lythrum junceum*, *Potentilla erecta*, *Polytrichum strictum*, *Sphagnum auriculatum*). This suggests a possible evolution towards peat-forming communities, through the so-called terrestrialization process that is common in Boreal countries (Korhola, 1995; Muller et al., 2003). On the opposite, the contrasted SAR between open water bodies and peat-forming wetlands linked with the roughly constant age-depth models of the studied sites (Fig. 4) suggest that the MF1 fen did not initiate by terrestrialization from a pre-existing pond. This is supported by the presence of sand and significant pollen degradation at the base of the core MF1b, features consistent with the fen spread from a stream flowing down a gentle slope, i.e. through paludification process (Lavoie et al., 2005). It is likely that the sand deposited in the lower portion of the sequences of BAR, MF3 and BOU/BEK (Cheddadi et al., 2016) reveals similar origins for the concerned wetlands. Such initiations by paludification agree with the present-day ecology of *Sphagnum auriculatum* in North Africa, where it constitutes loose carpets on waterlogged soils below springs or along streams, mainly in forest environments (Muller et al., 2010, 2011). Only two peat-forming wetlands of the Jebala Range could have originated through terrestrialization: the wet meadow of MAR and the degraded swamp RHE1 (Reille, 1977) (Table 1) have indeed formed from ponds, recorded in the basal pollen spectra by *Myriophyllum*, associated at RHE1 with *Ludwigia*, *Lythrum*, *Potamogeton* and *Glyceria*-type. Initially interpreted as cereals by Reille (1977), the last taxon presents, in the lowest part of the RHE1 sequence, a peak clearly linked to hydrophytic taxa, revealing its aquatic nature. This could explain the abnormally high SAR of this peat-forming wetland (1.13 mm.yr<sup>-1</sup>).

The plant communities that developed at the onset of wetlands varied between the sites that developed from slow-running waters, possibly along previous river beds. Some of them, such as MF3 and BAR, were initially covered by alder swamps, although others, such as MF1, were open and dominated by herbaceous communities evocating the *Sphagnum* pond MF4.

#### 4.4. Controls of the past dynamics of peat-forming wetlands in the Rif

Sometime after the initial phase of sand deposition in slow-moving waters (ca. 13,000-5000 cal. BP at BAR; ca. 9100-8000 cal. BP at BOU/BEK; 5100-3500 cal. BP at MF1b; 5400-2400 cal. BP at MF3), these four sites evolved towards peaty clay-accumulating wetlands (around 2500-2000 cal. BP at BAR, 6700 cal. BP at BOU/BEK, 930 cal. BP at

MF1b and 850 cal. BP at MF3). BAR and MF3, located on two different reliefs, were covered by alder swamps that were probably similar to the relictual MF5 that remains home to a rich peat-forming community including *Alnus glutinosa*, *Frangula alnus*, *Ilex aquifolium*, *Prunus lusitanica* and *Salix atrocinerea*. However, the MF3 sequence (Fig. 6) reveals that while the composition of the swamp undergrowth remained relatively unchanged for at least 5300 years, the respective abundance of each taxon has varied over time, at least at the edge of the pond: *Ilex* dominates the first half of the swamp's history until ca. 2500 cal. BP, at which point *Frangula* replaced it for about 4 centuries, and finally *Salix* spread, perhaps as a result of the contemporary opening of the alder grove. Approximately 900 cal. BP, the alder swamp closed again, which may have led to the regression of willow that regressed in its turn again a few centuries later.

The related sediment composition and wetland vegetation dynamics are controlled by autogenic (hydroseral plant succession) and allogenic factors (watershed forest cover, rainfall regime) (Payette, 1988; Korhola, 1996; Muller, 2001). Past changes affecting the nature of the sediment and/or hydrophytic plant communities should therefore reveal changes of one or more of these factors. With the sole exception of RHE1 (Reille, 1977), no local hydrophytic vegetation changes recorded in the Rif Mountains (Reille, 1977; Muller et al., 2015; Cheddadi et al., 2016; Abel-Schaad et al., 2018) (Figs. 5 to 7) are compatible with the hydroseral succession model initially described by Weber (1908) and Clements (1916). The climatic boundary conditions for peatland development, which induced high decomposition rates barely compensated for by production rates, may explain why the hydroseral succession is so poorly expressed in Northern Morocco. In contrast with the constancy of local hydrophytic plant communities, the regional forest cover underwent one major change, namely the late-Holocene decline of *Cedrus* (Reille, 1977; Muller et al., 2015; Cheddadi et al., 2016, 2017; Abel-Schaad et al., 2018). Available pollen sequences record this event at different periods: 4000-3000 cal. BP at BAR, 2900-2600 cal. BP at MF3, 2300-2000 cal. BP at MF1b, and 1500-800 cal. BP at BOU/BEK (Figs. 5 to 7) (Cheddadi et al., 2016, 2017; Abel-Schaad et al., 2018). While Cheddadi et al. (2017) attribute this decline to the late-Holocene climate aridification, its non-contemporaneity rather suggests the influence of human activities. On Jbel Bou Hachem, the first significant structural changes affecting peat-forming wetlands occurred soon after the cedar decline (Figs. 5 and 6), which probably reflects changes in the hydrology of watersheds induced by the regression of the tree cover. A similar hydrological change is reported on Jbel Tizirene by Cheddadi et al. (2015), who link the reduction in tree cover to enhanced soil erosion.

These results indirectly highlight human activities in the Rif since 3000 cal. BP, as cedar forest clearing impacted the hydrology of watersheds and sediment accumulation in wetlands. However, as previously noted (Cheddadi et al., 2015; Muller et al., 2015), and unlike contemporary pollen records in Europe, the pollen data from the Jebala Range show no clear evidence of past agriculture. It appears notably that although cereal cultivation was reported for more than 7,000 years on the coast of Northern Rif (Ballouche and Marinval, 2003; Zielhofer and Linstädter, 2006; Zapata et al., 2013), the cereal-type pollen signal recorded in the central Rif by Reille (1977) and Muller et al. (2015) is clearly related to the open-water nature of the wetlands and can be assigned to *Glyceria*-type pollen, mainly produced by *in-situ* floating populations of *Glyceria spicata*. Consequently, the changes that

affected the mountain forests of Rif before the end of the Middle Ages (Reille, 1977; Cheddadi et al., 2015, 2016, 2017; Muller et al., 2015) may be primarily attributed to animal husbandry. This is supported by the contemporary increases of *Plantago* in the BAR sequence (Reille, 1977) (Fig. 7) and of coprophilous fungi in the BEK one (Abel-Schaad et al., 2018), which indicate the local occurrence of grazing. Such differences in human activities could explain the delay of the anthropogenic impact on landscapes between coastal and mountain areas (Cheddadi et al., 2018): while cereal cultivation seems to have triggered the early Holocene decline of forest ecosystems on the coast (Zapata et al., 2013), animal husbandry should have prevailed for millennia in the Jebala Range, with a moderate and later impact on vegetation cover.

## 5. Conclusion

First, our results highlight that the consideration of the pollen record of hydrophytic plant communities clearly improve the interpretation of pollen spectra. Some hydrophytic taxa have indeed been misinterpreted as anthropogenic indicators in previous studies conducted in the Rif (e.g., *Cerealia*-type, *Galium*-type, *Potentilla* and Ranunculaceae; Reille, 1977; Cheddadi et al., 2018), leading to overestimating the past role of human populations. In particular, our study showed that it is difficult to distinguish between the pollen of cereals and that of certain wild Poaceae species including *Glyceria* spp., and that such confusion could lead to possible misinterpretations, as in Andrieu-Ponel et al. (2021) at Lake Acigöl in Turkey. Another ecological misinterpretation was reported for the *Erica*-type pollen record that is generally interpreted in North Africa as revealing regional evergreen shrublands (Reille, 1977; Benslama et al., 2010; Cheddadi et al., 2018), while it can come from local hydrophytic populations of *Erica ciliaris* (Northern Morocco) or *E. scoparia* (Northern Tunisia and Northeastern Algeria (Ghit et al., 2018)).

Second, our work provides a historical perspective for the conservation of the invaluable and highly threatened “peatlands” of Northern Morocco. It notably reveals the ancient wooded status of some of them, which were dominated by complex tree communities (including *Alnus glutinosa*, *Frangula alnus*, *Ilex aquifolium*, *Laurus nobilis* and *Prunus lusitanica*) and surrounded by deciduous oak forests before recent anthropogenic clearing. Previous studies show that the situation is similarly worrying at the scale of Maghreb. The rapid demographic increase in the three countries of the Maghreb and the difficult economic context in remote and landlocked regions (such as mountainous areas) have led in the past decades to severe degradation and destruction of most of the North African peatlands. That some of these benefit from a protected status has been clearly inadequate for guaranteeing their durability: the Tunisian Dar Fatma peatland reserve, for example, was damaged and over-pastured after the 2011 revolution; the alder swamps of the Algerian El Kala National Park are disappearing progressively because of illegal cutting and draining (De Bélair and Samraoui, 1994; Belouahem-Abed et al., 2011); and the Northern Moroccan peatlands of Jbel Bou Hachem were severely damaged by overgrazing and forest clearing and burning (Muller et al., 2015). In the coming decades, climate change will constitute an additional constraint for these habitats already greatly weakened by human activity. Based on the historical background, protection policies that guarantee their long-term survival must be urgently

implemented given their inestimable historical and patrimonial value as well as their biological and ecological richness.

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## Table and Figures

Jbel	Site	Code	Nature	Altitude (m a.s.l.)	Latitude N	Longitude W	Phytosociological relevés	Floristic richness	Mean SAR (mm/yr)
Bou Hachem	Maison Forestière-1	MF1	Fen	1064	35°15'12"	05°25'14"	20.05.2010	32	0.26
	Maison Forestière-2	MF2	Fen	1092	35°15'22"	05°25'40"	20.05.2010	26	
	Maison Forestière-3	MF3	Swamp/pond	1096	35°15'32"	05°25'54"	13.06.2012	52	1.01
	Maison Forestière-4	MF4	<i>Sphagnum</i> pond	1213	35°15'13"	05°25'58"	16.06.2012	40	
	Maison Forestière-5	MF5	Swamp	1300	35°15'04"	05°26'21"	21.10.2014	25	
Sougna	Tayenza-1	TAY1	Temporary pond	980	35°16'11"	05°26'09"	23.10.2014	26	
	Bartete	BAR	Fen	1249	35°01'51"	05°14'59"	14.06.2012	37	0.19
	Bazoukout	BAZ	Fen	1143	35°02'10"	05°14'38"	14.06.2012	30	
	Marzine	MAR	Pond/wet meadow	720	35°06'02"	05°20'09"	21.05.2010	37	0.88
	Tanakob Lake	TAN	Acid lake	840	35°07'42"	05°26'31"			1.17
Khezana	Tanakob Fen	TANT	Fen	791	35°07'21"	05°26'20"	20.05.2010	22	
	Al-Bayda Fen	ABF	Fen	1125	35°01'46"	05°12'33"	22.05.2010	27	
	Boujdayem	BOU	Temporary pond	1202	35°01'22"	05°12'24"	21.05.2010	39	0.93
Tizirène	Rhesana-1	RHE1	Swamp	1300	<i>n.a.</i>	<i>n.a.</i>			1.01
	Dayla-1	DAY1	Alkaline lake	1393	35°01'09"	05°00'02"			
	Dayla-2/Aanasser	DAY2	Alkaline lake	1300	35°01'02"	04°59'30"	22.05.2010	33	5.59

**Table 1.** Sites studied in the Rif. Certain sites were previously studied and sometimes differently named: BAR, *Daya Arbatète* (Reille 1977); BOU, Bab el Karn (Cheddadi et al., 2016; Abel-Schaad et al., 2018); DAY1, *Mare à Cypéracées, jbel Tizirène* (Reille 1977); DAY2, *Etang près d'el Anasser, jbel Tizirène* (Reille 1977) and *Aanasser* (Cheddadi et al., 2015); MF1 (Muller et al., 2015); MF3, *Mare à sphaignes du jbel Bou Hachem* (Reille 1977); RHE1, *Tourbière à sphaignes entre Bab Taza et Fifi* (Reille 1977); TAN and TANT (Reille 1977). SAR: sediment accumulation rate; *n.a.*: not available.

	ABF	BAR	BAZ	BOU	DAY2	MAR	MF1	MF2	MF3	MF4	MF5	TANT	TAY1
Date	22.05.2010	14.06.2012	14.06.2012	21.05.2010	22.05.2010	21.05.2010	20.05.2010	20.05.2010	13.06.2012	16.06.2012	21.10.2014	23.10.2014	20.05.2010
Water depth (cm)	0	0	5	50	150	150	0	0	0	80	0	0	20
Species richness	27	37	30	39	33	37	32	26	52	40	25	22	26
Wetland surface (ha)	0.03	0.7	0.1	0.4	6.6	0.7	0.12	0.18	0.8	0.07	0.5	0.2	0.15
<b>Charophytes and Bryophytes</b>													
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	2	1	1				1		1	1-2			
<i>Chara globularis</i> Thuillier					1								
<i>Nitella opaca</i> C.Agardh				2									
<i>Polytrichum commune</i> Hedw.										2-3			1-2
<i>Sphagnum auriculatum</i> Schimp.		+	1				4	2	2	4-5		1	1
<b>Tracheophytes (Lycopodiophytes, Polypodiophytes and Spermatophytes)</b>													
<i>Acis autumnalis</i> (L.) Herb.												+	
<i>Acis longifolia</i> J.Gay ex M.Roem.									+				
<i>Agrostis capillaris</i> L. subsp. <i>castellana</i> (Bois. & Reut.) O.Bolos, Massales & Vigo										2			
<i>Agrostis stolonifera</i> L.												+	
<i>Aira cupaniana</i> Guss.			+							1			
<i>Alisma lanceolatum</i> With.					1-2								
<i>Alnus glutinosa</i> (L.) Gaertn.									2		4		
<i>Alopecurus aequalis</i> Sobol.					+								
<i>Anthemis praecox</i> Link										1			
<i>Anthoxanthum odoratum</i> L.						1	4		3				
<i>Athyrium filix-femina</i> (L.) Roth.											1		
<i>Baldellia ranunculoides</i> (L.) Parl.	1	2							2-3	2			
<i>Baldellia repens</i> (Lam.) van Ooststr. ex Lawalrée			2	2		4	2	2-3			1		2-3
<i>Bellis sylvestris</i> Cirillo				1		+							
<i>Blechnum spicant</i> (L.) Roth									+		1-2		
<i>Briza maxima</i> L.									+				
<i>Briza minor</i> L.	+	1-2	1			+	+		1	1			
<i>Bromus madritensis</i> L.										1			
<i>Callitriche brutia</i> Petagna				1-2					+				2
<i>Callitriche stagnalis</i> Scop.			+		2				1				1
<i>Callitriche truncata</i> Guss.									1				
<i>Calluna vulgaris</i> (L.) Hull							1						
<i>Carex cuprina</i> (Sandor ex Heuff.) Nendtv. ex A.Kern.						1							
<i>Carex distans</i> L.	2	5	2				1-2	2	+	1			
<i>Carex divulsa</i> Stokes						+							
<i>Carex echinata</i> Murray		1					1	2					
<i>Carex flacca</i> Schreb.						+							
<i>Carex ovalis</i> Good.	3	2		1			1		1				
<i>Carex pseudocyperus</i> L.					1-2								
<i>Carex remota</i> L.											1		
<i>Carex serotina</i> Mérat								3	+				

<i>Chamaemelum fuscatum</i> (Brot.) Vasc.				1	+	+	1		1				1-2
<i>Cicendia filiformis</i> (L.) Delarbre				1			+	1	1	1			1-2
<i>Cistus creticus</i> L.				+									
<i>Cistus monspeliensis</i> L.				+						+			
<i>Cistus salviifolius</i> L.													
<i>Crataegus monogyna</i> Jacq.									+				
<i>Cuscuta epithymum</i> L.	1					+							
<i>Cyperus longus</i> L.	2	1	1			2			+			2	
<i>Dactylorhiza maurusia</i> (Emb. & Maire) Holub							+						
<i>Danthonia decumbens</i> (L.) DC.							2	1-2	1	1			
<i>Dittrichia viscosa</i> (L.) Greuter					+	3		1				1	
<i>Dorycnium rectum</i> (L.) Ser.					+								
<i>Eleocharis multicaulis</i> (Sm.) Desv.	5	3	4-5				5	5	2	2	1	3	2-3
<i>Eleocharis palustris</i> (L.) Roem. & Schult.				2-3		2-3						4-5	
<i>Erica arborea</i> L.								1	+	+	+		
<i>Erica ciliaris</i> L.							1						
<i>Erica umbellata</i> L.										+			
<i>Exaculum pusillum</i> (Lam.) Caruel										1			
<i>Frangula alnus</i> Mill. subsp. baetica (Willk. & E.Rev.) Rivas Goday ex Devesa									1			2	
<i>Galium palustre</i> L.				1							+		1
<i>Galium palustre</i> L. subsp. <i>elongatum</i> (C.Presl) Lange		1							1-2	2			
<i>Gaudinia fragilis</i> (L.) P.Beauv.		4											
<i>Genista ancistrocarpa</i> Maire							2	1	+	1-2			
<i>Glyceria spicata</i> (Biv.) Guss.				2	2				1-2				1
<i>Gratiola mauretana</i>										2			1
<i>Hedera helix</i> L. subsp. <i>maroccana</i>											+		
<i>Helosciadium inundatum</i> (L.) W.D.J.Koch				3		2							
<i>Helosciadium nodiflorum</i> (L.) W.D.J.Koch	1-2	1			3		1					1	
<i>Holcus lanatus</i> L.					3			1					+
<i>Hypericum humifusum</i> L.	1	+					1			1	1	+	+
<i>Hypericum perforatum</i> L.	1-2					+							
<i>Hypericum tetrapterum</i> Fr.		2											
<i>Hypericum tomentosum</i> L.	2-3					+							
<i>Ilex aquifolium</i> L.											1		
<i>Illecebrum verticillatum</i> L.				1-2					+				1-2
<i>Isoetes histrix</i> Bory				1-2			1			1			
<i>Isoetes velata</i> A.Braun				2-3									
<i>Isolepis cernua</i> (Vahl.) Roemer & Schultes	2			1					2	1			1
<i>Isolepis setacea</i> (L.) R.Br.	1	+	+		+			+	+				



<i>Juncus bufonius</i> L.		+	1	1				2	1-2		1-2
<i>Juncus bulbosus</i> L.		1-2	3			3	2	1	2-3		
<i>Juncus capitatus</i> Weigel									1		
<i>Juncus conglomeratus</i> L.		1					2	3-4		1	
<i>Juncus effusus</i> L.	1										
<i>Juncus foliosus</i> Desf.					1	1					
<i>Juncus heterophyllus</i> Dufour			1	1-2				1		2	5
<i>Juncus pygmaeus</i> L.C.M.Richard				+		1	+				1
<i>Juncus tenageia</i> L.fil.								1			
<i>Lemna minor</i> L.					1						
<i>Leontodon tuberosus</i> L.				1-2							
<i>Lobelia urens</i> L.							1			1	
<i>Lotus angustissimus</i> L. subsp. <i>hispidus</i> (Desf. ex DC.) Bonnier & Layens		+	+	1	+	1			1-2		+
<i>Lotus pedunculatus</i> Cav.		1-2	1-2				3	2	1	1	1
<i>Ludwigia palustris</i> (L.) Elliot		+	1		2-3				1	+	
<i>Lycopus europaeus</i> L.					1						
<i>Lysimachia arvensis</i> (L.) U.Manns & Anderb.										+	
<i>Lysimachia tenella</i> L.	3										
<i>Lysimachia tyrrenia</i> (Thore) U.Manns & Anderb.		+	3			1	2	+		1	2
<i>Lythrum borysthenicum</i> (Schrank) Litv.				1							
<i>Lythrum junceum</i> Banks & Sol.	2	1-2	2			1-2	1	1-2	1	1	2
<i>Lythrum portula</i> (L.) D.A. Webb		+	1						1-2	1-2	3-4
<i>Mentha pulegium</i> L.	1-2	2-3	2	1-2		2	1	1	2	2	1
<i>Mentha suaveolens</i> Ehrh.	+				1						2
<i>Montia minor</i> C.C.Gmel. subsp. <i>chondrosperma</i> (Fenzl) Walters		1	1	1	3				1-2		
<i>Myosotis welwitschii</i> Boiss. & Reut.		1	+		1	1	+	2			
<i>Nardus stricta</i> L.			2								
<i>Nasturtium officinale</i> R.Br.	+				2-3					1	
<i>Oenanthe lachenalii</i> C.C.Gmel.									1		
<i>Ornithopus pinnatus</i> (Miller) Druce									1		
<i>Panicum repens</i> L.					1						
<i>Parentucellia viscosa</i> (L.) Caruel						+					
<i>Paspalum distichum</i> L.											1
<i>Phragmites australis</i> (Cav.) Steud.					2-3						
<i>Plantago coronopus</i> L.	+		+	1			+		1		+
<i>Poa annua</i> L.	+	+		1		1					1
<i>Polypogon monspeliensis</i> (L.) Desf.				2							
<i>Potamogeton polygonifolius</i> Pourr.		1	1		1		1	2	1		3

<i>Potentilla erecta</i> (L.) Rauschel			1			1-2	1	1	1	1		+
<i>Prunella vulgaris</i> L.	2-3	1							1	+	1	
<i>Prunus lusitanica</i> L.										4		
<i>Pteridium aquilinum</i> (L.) Kuhn	+			1	1	1	1	+	+	1		
<i>Pycreus flavescens</i> (L.) P.Beauv. ex Rchb.											1	
<i>Quercus canariensis</i> Willd.											+	
<i>Radiola linoides</i> Roth.				+					1			
<i>Ranunculus baudotii</i> Godr.				3	2	2						2
<i>Ranunculus bulbosus</i> L.		1		2								
<i>Ranunculus ficaria</i> L.						1						
<i>Ranunculus flammula</i> L.		2-3	1-2									
<i>Ranunculus hederaceus</i> L.		+										1-2
<i>Ranunculus ophioglossifolius</i> Vill.					1	2						
<i>Ranunculus tripartitus</i> DC.	+							1	1			
<i>Rubus ulmifolius</i> Schott.							+	1		2		
<i>Rumex conglomeratus</i> Murray				1	1	1						
<i>Rumex pulcher</i> L.						+						
<i>Salix atrocinerea</i> Brot.					1					2		
<i>Salix pedicellata</i> Desf.		+										
<i>Samolus valerandi</i> L.	1-2							+				
<i>Scrophularia auriculata</i> L. ex L.						1						
<i>Serapias lingua</i> L.										+		
<i>Serapias strictiflora</i> Welw. ex Da Veiga										+		
<i>Sherardia arvensis</i> L.				+								
<i>Silene laeta</i> (Aiton) Godr.	1	+					1	1	1-2		2	
<i>Solenopsis laurentia</i> (L.) C.Presl.			1	1								+
<i>Sparganium erectum</i> L.					2							
<i>Tolpis barbata</i> (L.) Gaertn.										+		
<i>Trifolium filiforme</i> L.						1	+		1	1	+	
<i>Trifolium michelianum</i> Savi		2	1-2									
<i>Trifolium nigrescens</i> Viv.				1	1							
<i>Trifolium resupinatum</i> L.				+		1						
<i>Trifolium strictum</i> L.									+			
<i>Trifolium subterraneum</i> L.				1		+						
<i>Typha latifolia</i> L.					1-2							
<i>Utricularia australis</i> R.Br.			1-2						1-2			
<i>Verbena supina</i> L.						+						
<i>Veronica anagalloides</i> Guss.						+						
<i>Vulpia myuros</i> (L.) C.C.Gmel				1								

**Table 2.** Vegetation surveys in 13 wetlands of the Jebala Range. The signification of site codes is given [Table 1](#).

Taxon	Number of slides	Number of measured grains	Polar length ( $\mu$ )			Equatorial length ( $\mu$ )			Annulus diameter ( $\mu$ )			Pore diameter ( $\mu$ )		
			Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
<i>Avena barbata</i>														
subsp. <i>wiestii</i>	1	33	45.8 $\pm$ 0.7	41.0	50.0	41.0 $\pm$ 0.7	37.0	45.0	11.2 $\pm$ 0.3	9.1	12.8	4.7 $\pm$ 0.1	3.8	6.0
<b><i>Avena sativa</i></b>	1	34	47.2 $\pm$ 0.8	41.0	53.0	43.0 $\pm$ 0.9	39.0	52.0	11.9 $\pm$ 0.2	10.5	13.0	5.4 $\pm$ 0.2	4.3	7.4
<i>Bromopsis inermis</i>														
subsp. <i>inermis</i>	1	20	41.6 $\pm$ 1.1	37.0	47.0	38.2 $\pm$ 0.6	35.0	41.0	9.8 $\pm$ 0.3	8.3	11.6	5.0 $\pm$ 0.2	4.1	5.9
<i>Dactylis glomerata</i>	1	8	33.0 $\pm$ 2.4	28.0	42.0	31.0 $\pm$ 1.6	27.0	35.0	6.7 $\pm$ 0.3	6.0	7.5	3.4 $\pm$ 0.1	3.1	3.8
<i>Elytrigia campestris</i>	1	18	39.3 $\pm$ 0.8	35.0	42.0	36.1 $\pm$ 0.9	32.0	40.0	9.5 $\pm$ 0.4	7.6	11.0	4.5 $\pm$ 0.2	3.7	5.5
<i>Glyceria fluitans</i>	2	43	45.0 $\pm$ 0.8	40.2	55.3	42.5 $\pm$ 0.6	38.2	48.1	13.8 $\pm$ 0.4	11.1	18.2	6.5 $\pm$ 0.3	4.8	10.7
<i>Glyceria notata</i>	2	49	47.8 $\pm$ 0.6	40.9	52.7	45.1 $\pm$ 0.8	37.9	52.0	12.0 $\pm$ 0.6	6.7	17.7	6.1 $\pm$ 0.5	3.1	9.9
<i>Hordeum brevisubulatum</i>	1	39	45.7 $\pm$ 0.6	42.0	50.0	39.4 $\pm$ 0.7	35.0	44.0	11.7 $\pm$ 0.2	10.5	13.2	4.6 $\pm$ 0.1	3.6	5.6
<b><i>Hordeum vulgare</i></b>														
subsp. <i>distichon</i>	2	18	56.3 $\pm$ 2.3	45.9	67.5	49.2 $\pm$ 3.1	41.8	66.7	14.1 $\pm$ 0.8	11.1	17.5	5.1 $\pm$ 0.5	3.4	7.5
<i>Leymus condensatus</i>	1	30	45.5 $\pm$ 0.9	42.0	51.0	42.0 $\pm$ 0.9	37.0	48.0	9.8 $\pm$ 0.2	7.6	11.3	5.0 $\pm$ 0.1	4.0	6.2
<i>Phragmites communis</i>	1	29	40.7 $\pm$ 1.4	33.0	50.0	36.5 $\pm$ 1.3	26.6	44.0	9.7 $\pm$ 0.3	8.1	12.0	4.5 $\pm$ 0.2	3.6	6.6
<i>Schedonorus arundinaceus</i>	1	12	36.9 $\pm$ 2.7	24.0	45.0	34.2 $\pm$ 2.1	24.0	41.0	7.0 $\pm$ 0.5	5.3	8.9	3.4 $\pm$ 0.3	2.5	4.3
<b><i>Secale cereale</i></b>	2	28	82.1 $\pm$ 3.3	51.0	97.0	68.2 $\pm$ 3.6	42.0	87.0	16.8 $\pm$ 0.8	11.2	22.0	6.9 $\pm$ 0.3	4.3	9.0
<i>Thinopyrum elongatum</i>	1	27	44.8 $\pm$ 1.2	36.0	51.0	41.6 $\pm$ 1.0	36.0	48.0	10.3 $\pm$ 0.3	7.8	12.0	4.5 $\pm$ 0.2	3.3	5.7
<b><i>Triticum aestivum</i></b>														
subsp. <i>aestivum</i>	3	22	72.0 $\pm$ 1.7	61.0	79.0	67.0 $\pm$ 2.3	52.0	77.0	19.0 $\pm$ 0.3	16.9	21.1	8.4 $\pm$ 0.4	7.1	11.2
subsp. <i>spelta</i>	4	36	68.9 $\pm$ 1.3	56.0	80.0	63.0 $\pm$ 1.2	54.0	70.0	17.2 $\pm$ 0.4	14.7	20.5	7.4 $\pm$ 0.3	5.9	10.2
<b><i>Triticum compactum</i></b>	1	30	80.3 $\pm$ 2.3	65.0	98.0	70.2 $\pm$ 1.7	57.4	78.0	21.6 $\pm$ 0.7	16.8	27.8	10.2 $\pm$ 0.4	7.8	14.4
<b><i>Triticum turgidum</i></b>														
subsp. <i>dicoccon</i>	1	29	69.5 $\pm$ 1.0	63.0	75.0	63.8 $\pm$ 1.4	55.0	73.0	17.4 $\pm$ 0.3	13.8	19.8	6.1 $\pm$ 0.2	4.6	7.2
subsp. <i>durum</i>	4	38	65.0 $\pm$ 2.0	47.0	85.0	59.6 $\pm$ 2.0	46.0	79.0	15.9 $\pm$ 0.4	13.1	18.9	6.3 $\pm$ 0.2	4.2	7.9
subsp. <i>turgidum</i>	1	16	80.0 $\pm$ 4.5	56.6	95.8	72.5 $\pm$ 4.1	52.8	89.1	21.5 $\pm$ 1.5	15.6	28.2	8.3 $\pm$ 0.8	5.9	12.4
<b><i>Zea mays</i></b>	1	15	126.9 $\pm$ 4.3	108.0	148.0	116.5 $\pm$ 3.2	106.0	130.0	23.5 $\pm$ 0.6	22.0	27.4	8.5 $\pm$ 0.7	6.4	10.9

**Table 3.** Biometric data of selected Poaceae pollen grains from the pollen collection of ISEM, Univ. Montpellier (France). Pollen is mounted in glycerol. Cultivated taxa are noted in bold. Mean values are given with the standard error.

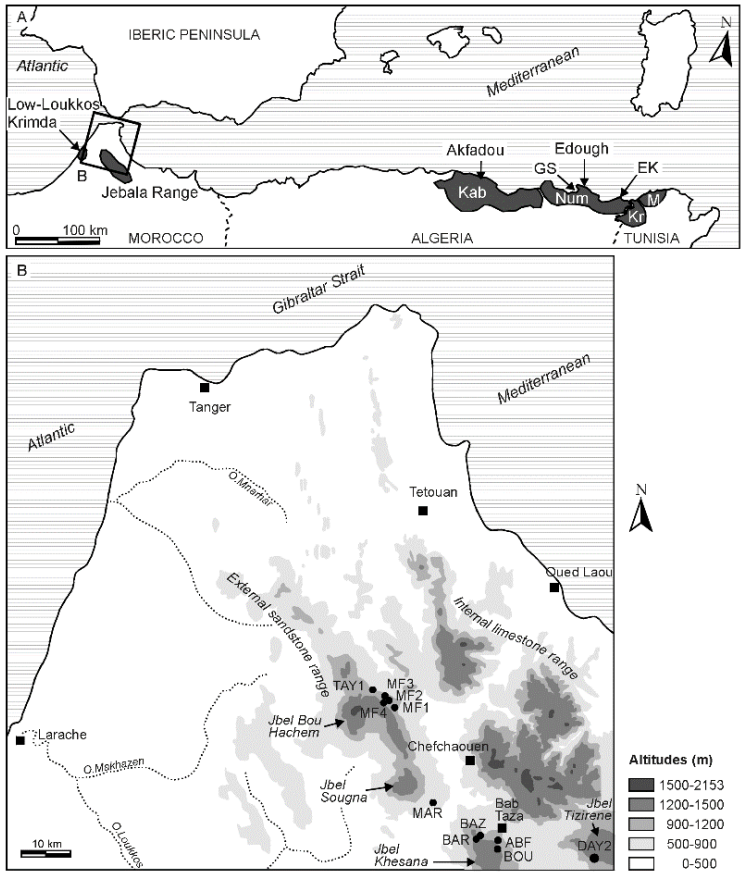
Representation	Pollen taxa	A		U		O	
Strongly associated taxa	<i>Alisma</i> -type	100	(82-100)	0	(0-18)	0	(0-18)
	Asterioideae	67	(43-84)	0	(0-25)	33	(16-57)
	Cyperaceae	100	(82-100)	0	(0-18)	0	(0-18)
	<i>Lobelia</i>	67	(25-92)	0	(0-57)	33	(8-75)
	<i>Lysimachia tenella</i> -type	67	(40-86)	14	(3-45)	25	(9-54)
	Poaceae	92	(70-98)	0	(0-20)	8	(2-30)
	<i>Ranunculus</i> -type	91	(68-98)	0	(0-21)	9	(2-32)
	Rubiaceae	67	(40-86)	0	(0-31)	33	(14-60)
	<i>Sphagnum</i>	100	(72-100)	0	(0-28)	0	(0-28)
	Associated taxa	Apiaceae	55	(32-76)	14	(3-45)	40
<i>Cicendia/Exaculum</i>		57	(29-81)	20	(5-56)	33	(12-65)
<i>Ilex</i>		50	(12-88)	0	(0-73)	50	(12-88)
Juncaceae		50	(29-71)	45	(24-68)	14	(3-45)
<i>Lotus</i> -type		64	(39-82)	36	(18-61)	0	(0-28)
<i>Plantago coronopus</i> -type		50	(29-71)	0	(0-31)	50	(29-71)
<i>Potamogeton</i> -type		50	(25-75)	33	(12-65)	33	(12-65)
<i>Potentilla</i>		56	(30-78)	29	(10-59)	29	(10-59)
<i>Samolus</i>		50	(12-88)	0	(0-73)	50	(12-88)
Weakly associated taxa		<i>Callitriche</i>	11	(3-38)	80	(44-95)	80
	<i>Dryopteris</i> -type	20	(5-56)	50	(12-88)	75	(36-94)
	<i>Frangula</i>	17	(4-50)	50	(12-88)	80	(44-95)
	<i>Genista</i> -type	22	(8-50)	50	(18-82)	71	(41-90)
	<i>Gratiola</i>	25	(6-64)	50	(12-88)	67	(25-92)
	<i>Illecebrum/Paronychia</i>	14	(3-45)	67	(25-92)	80	(44-95)
	<i>Lysimachia arvensis</i> -type	0	(0-57)	100	(27-100)	100	(27-100)
	<i>Prunus</i> -type	14	(3-45)	67	(25-92)	80	(44-95)
	<i>Salix</i>	18	(6-43)	50	(18-82)	78	(50-92)
	Over-represented taxa	<i>Alnus glutinosa</i> -type	25	(9-54)	0	(0-57)	75
Brassicaceae		25	(10-49)	0	(0-47)	75	(51-90)
<i>Calluna</i>		20	(5-56)	0	(0-73)	80	(44-95)
<i>Cerealia</i> -type		33	(16-57)	0	(0-40)	67	(43-84)
Cichorioideae		17	(6-40)	0	(0-57)	83	(60-94)
<i>Cistus</i>		17	(6-40)	0	(0-57)	83	(60-94)
<i>Erica</i> -type		42	(22-64)	0	(0-35)	58	(36-78)
Fabaceae		22	(8-50)	0	(0-57)	78	(50-92)
<i>Hedera</i>		20	(5-56)	0	(0-73)	80	(44-95)
<i>Isoetes</i>		43	(19-71)	0	(0-47)	57	(29-81)
<i>Lythrum salicaria</i>		0	(0-57)	0	(0-57)	100	(43-100)
<i>Myriophyllum alterniflorum</i>		0	(0-35)	0	(0-35)	100	(65-100)
<i>Nymphaea</i>		0	(0-73)	0	(0-73)	100	(27-100)
<i>Ophioglossum</i>		0	(0-57)	0	(0-57)	100	(43-100)
<i>Osmunda</i>		0	(0-57)	0	(0-57)	100	(43-100)
<i>Quercus canariensis</i> -type		8	(2-30)	0	(0-73)	92	(70-98)
<i>Radiola</i>		0	(0-57)	0	(0-57)	100	(43-100)
<i>Sparganium/Typha</i>	33	(8-75)	0	(0-73)	67	(25-92)	

**Table 4.** Indices (%) of association (A), under-representation (U) and over-representation (O) for taxa present in both plant and pollen datasets in the Jebala Range wetlands, with 90% confidence intervals given into brackets. See text for explanations.

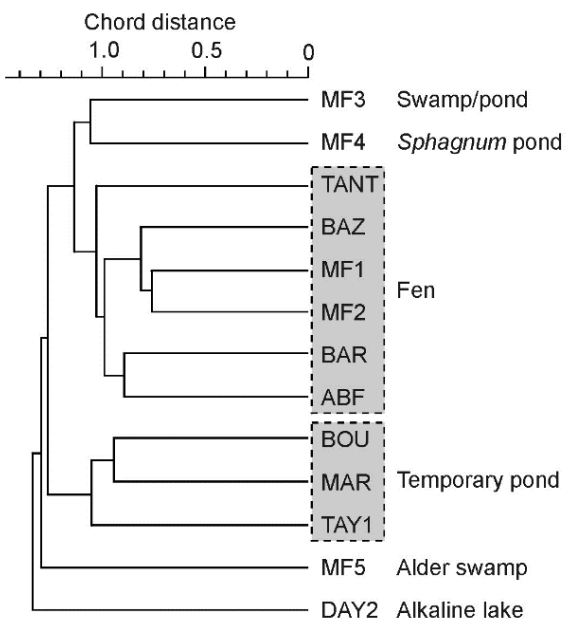
Site	Core	Depth (cm)	Code laboratory	Age <sup>14</sup> C (BP)	Calendar age 2σ (cal. BP)	Dated material	Reference
Bartete	BAR1bis	49-50	Poz-82703	55 ± 30	Modern	Sediment	This study
		50-51	Poz-87231	55 ± 30	Modern	Sediment	–
		61-62	Poz-94942	2485 ± 30	2720-2430	Sediment	–
		81-82	Poz-94943	4000 ± 35	4570-4410	Sediment	–
		99-100	Poz-82921	3795 ± 35	4350-4010	Sediment	–
		149-150	Poz-82922	5775 ± 30	6660-6490	Sediment	–
		190	Poz-51919	2350 ± 35	2660-2320	Charcoal: <i>cf. Lamiaceae</i>	Muller et al., 2015
		199-200	Poz-82923	8290 ± 50	9450-9040	Sediment	This study
		247-248	Poz-82924	11040 ± 70	13100-12780	Sediment	–
			BAR3-1977	125-130	Lv-635	1010 ± 50	1050-790
Maison Forestière-1	MF1b	35-36	Poz-61157	315 ± 30	460-300	Sediment	Muller et al., 2015
		65	Poz-51918	2060 ± 30	2110-1930	Charcoal: <i>Frangula alnus</i>	–
		83-84	Poz-57995	2125 ± 30	2290-2000	Sediment	–
		117	Poz-51917	11070 ± 60	13100-12840	Charcoal: Deciduous <i>Quercus</i>	–
		131.5-132	Poz-57997	4480 ± 60	5310-4880	Sediment	–
			MF3	95-96	Poz-76701	1040 ± 30	1050-840
Maison Forestière-3	MF3	200-201	Poz-76703	2440 ± 30	2700-2360	Sediment	–
		301-302	Poz-80990	3375 ± 35	3690-3490	Sediment	–
		400-401	Poz-76704	3980 ± 35	4530-4300	Sediment	–

**Table 5.** Radiocarbon ages of the studied sites (BAR, MF1b and MF3) and basal ages of other sites in the Jebala Range (from Reille 1977; Cheddadi et al., 2015, 2016). Ages highlighted in grey are rejected.

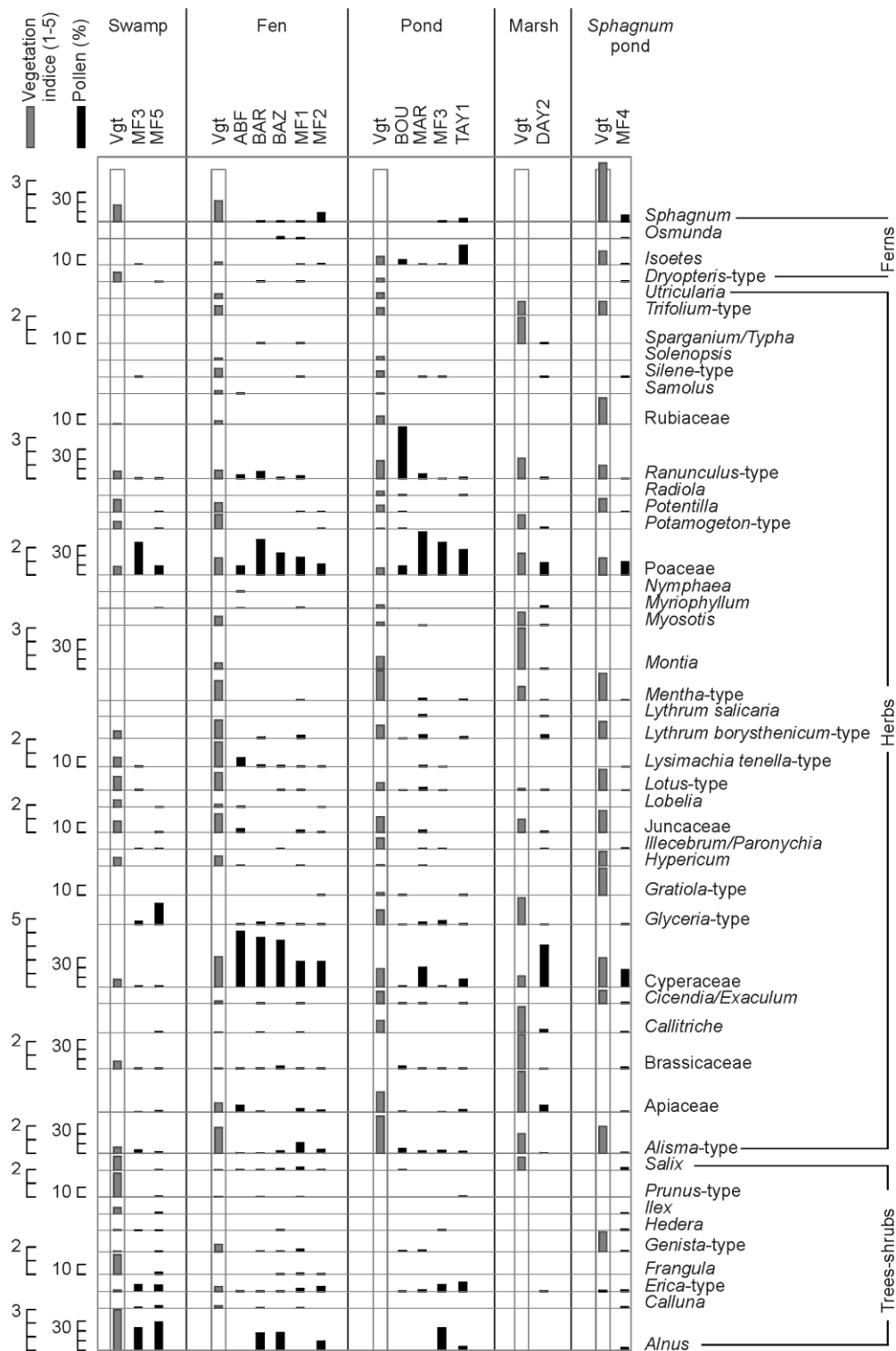




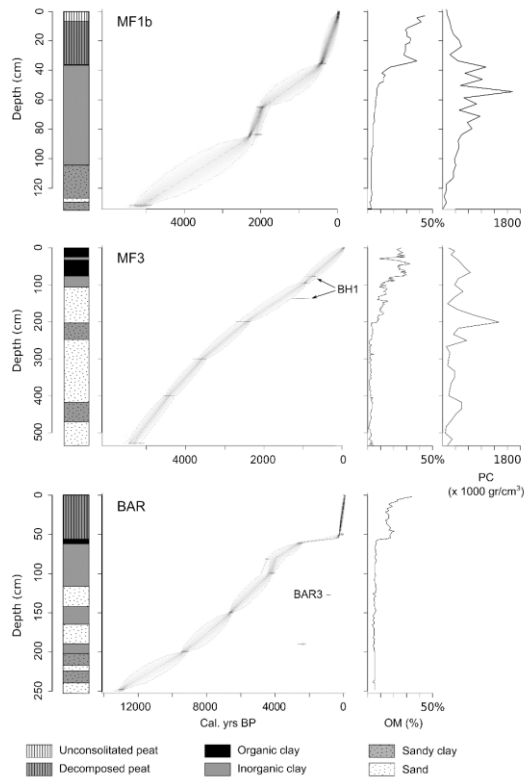
**Figure 1.** Location of studied regions and sites. (A): North African regions harbouring peat-forming wetlands. EK, El Kala National Park; GS, Guerbès-Senhadja wetland complex; Kab, Kabylia; Kr, Kroumiria; M, Mogods; Num, Numidia. (B): Reliefs and studied sites of Northern Morocco



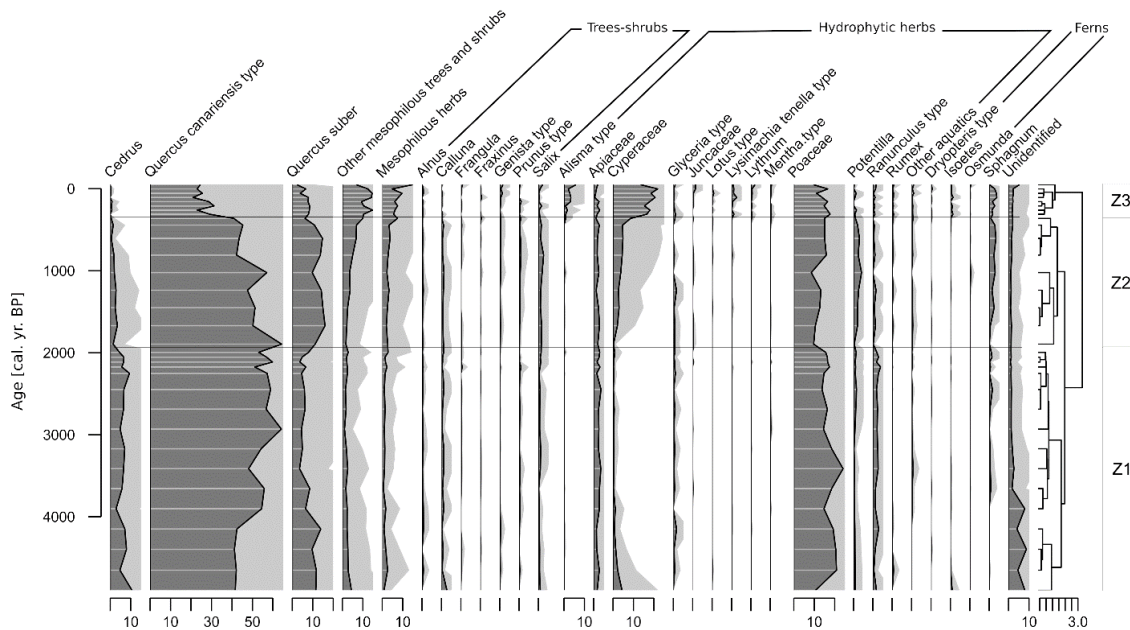
**Figure 2.** Ascendant hierarchical classification performed on phytosociological relevés (13 sites, 80 species)



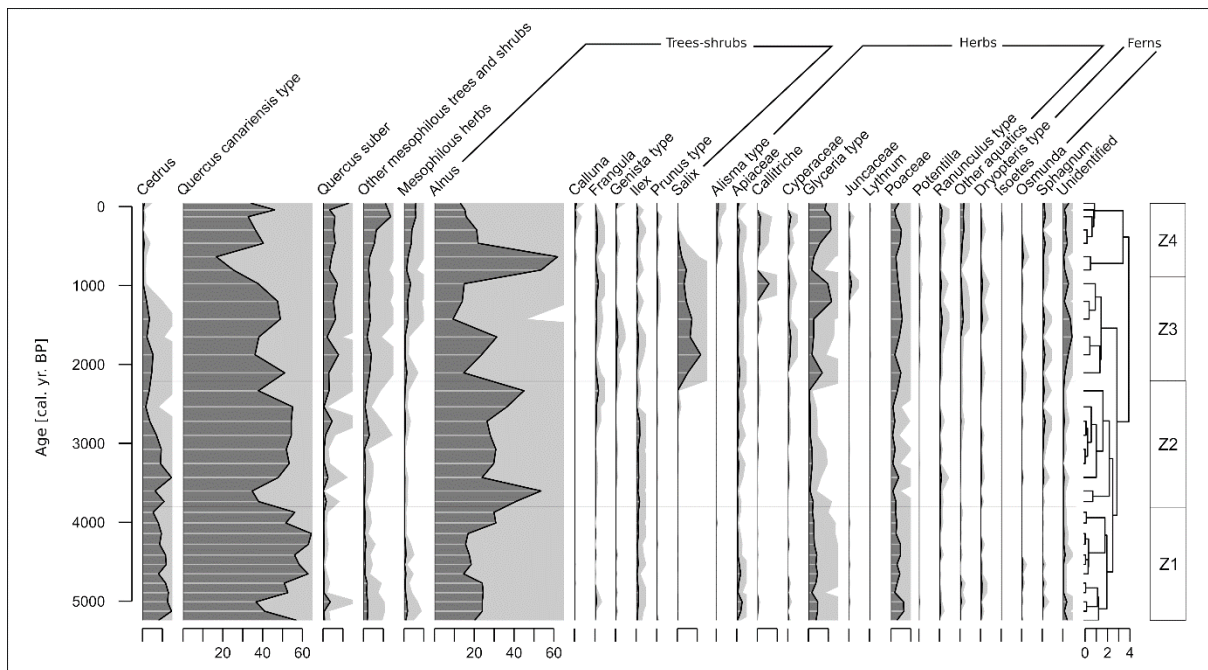
**Figure 3.** Surface percentage pollen diagram of hydrophytic taxa. Sites are grouped according to the classification in Figure 2. Grey histograms noted Vgt (in grey frames) correspond to mean abundance-dominance indices of vegetation surveys (1-5). Pollen percentages are calculated on pollen sums including terrestrial taxa but excluding ferns.



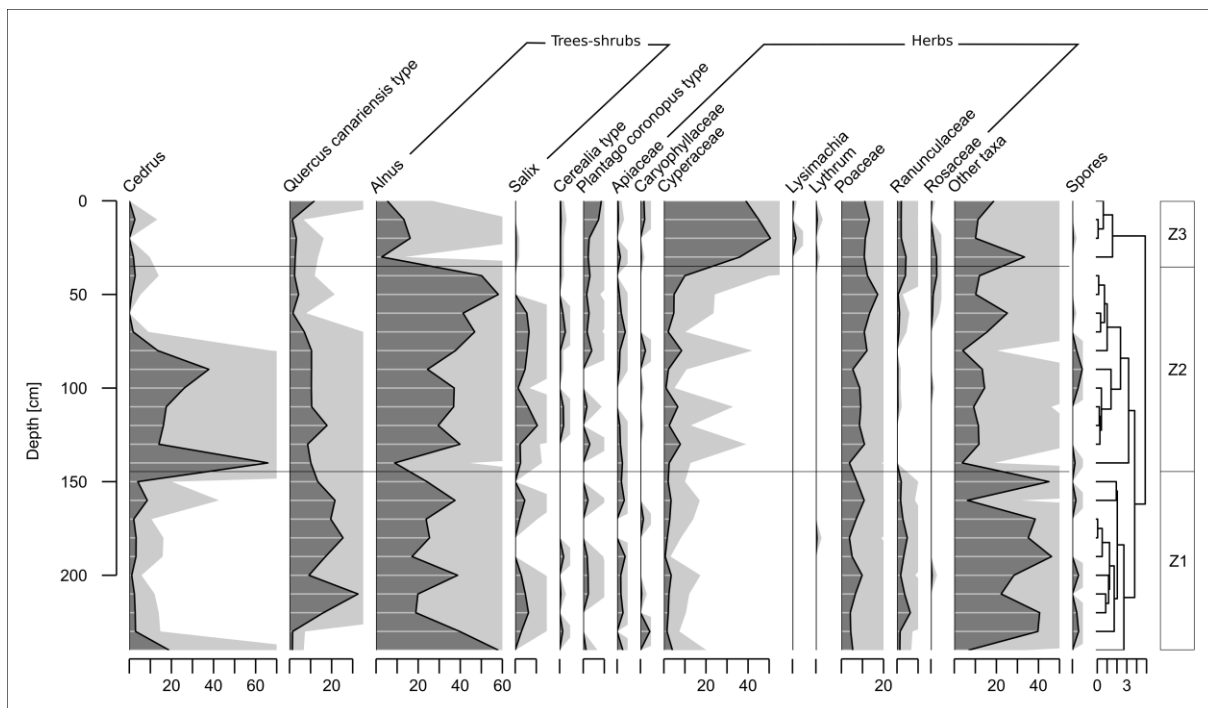
**Figure 4.** Age-depth models and content of organic matter (OM, %) of BAR, MF1b and MF3 cores and pollen concentrations (PC, x 1000 gr/cm<sup>3</sup>) of MF1b and MF3 cores. The ages in red are from other cores previously taken in the same wetlands (Reille 1977).



**Figure 5.** Local pollen percentage diagram of MF1b. Y axis is in years cal. BP. For each curve, is given the 5-fold exaggerated curve.



**Figure 6.** Local pollen diagram of MF3. Y axis is in years cal. BP. For each curve, is given the 5-fold exaggerated curve.



**Figure 7.** Local pollen diagram of BAR (from [Reille 1977](#)). Y axis is in cm. For each curve, is given the 5-fold exaggerated curve.