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The Holocene

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3 **Human demography changes in Morocco and environmental imprint** 4 **during the Holocene**

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26 **Keywords:** Human demography; Holocene; Morocco; anthropogenic pollen markers; fossil records; land
27 cover

28 **Abstract**

29 The aim of this work is to reconstruct the periods of growth and decline of human
30 populations in Morocco and their potential impacts on the landscape over the last 10,000 years.
31 In order to estimate trends in human population size between 10,000 and 3,000 years ago we
32 used a Summed Probability Distribution (SPD) of radiocarbon dates from a wide range of
33 archaeological sites throughout Morocco. Landscape changes were identified and quantified
34 from a data set of fossil pollen records. Different anthropogenic pollen markers, as well as
35 natural vegetation groups and taxonomic richness were used to analyze the relationship
36 between long-term trends in human population expansion or regression and type of impact on
37 the landscape.

38 Sub-regions of Morocco have different topographies and climates, which have either
39 favored or prevented the establishment and/or spread of human populations. In order to
40 identify areas most significantly impacted by humans and the timing of such impacts we have
41 reconstructed and compared the same past anthropogenic and landscape proxies along with
42 population trends within the lowlands and the mountainous areas. The lowlands were more
43 strongly impacted earlier in the Holocene than the mountainous areas. Anthropogenic markers
44 indicate that farming expanded in the lowlands during the first major expansion of human
45 populations between ca. 7200 and 6700 calibrated years BP at the start of the Neolithic period.
46 In the Atlas and Rif Mountains anthropogenic impact is not clearly detectable in any of these
47 areas before 4000 cal. BP.

48 **Introduction**

49 Humans have been present in the northwest corner of Africa throughout the Quaternary.
50 For example, fossil remains of *Homo sapiens* more than 300,000 years old were recently
51 discovered in Jebel Irhoud, near the town of Safi in Morocco (Hublin et al. 2017). This time span,
52 which encompasses the latter part of the Palaeolithic period, witnessed three climatic cycles
53 with marked interglacials that were similar to the Holocene, and long glacial periods (e.g. Hays
54 et al. 1976). . During the most recent glacial period, around 20,000 years BP, glaciers developed
55 even at low latitudes, such as within the Mediterranean (Hughes et al. 2006) including North
56 Africa at elevations as low as 2000 m a.s.l. (Hughes et al. 2011, Hughes et al., 2018). As a
57 consequence, plant and animal species were naturally constrained, which reduced their range
58 substantially and allowed them to persist only in refugial areas (e.g. Hewitt, 2000). Likewise,
59 humans would have adapted their population size and habitats locations in response to past
60 climate fluctuations (Roberts et al. 2018; van de Loosdrecht et al., 2018).

61 The recolonisation of new suitable habitats by humans after the last glacial period from
62 scattered populations was probably neither synchronous throughout the Mediterranean nor
63 continuous and homogeneous during the Holocene warm period (Hajar et al. 2010; Mercuri and
64 Sadori 2012). This may explain the asynchronous dating of the beginning and end of the
65 Neolithic in the Mediterranean (Morales et al. 2013; Linstädter et al. 2018). In terms of impact
66 on the landscape, as soon as human populations began to settle and/or to spread in the
67 Mediterranean basin they left clear imprints of their activities (cultivation, fire, domestication,
68 clearing, use of tools etc.) directly in the areas they occupied and indirectly in the fossil records
69 preserved in wetlands sediment archives and lakes. Most Holocene fossil records tend to show
70 that there were natural changes during the first thousand years of the Holocene when climate
71 mainly forced ecosystem changes, which was followed by complex interactions with increasing
72 human interference. Some authors have proposed that climate was the main driver of
73 synchronous ecosystem changes in the Mediterranean during the entire Holocene and that
74 landscape changes cannot be attributed to human activity alone (Jalut et al. 2009). Other
75 scholars have argued that there is an interplay between climate, humans and Mediterranean
76 ecosystems, which becomes complex to unravel when aridity increased during and after the
77 mid-Holocene (Carrión et al. 2010; Mercuri 2008; Sadori et al. 2011).

78 In Morocco, the earliest Holocene human use of plant resources was detected in the semi-
79 arid lowlands of the Northeast Moroccan hinterland. Charcoal samples from rock shelters
80 (Grösdorf and Eiwanger, 1999) and Epipalaeolithic open air sites (Ibouhouten et al., 2010,
81 Linstädter et al., 2012; Mikdad et al., 2000) provide ¹⁴C ages between 11,700 and 7,800 years
82 cal. BP. In the Middle Atlas Mountains, there are indications of early Holocene occupation
83 during the Epipalaeolithic with chronological evidence dating to around 8,400 cal BP from
84 Ouberid cave (Mikdad et al. 2012). However, the ecological impact of Epipalaeolithic hunter-
85 gatherers on the Early Holocene landscape was minor, therefore this early occupation is not
86 clearly reflected in secondary environmental archives. The first evidence for human impact on
87 vegetation cover is provided by recent and precise archaeobotanical studies that have dated
88 the onset of Early Neolithic occupation in northern Morocco, close to the Mediterranean Sea,
89 between 7700-7200 years cal. BP (Linstädter et al. 2016; Zapata et al. 2013).

90 Indirect evidence from fossil pollen records suggests that human impact has strongly
91 increased over the last four thousand years in Morocco and became increasingly apparent at
92 both low and high elevations (Lamb et al. 1991; Cheddadi et al. 2015, Campbell et al. 2017). In
93 addition to fossil pollen records, model simulations show that during the historic period, forest
94 cover on usable land may have dropped dramatically from an estimated 98% in 3000 BP to
95 31.7% in 1850 AD (Kaplan et al. 2009) in relation to the expansion of human population. In
96 Morocco, cedar forest cover in the Rif mountains decreased by about 75% between 1960 and

97 2010 (Cheddadi et al. 2017).

98 Human activities can be identified in the fossil pollen records through the occurrence and
99 abundance of those taxa that are considered anthropogenic indicators (Behre 1981; Mercuri et
100 al. 2011). Changes through time in human population size can also be estimated from the
101 summed probability distributions (SPD) of archaeological (e.g. anthropogenic) radiocarbon
102 dates (Crema et al. 2016; Gamble et al. 2004; Palmisiano et al. 2017 and in press; Shennan et al.
103 2013; Timpson et al. 2014; Weninger et al. 2009; Williams 2012; Zielhofer et al. 2008).

104 In the present study, we estimated the size of human population in Morocco for the time
105 period between 10,000 and 3000 cal BP and compared population variation during the
106 Holocene to several anthropogenic pollen indicators as well as to reconstructed natural
107 vegetation groups and past taxonomic richness derived from an extensive data-set of fossil
108 pollen records.

109 Morocco has a wide range of topographies with highest elevations ranging from 2500 in
110 the Rif mountain chain up to more than 4000masl in the High Atlas. There are also large coastal
111 lands and plains, which are intensively cultivated today. These complex topographic features
112 have almost certainly constrained the spread and settlement of humans throughout the
113 Moroccan landscape. The main objectives of this study are threefold (1) to reconstruct overall
114 human demographic changes in Morocco during the later prehistory (2) to identify different
115 past human activities in different areas using a set of anthropogenic markers from a dataset of
116 fossil pollen records and (3) to evaluate the spread of human activities and their impacts both
117 on the lowlands and mountain landscapes.

118 ***Materials and Methods***

119 ***Anthropogenic markers, natural vegetation groups and taxonomic richness***

120 The pollen data-set used in the present study includes 22 records from different areas
121 in Morocco, obtained from both original authors and digitized published work (figure 1A, table
122 1). There are two sites, Lake Hachlaf and Lake Sidi Ali, where two records were collected in
123 each lake. We integrated these duplicated records because they encompass different time
124 periods. The Moroccan pollen records were produced by various analysts over a ca. 40 year
125 period, between 1976 and 2017 and have been dated relatively accurately by conventional and
126 AMS radiocarbon dating. Some of the oldest pollen records (Reille, 1976; 1977 and 1979) have
127 been dated using very few radiocarbon dates. Three pollen records (Marzine in the Rif,
128 Tessaout and Tizi Inouzane in the High Atlas) for which the published chronologies were based
129 on just one ¹⁴C date (Reille, 1976; 1977), while one record (Iguerda-Ait-Amama in the Middle
130 Atlas) has not been dated by any radiometric methods (Reille, 1976). The age/depth models
131 that we have built for these four pollen records are based on the published original author's
132 assumptions based on stratigraphic markers and expertise. The time spans proposed by the
133 original author (Atlantic, Sub-boreal and Sub-Atlantic periods) have been used to build a
134 quantitative chronology for the four pollen records.

135 Within the dataset, there are five pollen records located at elevations lower than 800m
136 asl. Two of them encompass the Early Holocene and three others only cover the mid- late
137 Holocene (after 6500 BP). Thus, in the data-set used in this study, there are more pollen records
138 that encompass the entire Holocene period in the mountains than in the lowlands. Such bias in
139 the duration and the spatial distribution of the pollen records in Morocco must be taken into
140 account when interpreting the occurrence of anthropogenic markers and overall vegetation
141 changes. All of the pollen records compiled have been archived in a MySQL database, which has
142 a compatible structure with the European Pollen Database
143 (www.europeanpollendatabase.net). The Moroccan pollen data will be contributed to the
144 European Pollen Database (Leydet, 2007-2018).

145 We defined five anthropogenic pollen markers (APMs) from the taxa identified in the
146 fossil pollen records (table 2). These APMs are based on earlier published research and are
147 considered indicative of human activities (Behre 1981; Mercuri 2008; Mercuri et al. 2011;
148 2013a; 2013b; Sadori et al. 2011). The reconstructed APMs include:

- 149 - Anthropogenic pollen index (API)
- 150 - Regional pastoral indicators (RPI)
- 151 - Anthropogenic nitrophilous herbs (ANH)
- 152 - Cultures and crops (CC)
- 153 - *Olea-Juglans-Castanea-Vitis* (OJCV)

154 We selected these five APMs to allow comparisons with a selection of similar studies
155 based on six other regions spanning the Mediterranean and a Mediterranean-wide synthesis of
156 Holocene population and landscape change (see Bevan et al., in press, Roberts et al., in press).
157 In Morocco, these APMs were reconstructed for three separate regions: the Rif Mountains, the
158 Atlas Mountains and lowland sites (located at an elevation lower than 800m asl). The three sub-
159 regions were then amalgamated and reconstructions produced, for the entire country as one
160 overall entity that takes all of the pollen records into account (figure 2). One palynological
161 difference with these similar studies carried out in other Mediterranean regions is the exclusion
162 of *Artemisia* from the APMs because it is a natural dominant taxon in Moroccan steppe
163 landscapes which occurs in the mountainous areas (e.g. Saadi and Bernard, 1991). Thus,
164 *Artemisia* was not considered an anthropogenic marker in the present study. In addition to the
165 APMs, we reconstructed the pollen taxonomic richness (figure 3) using rarefaction analysis
166 (Birks and Line 1992) for the same areas and pollen records as the APMs. Fossil pollen samples
167 represent a partial representation of the anemophilous plants, due to the differing pollen
168 productivity of different plants and their dissimilar dispersal capacity. The number of identified
169 and counted pollen grains is also often, if not always, different from one analyzed sample to
170 another within the same record. Rarefaction analysis provides an unbiased estimate of the
171 number of taxa in a fossil sample which allows a comparison of the pollen analyses from
172 different samples in the same record (Birks and Line 1992). However, one should keep in mind
173 that the pollen taxonomic richness does not represent a measure of the species diversity, *sensu*
174 Shannon or Simpson indices, as one pollen taxon may correspond to one or several species and
175 the pollen percentage in a fossil sample does not correspond to the number of occurrences of
176 the species in the studied site. Modern human activities often result in negative impact on
177 species diversity. Pollen taxonomic richness is not a direct indicator of past human
178 disturbances, but it may help comprehend whether the past human demographic changes had
179 a negative or positive impact on species diversity.

180 In addition to the APMs and pollen taxonomic richness, we also used clusters of pollen
181 taxa to identify four natural vegetation groups (figure 4) that represent the main ecosystem
182 types in Morocco (Quézel and Médail, 2003). These natural vegetation groups are ordered by
183 increasing elevation (1) evergreen trees and shrubs, (2) deciduous trees, (3) mountain conifers,
184 and (4) steppe (table 3). This is based on grouping pollen samples into 'vegetation clusters'
185 according to their taxa assemblages and builds on the cluster analysis approach used by
186 Woodbridge et al. (2018) and Fyfe et al. (2018).

187 **Demographic change over the Holocene**

188 In the past two decades one of the most popular proxies for inferring demographic trends
189 in the prehistoric period has involved summed probability distributions (SPDs) of
190 archaeological radiocarbon dates as a result of increasingly sophisticated methods (Rick, 1987;
191 Shennan and Edinborough, 2007; Bocquet-Appel et al., 2009; Shennan et al., 2013; Timpson et
192 al., 2014; Balsera et al., 2015; Crema et al., 2016; Bevan et al., 2017; Palmisano et al.; 2017;
193 Capuzzo et al. 2018). The SPD results from 'counting up' (summed in the manner of a

194 histogram) the calibrated raw radiocarbon years of each organic sample, which are expressed
195 as probability statements with error ranges. This is based on the assumption that the more
196 people living in a given region, the more archaeological remains, the more organic materials,
197 and the more samples can be collected for radiocarbon dating (Rick 1987). Such indicators do
198 not offer good evidence for absolute numbers of a human population but rather give an idea of
199 relative intensities of population and proportional change through time. Although SPDs of
200 radiocarbon dates has been extensively used by archaeologists for modelling population
201 fluctuations in prehistory, it faces several challenges such as biases in research strategies,
202 budgets and interests that can undermine a random sample of human activity in every
203 archaeological phase.

204 Over the past ten years, both the number and the accuracy of radiocarbon dates have
205 increased in most newly investigated archaeological sites. This is the case in Morocco, where
206 more than two-thirds of the radiocarbon dates used in the present study were published in the
207 past decade. In the present study we have estimated human population size in Morocco from
208 270 uncalibrated radiocarbon dates which have been collected from 83 archaeological sites
209 (figure 1B) between 10,000 and 3000 cal BP. To our knowledge, the dataset used in this work
210 represents the largest existing collation of archaeological radiocarbon data for Morocco. This
211 number of dates collected ($n=270$) exceeds the suggested minimum threshold of 200-500 dates
212 to produce a reliable SPD with reduced statistical fluctuation for a time interval of 10,000 years;
213 specific issues about sample size will be discussed below (Michczyńska and Pazdur, 2004;
214 Michczyńska et al., 2007; Williams, 2012, 580-581). We are aware of the limitations of our
215 dataset and the results are a preliminary attempt to reconstruct demographic change given the
216 spatially restricted archaeological data available in the area.

217 All of the radiocarbon dates are from archaeological contexts, with the majority based on
218 samples of bone, charcoal and wood. Radiocarbon dates obtained from marine sources, such as
219 shells have been removed (and are not part of the above total) to avoid the complicated issues
220 arising from unknown or poorly understood marine reservoir offsets. The probabilities from
221 each calibrated date have been combined to produce a summed probability distribution (SPD,
222 figure 5)¹. The potential bias of oversampling particular site-phases has been reduced by
223 aggregating multiple uncalibrated radiocarbon dates from the same site that are within 100
224 years of each other and dividing by the number of dates that fall within this time 'bin' (see
225 Timpson et al. 2014). Following this process, the probabilities of each bin are summed: in our
226 case, 270 radiocarbon dates have been aggregated into 207 bins. Following previous works
227 (Weninger et al. 2015; Williams 2012), which show that normalized calibrated dates emphasize
228 narrow artificial peaks in SPDs due to steepening portions of the radiocarbon calibration curve,
229 we opted to use unnormalized dates prior to summation and calibrated via the IntCal13 curve
230 (Reimer et al. 2013; see former applications of calibrated unnormalized radiocarbon dates in
231 Bevan et al. 2017; Palmisano et al. 2017; Roberts et al. 2018). A logistic null model representing
232 expected population increase has been fitted to the observed SPD in order to produce a 95%
233 confidence envelope (composed of 1,000 random SPDs) and statistically test if the observed
234 pattern significantly departs from this model (for the general approach see Shennan et al 2013;
235 Timpson et al 2014; as specifically implemented in Bevan and Crema 2018: modelTest,
236 'uncalsample'). Deviations above and below the 95% confidence limits of the envelope
237 respectively indicate periods of population growth and decline greater than expected according
238 a logistic model of population growth. However, it is important to recognize that a logistic
239 model cannot strictly be considered as a realistic model for population growth, but rather as
240 an elementary model useful for quantitatively testing population fluctuations (cf. Turchin

¹ The analysis has been performed in R v. 3.3.3 by using the package *rcarbon* developed by Crema and Bevan (2018).

241 2001). In this case, a logistic model was selected as a more suitable option as opposed to other
242 possible null-models (e.g. uniform, exponential) given the observed shape of radiocarbon date
243 SPDs in our study area (see Fig. 5).

244 As proxies for past population estimates from the SPDs of radiocarbon dates can be used
245 as recently as ~3000 Cal yr BP in Morocco, that is prior to the historical time period when
246 archaeological chronologies rely more on specific evidence such as datable coins, written
247 source and fine-ware pottery rather than on radiometric dating.

248 **Chemical elements**

249 A chemical elements analysis was carried out, using portable X-ray fluorescence (XRF)
250 technique, on a sediment core retrieved in Ait Ichou swamp in the south of the Middle Atlas
251 (Tabel et al., 2016). XRF analyses allowed the variation of more than 20 chemical elements to
252 be measured over the past 25,000 years covered by the Ait Ichou core. However, only four
253 chemical elements were used in this study (figure 6). These elements are iron (Fe), lead (Pb),
254 zinc (Zn) and copper (Cu). These elements were selected as indicators of human activity and
255 marked increase of their concentration in the sedimentary record is related to different human
256 activities in the area.

257 **Results**

258 The compiled fossil pollen data-set (figure 1A) and archaeological radiocarbon dates
259 (figure 1B) allow us to reconstruct of several anthropogenic markers (figure 2), past plant
260 taxonomic richness (figure 3), natural composition of past ecosystems (figure 4) as well human
261 demography changes (figure 5) during the Holocene. The anthropogenic pollen markers allow
262 us to identify of potential relationships between natural ecosystems and superimposed human
263 disturbances. A spatial and temporal analysis of these pollen markers may provide information
264 on the timing of human interference throughout the Holocene and the types of impact. The
265 proportions of the reconstructed anthropogenic markers correlate with the estimated human
266 demography, which may provide information about the intensity of human impacts on the
267 landscape.

268 The archaeo-demographic results (Figure 5) show some significant overall departures
269 of the SPD of observed data from the envelope of the logistic model ($p = 0.006$), which indicates
270 that population did not grow logistically from 10,000 to 3000 BP in Morocco. The population
271 was greater than predicted by the logistic null model in the Middle Holocene between ~7200-
272 6700 cal. BP and ~6300-6200 cal. BP. In contrast, population was significantly below expected
273 values in the Early Holocene (~9200-9000 cal. BP, ~8450-8370 cal. BP and ~8200-8000 cal.
274 BP). Another marked decline in population occurs during 4800-4500 cal. BP. Generally, the
275 level of population was lower in the Early Holocene and started increasing substantially with
276 the onset of the Neolithic in the 8th millennium cal BP. The duration of these periods of
277 decreasing and increasing human population differ and varies between ca. one and ca. four
278 centuries (figure 5).

279 The anthropogenic pollen markers API, ANH and CC show a marked increase (figure 2)
280 that matches the first significant expansion of human populations between 7180 and 6740 cal
281 BP (event 4 in figure 5). This first increase in pollen indicators of human activity is recorded
282 mainly in the lowland sites rather than in the Rif and Atlas Mountains. The arboreal pollen
283 percentages decrease most significantly within sites located at lower altitude. Human
284 demographic changes (figure 5) and the three APMs (API, ANH and CC) from the lowland sites
285 are positively correlated (table 4). Pollen taxonomic richness shows a significant correlation
286 with SPDs (table 4) with a marked increase between 7180 and 6740 then between 6330 and
287 6240 when human population also increased (events 4 and 5). This correlation is more

288 significant in sites located in the lowlands than in the Rif and Atlas Mountains (figure 3). Periods
289 of decreasing human population (events 1, 2, 3 and 6, figure 5) are not marked in the lowlands
290 or in the mountains. In order to evaluate the impact of human demographic changes on natural
291 ecosystems we have reconstructed four groups of vegetation (figure 4, table 3), which are well
292 defined in Morocco (Quézel and Médail, 2003) and pollen grains representing these plant
293 species have been identified in the fossil records. These vegetation groups include montane
294 conifers, deciduous trees, evergreen trees and shrubs and steppic plants (figure 4). None of
295 these groups shows a significant correlation with human demographic changes during the
296 Holocene (table 4) and none of the human population increases (event 4 and 5) or decreases
297 (events 1, 2, 3 and 6) clearly reflect changes in any vegetation group.

298 **Discussion**

299 The modern challenges facing the Mediterranean region in terms of managing the impacts
300 of both the climate change and human population growth are intensifying. Human pressures on
301 Mediterranean biodiversity has steadily increased over the last century and reached a critical
302 threshold within the last few decades. Understanding of past relationships between human
303 demography and ecosystem changes is paramount to managing ongoing landscape changes and
304 requires studies integrating longer time scales than the last few decades.

305 Morocco is within the Mediterranean floristic area, which is considered a hotspot of
306 biodiversity (Myers et al. 2000) with approximately 22% of endemic vascular plants (Rankou
307 et al. 2013). Due to the geographical expansion of human population and related activities,
308 several species have become extinct over the last century and many species are endangered or
309 in threat of extinction today (IUCN, 2018). Forest cover in Morocco has been decreasing steadily
310 and substantially over the past century (Kaplan et al. 2009) and all ecosystems, from the
311 seashore to the highest elevation mountains, have been impacted by expanding human
312 activities and increasing exploitation of ecosystem resources. For example, cedar forest cover
313 in the Rif Mountains has decreased by about 75% over the last 50 years, from more than 45k
314 ha to ca. 10k ha today (Cheddadi et al. 2017). Simultaneously, human population more than
315 quintupled between 1900 and 2014, from ca. 6 to ca. 34 million inhabitants. In this context,
316 today more than ever it is important to analyze and understand past impacts of human
317 demographic change on different ecosystem types. The Neolithic is a very interesting period for
318 exploring the impact of early human expansions and regressions, on landscapes and the
319 increasingly complex ways in which such activities are superimposed on climate change
320 records. This may help to evaluate the ecosystem's capacity for adaptation and resilience to the
321 combined effects of natural and human induced changes.

322 Evaluation of human demography during the Neolithic can be performed using
323 radiocarbon dates available from archaeological sites and *ad hoc* statistical tools (Crema et al.
324 2016; Gamble et al. 2004; Palmisiano et al., 2017; Shennan et al. 2013; Williams 2012).
325 However, one should be cautious as archaeological sites are often not exhaustively studied and
326 there may be important differences in the number of dates available at each site. This is clearly
327 the case for Morocco where the number of ¹⁴C dates used in this study could certainly be
328 improved with additional archaeological sites and more ¹⁴C dates per site. Other additional
329 potential biases related to ¹⁴C date measurements and their calibration may also introduce
330 some errors in estimating human demographic trends using SPDs (Shennan et al. 2013), as well
331 as the duration of the expansion/regression of human populations (Manning et al. 2014). Used
332 as a demographic proxy, SPDs may reflect only a local (or regional) expansion of human
333 population rather than representing a spatially large spread (Shennan et al. 2013).

334 There is a large literature focused on human expansion and related activities in the
335 Mediterranean basin during the Neolithic (summarized in Shennan, 2018). However, the timing

336 of expansion and, the type and intensity of the impacts are not synchronous and probably not
337 comparable throughout the Mediterranean region. Today, human population in Morocco is
338 composed mainly of Berbers (autochthonous population) and Arabs. Genetic analyses of North-
339 Western African populations reveal that lineages of different Berber groups may date back to
340 at least the last glacial period and that the omnipresence of a certain mitochondrial DNA motif
341 suggests a continuous presence of these populations in Morocco over more than 20,000 years
342 (Rando et al., 1998). All recent genetic studies agree that the spread of human populations in
343 North Africa originated from the East-West (Bentayebi et al. 2014), rather than originating from
344 sub-Saharan populations (Desanges, 1981). The genetic contribution of sub-Saharan
345 populations to the modern North African populations seems to be minor (Bosch et al., 1997;
346 Brakez et al., 2001). Recent archaeological findings in Northern Morocco indicate the absence
347 of Saharan influences during the Early Neolithic until 6.0 cal ka BP (Linstädter et al., 2018).
348 Thus, even if the timing, continuity and degree of expansion of the migrating original
349 populations is still under scientific debate, the Eastern origin of the modern North African
350 populations is now genetically proven. Rando et al. (1998) state that the modern dominating
351 lineages arrived in North Africa, during the Mesolithic and Neolithic in waves while Arredi et
352 al. (2004) propose that the Neolithic transition in North Africa was accompanied by demic
353 diffusion (see Cavalli-Sforza et al. 1993). The marked variations in ¹⁴C date SPDs (figure 5) and
354 the discontinuous occurrences of the fossil anthropogenic markers (figure 2) suggest that
355 human population in Morocco did not increase steadily during the Holocene, but involved
356 marked periods of 'booms' and 'busts' that impacted upon the landscape intermittently. These
357 past demographic variations (figure 5) and discontinuous landscape changes could probably
358 have resulted from waves of immigrating populations rather than demic diffusion into Morocco
359 during the Holocene.

360 The SPD data suggest that human demography fluctuated during the Holocene with two
361 periods of noticeable population increase and four others with noticeable population decrease
362 (figure 5; table 4). Human population increased substantially with the onset of the Atlantic
363 Neolithic around 7400/7300 cal BP. In agreement with the SPD data, pollen markers of cultures
364 and crops and farming increased in sites located at low elevation. The correlation between the
365 anthropogenic markers and SPD (table 5) suggests that human impact was not only local or
366 regional, but probably took place over a larger area. However, this positive correlation is based
367 on only five lowland records, which includes two Holocene archaeological sites (figure 1B, table
368 1) and three pollen records that encompass the second half of the Holocene (younger than 6500
369 cal. BP). To confirm that human impact in the lowlands was spatially more extended would
370 require additional Holocene data from off-site contexts, such as lake sediments at low elevation.
371 The pollen records available in the Rif and Atlas Mountains are more numerous, well dated and
372 many of them encompass the entire Holocene (table 1). In these montane records we do not
373 observe a significant correlation between the APMs and SPDs (table 5) which supports the
374 interpretation that human imprints were probably restricted to the lowland areas during the
375 Early Neolithic. Archaeological findings in the Moroccan coastal areas and lowlands confirm the
376 presence of cultivated landscapes as early as ca. 7000 cal BP (Ballouche and Marival 2003;
377 Linstädter et al. 2016; López-Sáez and López-Merino, 2008; López-Sáez et al., 2013; Morales et
378 al. 2013; Zapata et al. 2013). At higher elevations, several palaeoecological studies indicate late
379 Holocene human impacts on ecosystems in the Atlas and the Rif Mountains (Abel-Schaad et al.
380 2018; Campbell et al., 2017; Cheddadi et al. 2015; Lamb et al. 1991; Reille 1977; Zielhofer et al.
381 2017). The low correlation between forest ecosystems (figure 4), which occur mainly in the
382 mountain areas, and SPDs (table 5) suggest a lower level of human impact at higher elevations.
383 Inhabitants of the Moroccan mountains may have included populations of hunters-gatherers
384 rather than farmers, which could have delayed the expansion of cultivation and food production

385 "technologies" (Bosch et al. 1997) and, therefore, may explain the absence or low level of human
386 imprints during the Early Neolithic in the Rif and Atlas Mountains. Prior to the first period of
387 significant human expansion (ca. 7400 cal BP) there are high values of OJCV (>10%) that are
388 dominated by *Olea* pollen percentages, which may be interpreted as related to early
389 domestication of the olive tree in Morocco. However, these high *Olea* occurrences are recorded
390 during a time span of significantly lower human population (figure 2). The increase in *Olea*
391 pollen percentages during the early Holocene in Morocco likely corresponds to the spread of
392 wild stands (oleaster) under a warmer early Holocene climate (Cheddadi et al. 1998) rather
393 than to early domestication of the olive tree (see Langgut et al., this volume).

394 Reconstructed pollen taxonomic richness (figure 3) is not well correlated with human
395 demographic changes either in the lowlands or in the mountainous sites (table 5, figure 3),
396 which suggests that either human demographic fluctuations had a minor impact on the
397 structure and composition of the ecosystems or that such ecosystems are highly resilient. This
398 reflects the characteristics of modern Mediterranean ecosystems, which are considered highly
399 resilient to human disturbances due to their high ecological diversity (Lavorel, 1999; Pausas et
400 al. 2008).

401 After the first major increase in human population (7180-6740 cal BP) we observe a
402 quasi-steady decreasing trend, which reached a noticeable SPD minimum between ca. 4820 and
403 ca. 4530 cal BP (figure 5). The anthropogenic markers (API, ANH and CC) also decreased in the
404 lowlands and remained low in the Rif and Atlas Mountains (figure 2) during this time, which is
405 coherent with the reconstructed decreasing trend in human population. Within the Rif
406 Mountain archaeological sites cereals and anthropogenic herbs decreased between 6700 and
407 6000 cal BP, indicating reduced grazing and cultivation activities (Linstädter et al. 2016). The
408 SPD data indicate that human population remained low until 4000 cal BP, which probably
409 marks the end of the Neolithic in Morocco.

410 Unlike other parts of the Mediterranean, the metal ages (Bronze, Copper, Iron) are not
411 well dated in Morocco. X-Ray fluorescence measurements of the fossil record in the southern
412 part of the Middle Atlas (Tabel et al. 2016) show that iron (Fe), lead (Pb), copper (Cu) and zinc
413 (Zn) started to increase significantly after 4000 cal BP (figure 6) which seems to be earlier than
414 in other parts of the Mediterranean (Van Der Plicht et al. 2009), and coherent with earlier
415 archaeological studies in Morocco (Daugas et al. 1998; Ballouche and Marinval 2003). Chemical
416 elements (Fe, Cu, Zn and Pb) are often associated with human activities during the metal ages
417 (i.e. the Bronze and Iron Ages) probably mark the beginning of an "industrial" period dedicated
418 to their extraction. The SPD data cover the period between 10000 and 3000 cal BP, which does
419 not allow exploration of human demographic changes during the Iron age. In the northern part
420 of the Middle Atlas, and increase in lead concentration (Pb) in a fossil record (Nour El Bait et al.
421 2014) started around 2000 cal BP, which corresponds to the beginning of the Roman presence
422 in Morocco. In the Rif Mountains, the geochemical content of several records show similar
423 changes to those of the Middle Atlas after 2000 cal BP and are clearly related to Roman
424 industrial activities, which started to impact upon mountain ecosystems, such as through the
425 degradation of the Atlas cedar forests (Cheddadi et al. 2015). The impact of Roman activities in
426 Morocco seems to have been more critical for forest ecosystems with a decrease in arboreal
427 pollen percentages (figure 2), particularly those of the deciduous and evergreen trees (figure
428 4).

429 It is interesting to note that taxonomic diversity, as detected by pollen records, (figure 3)
430 was not altered during the Neolithic nor the Bronze/Iron Ages and not even during the Roman
431 period. Today, areas rich in endemic species are threatened by the wide range of human
432 activities particularly in areas identified as biodiversity hotspots such as the Mediterranean
433 (e.g. Cincotta et al. 2000). Pollen taxonomic richness in Morocco actually shows a relatively

434 steady increase throughout the Holocene and increases more over so throughout the last 3000
435 years during the metal ages. Elsewhere, several paleoecological studies have also shown that
436 the last thousand years of the Holocene are marked by an increase in pollen taxa richness (e.g.
437 Birks and Line 1992; Lotter 1998), which is paradoxical with the modern negative impacts of
438 human activities on ecosystems and their species richness, but perhaps consistent with the
439 well-known (but debated) intermediate-disturbance hypothesis (e.g. Fox, 2013). Unlike during
440 the modern industrial era, human activities during earlier periods of the Holocene, which
441 mainly involved livestock grazing and cultivation, were excellent means for the dispersal of
442 seeds, propagation of domesticated plants and the dispersal of ruderal plants that are often
443 subservient to crops.

444 Our study suggests that there are major differences between past and modern human
445 activities, such as modern artificial reduction of species ranges through the industrial
446 exploitation of forest resources (e.g. Pearson and Dawson 2003), mono-specific plantations
447 over large areas (Brockerhoff et al. 2008), the introduction of invasive and alien plant species
448 which strongly and negatively disturb ecosystem composition (Thuiller et al. 2005), the
449 widespread use of herbicides and pesticides, and the abruptness of ongoing climate change
450 (<http://www.ipcc.ch/>) which restricts species ranges. Modern human activities are causing
451 rapid, novel, and substantial changes to Earth's ecosystems (Vitousek et al. 1997; Nolan et al.,
452 2018) that we have not observed in our Holocene records in Morocco.

453 **Conclusions**

454 The last 10,000 years represent an informative time span encompassing the spectrum of
455 natural to anthropogenic forcing, which includes a period of natural climatic changes, with
456 negligible human impact in the early Holocene, followed by a period of interplay between
457 natural and anthropogenic impacts with the expansion of human populations.

458 The archaeological and environmental data used in this study indicate that prior to 7400
459 cal BP human populations had a limited impact on the lowland landscape and mountain
460 ecosystems. The earliest significant expansion of human population in Morocco during the
461 Holocene took place around 7000 cal BP and it is marked in the fossil pollen record by an
462 increase in farming indicators, particularly crop pollen markers. This time span is a few
463 hundred years later than the beginning of the Neolithic period in Morocco and ends around
464 4000 cal BP when iron, copper and zinc content started to increase in sedimentary records.
465 Geochemical elements were extracted to make metal tools, which marks the end of the Neolithic
466 period and probably the beginning of a prehistoric metallurgical industry era. We observe that
467 several anthropogenic indicators increase when human population increases. Likewise, natural
468 ecosystem changes, including forest species, are negatively or positively impacted by an
469 increase or a decrease in human population size during the Holocene, respectively.

470 The correlations we have performed between ¹⁴C date SPDs, as a proxy for population
471 change, and the fossil pollen data suggest that:

472 (1) early expansion of human populations around 7000 cal BP took place mainly in the
473 lowlands and if there was a spread towards the mountain areas then it was either minor or the
474 spreading populations had a negligible impact on natural ecosystems. However, early Holocene
475 anthropogenic evidence is derived from very few lowland sites. To confirm whether there was
476 a more extensive vegetation change additional data from archaeological off-site contexts, such
477 as lake sediments, are still needed.

478 (2) the principal human activity detected in the lowland records involved grazing and
479 farming until ca. 4000 cal BP.

480 (3) plant domestication seems not to have taken place before the early expansion of
481 human populations in Morocco, which is recorded during the Neolithic around 7000 cal BP.

482 The conclusions drawn in the present study have potential to be clarified through
483 integration of additional archaeological sites with more radiocarbon dates and new fossil pollen
484 records from lower elevations areas.

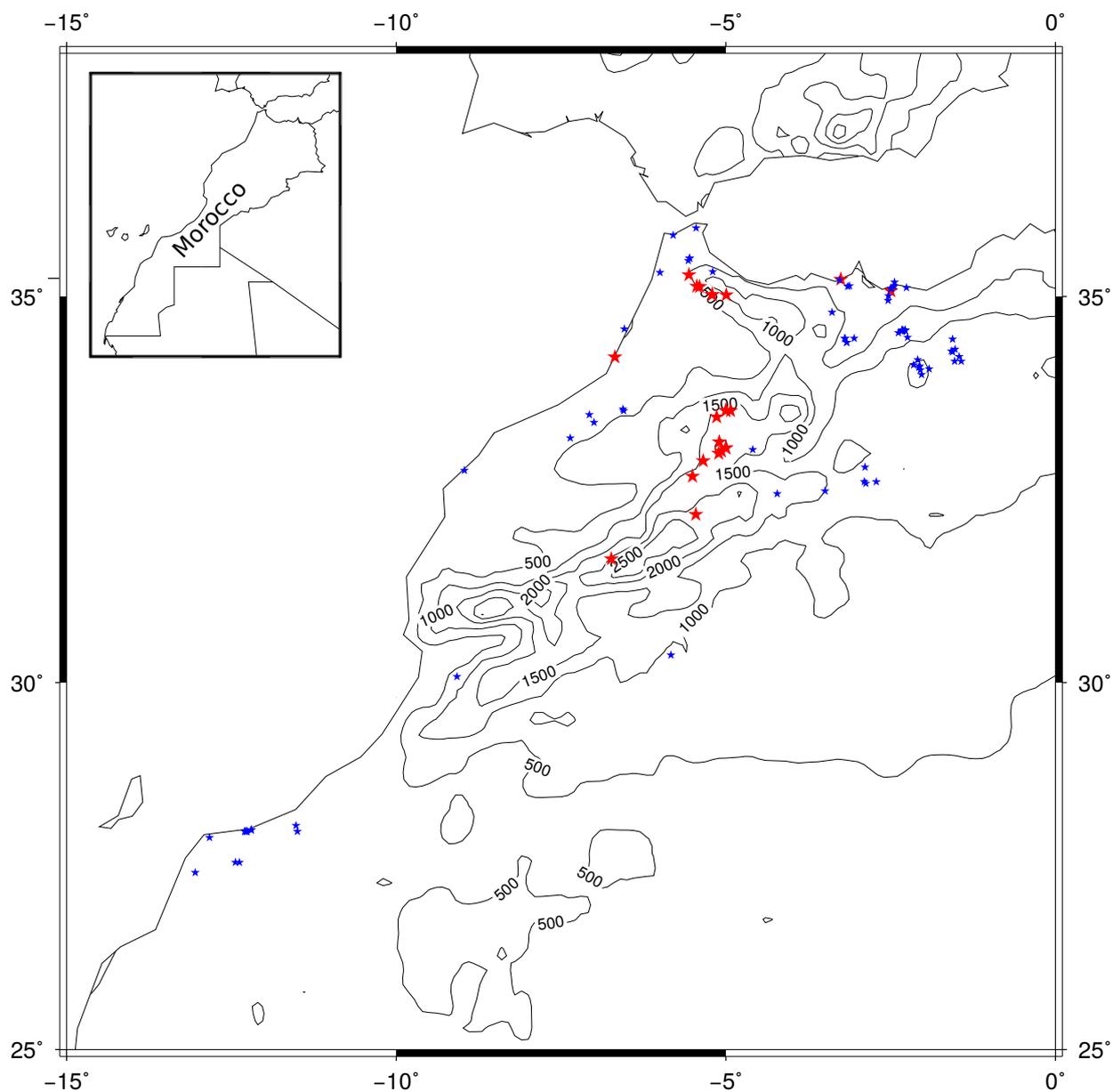
485 ***Acknowledgements***

486 This work stems from a workshop dedicated to the Leverhulme Trust-funded project
487 'Changing the face of the Mediterranean: land cover and population since the advent of farming'
488 organized in Mallorca in September 2017.

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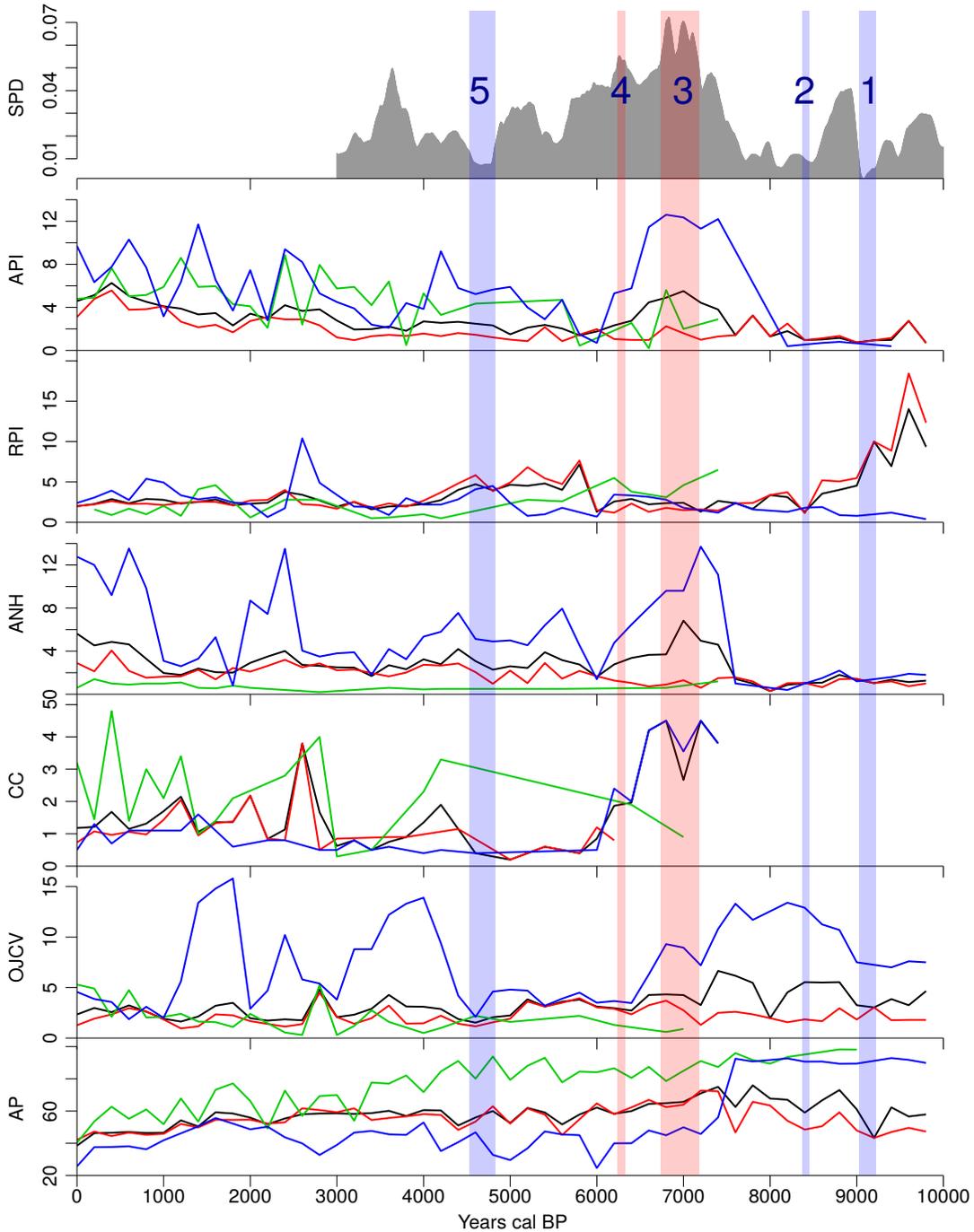
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491 **Figure 1.** A. Location of the fossil pollen records (red stars) used for reconstructing
492 anthropogenic markers, vegetation groups and pollen taxonomic richness. Pollen record
493 numbers refer to table 1. B. Location of the archaeological sites (blue stars) from which we have
494 obtained ^{14}C measurements for evaluating past changes in human population in Morocco (SPD).
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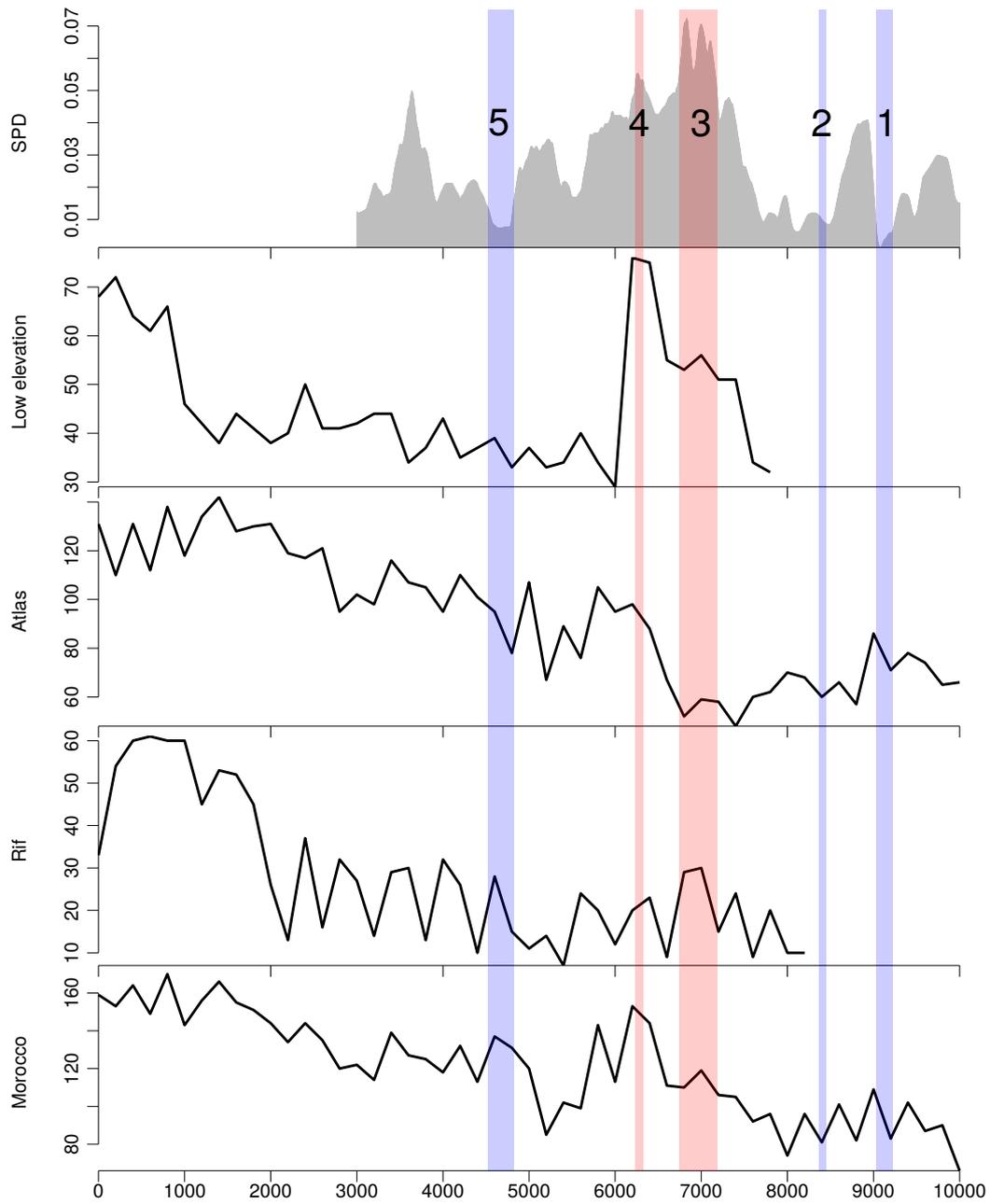
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498 **Figure 2.** Percentages of anthropogenic pollen markers (API, RPI, ANH, CC and OJCV) and
 499 arboreal pollen taxa (AP) during the Holocene in the Atlas mountains (red), the Rif
 500 mountains (green), the lowlands (sites below 800m asl, blue) and Morocco (black, including
 501 all pollen records). API = Anthropogenic Pollen index, RPI = Regional Pastoral indicators,
 502 ANH = Anthropogenic nitrophilous herbs, CC= Cultures and crops and OJCV = *Olea-Juglans-*
 503 *Castanea-Vitis*.
 504



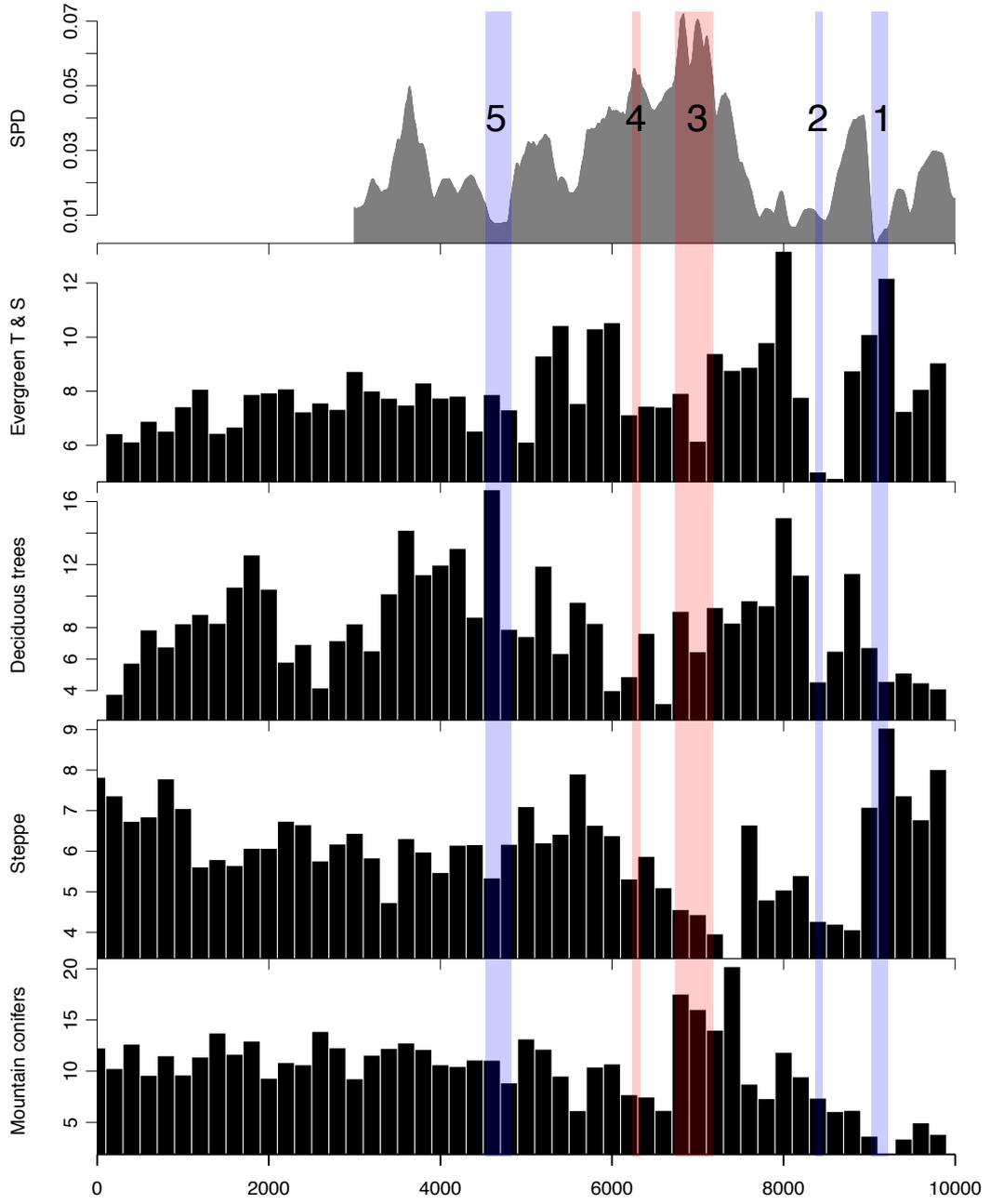
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507 **Figure 3.** Estimated pollen taxonomic richness using rarefaction analysis from the lowland
508 sites (below 800m asl), the Rif and Atlas Mountains, and all datasets from Morocco.
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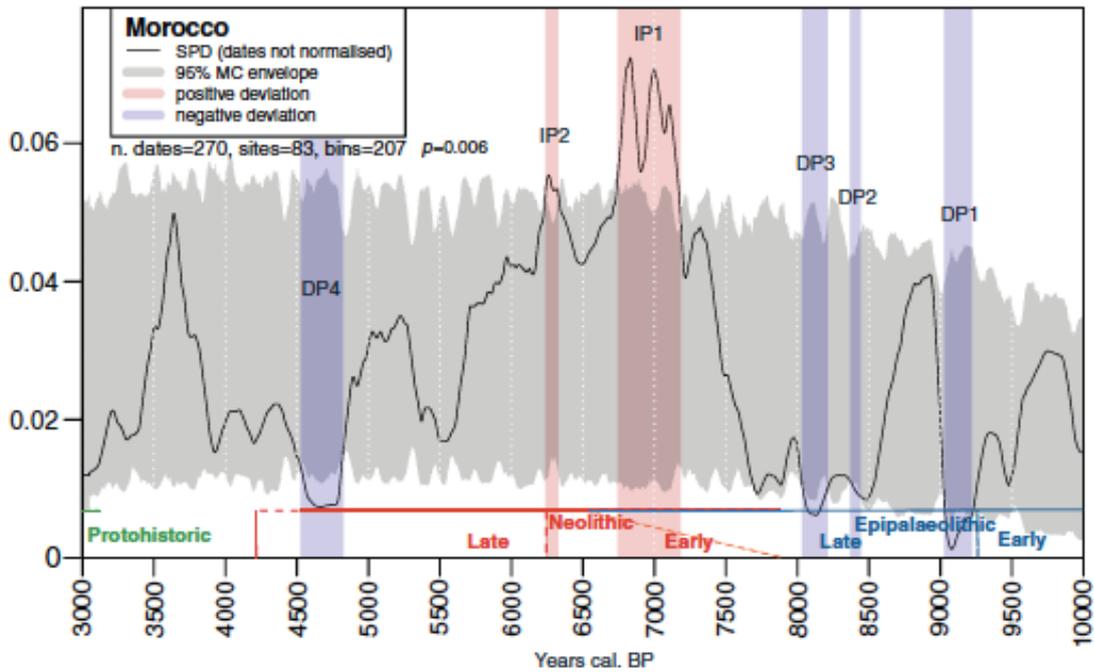
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512 **Figure 4.** Pollen percentages of four natural vegetation groups.
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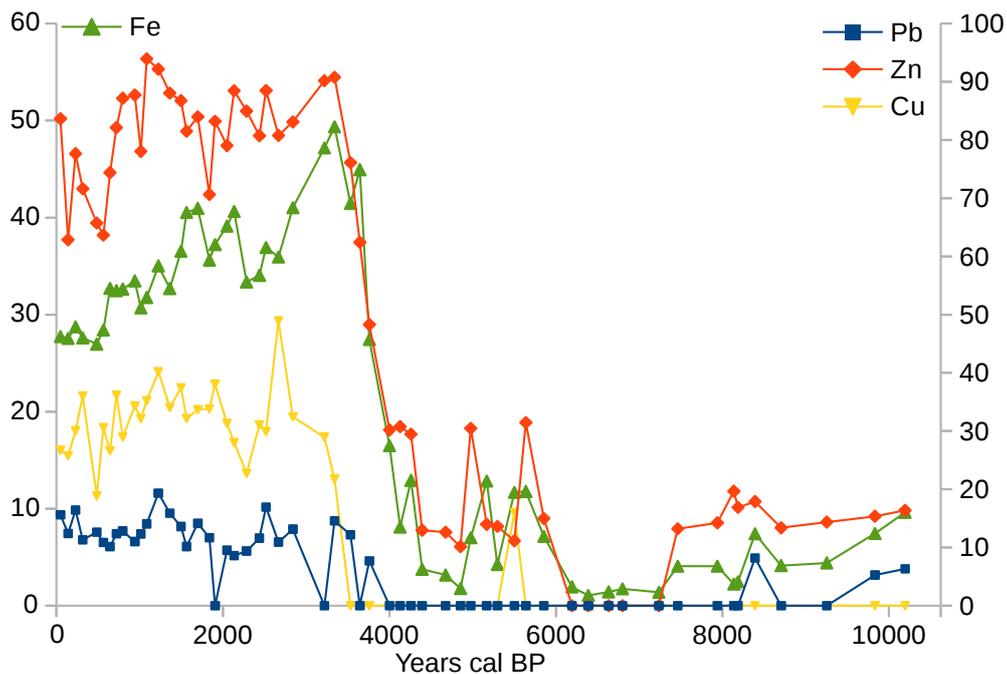


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516 **Figure 5.** Summed Probability Distribution (SPD) of unnormalised calibrated radiocarbon dates vs. a fitted logistic null model (95 % confidence grey envelope). Blue and red bands
 517 indicate that chronological ranges within the observed SPD deviates negatively and
 518 positively from the null model and corresponds to four significant decreases in human
 519 population (events 1, 2, 3 and 6) and two significant increases (events 4 and 5). The
 520 Epipalaeolithic and Neolithic periods have been defined according to Linstädter et al.
 521 (2018) in Northern Morocco.
 522



523 **Figure 6.** X-Ray measurements of Iron (Fe), Copper (Cu), Lead (Pb) and Zinc (Zn) in the Ait
 524 Ichou fossil record collected in the Middle Atlas (Tabel et al., 2016)
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527

528 **Table 1.** Pollen records used in the present study (displayed in figure 1A). All pollen records
 529 from Reille (1976, 1977 and 1979) have been digitized from the original published pollen
 530 diagrams and the raw data computed using the pollen sums.
 531

Site Name	Location	Elevation	Time span (approx)	Authors
Aanasser	Rif	1342	0-4000	Reille, 1977, Cheddadi et al., 2015; 2017
Abartete	Rif	1260	0-8000	Reille, 1976
Bab El Karn	Rif	1178	0-9000	Cheddadi et al., 2016
Col de Zad	Middle Atlas	2138	0-3000	Reille, 1976
Hachlaf	Middle Atlas	1700	0-6000; 0-16000	Nourelbait et al., 2016; Tabel & Cheddadi, unpublished
Ifrah	Middle Atlas	1610	4500-25000	Cheddadi et al., 2009
Ifri nEtsedda	Rif	300	4500-10000	Linstädter et al., 2016
Ifri Oudadane	Rif	50	6000-10000	Zapata et al., 2013
Iguerda-Ait-Amama	Middle Atlas	2052	0-2500	Reille, 1976
Ishou	Middle Atlas	1608	0-23000	Tabel et al., 2016
Marzine	Rif	1400	0-2000	Reille, 1976
Mhad	Rif	754	0-6000	Cheddadi et al., 2015; 2017
Ras El Ma	Middle Atlas	1633	0-18000	Nourelbait et al., 2014
Sidi Ali	Middle Atlas	2080	0-7500; 0-12000	Lamb et al., 1999; Zielhofer et al., 2017
Sidi bou Ghaba	Rabat province	20	0-6500	Reille, 1979
Tanakob	Rif	726	0-1200	Reille, 1976
Tessaout	High Atlas	2040	0-6000	Reille, 1976
Tifounassine	Middle Atlas	1921	0-13000	Tabel & Cheddadi, unpublished data
Tigalmamine	Middle Atlas	1626	0-10000	Lamb et al., 1995
Tizi Ninouzane	High Atlas	2591	0-2500	Reille, 1976

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534 **Table 2.** Taxa used to identify different human impacts within the Moroccan pollen records:
 535 Anthropogenic Pollen index = API; Regional Pastoral indicators =RPI; Anthropogenic
 536 nitrophilous herbs = ANH; Cultures and crops = CC; *Olea-Juglans-Castanea-Vitis* = OJCV.
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CC	API	API
Cerealia-type	Asteraceae subf. Cichorioideae	Urtica
Cerealia	Cannabaceae/Urticaceae	Urtica atrovirens
Secale	Centaurea	Urtica atrovirens-type
Zea mays	Centaurea cyanus	Urtica cf. U. dioica
	Centaurea cyanus-type	Urtica cf. U. pilulifera
OJCV	Centaurea scabiosa	Urtica dioica
Castanea sativa	Centaurea scabiosa-type	Urtica dioica-type
Juglans	Centaurea undiff.	Urtica dubia-type
Juglans regia	Cerealia	Urtica indeterminata
Olea	Cerealia (excl. Secale)	Urtica pilulifera
Olea europaea	Cerealia Indeterminata	Urtica pilulifera-type
Oleaceae	Cerealia sp.	Urtica undiff.
Vitis	Cerealia undiff.	Urtica urens
Vitis vinifera	Cerealia-type	Urtica-type
	Cerealia-type (excl. Secale)	Urtica/Humulus
RPI	Cerealia-type cf. Avena/Triticum-group	Urtica/Parietaria
Cirsium	Cerealia-type cf. Hordeum-group	Urticaceae
Cirsium-type	Cerealia-type undiff.	Urticaceae undiff.
Galium	Cerealia-type/Secale	Urticaceae/Moraceae
Galium-type	Cerealia-type/Triticum	Urticales
Plantago lanceolata	Cerealia-type/Triticum/Avena	
Plantago pp.	Cerealia-type/Zea	
Potentilla	Cerealia/Avena-type	
Potentilla undiff.	Cerealia/Hordeum-type	
Potentilla-type	Cerealia/Secale	
Ranunculaceae	Cerealia/Triticum-type	
	cf. Urtica	
ANH	Compositae subf. Cichorioideae	
Anthemis-type	Humulus/Cannabis/Urtica	
Aster-type	Plantago	
Boraginaceae	Plantago cf. P. coronopus	
Centaurea	Plantago cf. P. lanceolata	
Centaurea collina	Plantago cf. P. major	
Centaurea cyanus	Plantago cf. P. media	
Centaurea nigra-type	Plantago coronopus	
Centranthus	Plantago coronopus-type	
Cirsium	Plantago lanceolata	
Cirsium-type	Plantago lanceolata-type	
Convolvulaceae	Plantago major	
Convolvulus	Plantago major-type	
Dipsacaceae	Plantago major/P. maritima	
Echium	Plantago major/P. media	
Erodium-type	Plantago major/P. media-type	
Eryngium	Plantago major/P. minor-type	
Galium	Plantago maritima	
Galium-type	Plantago maritima-type	
Geraniaceae	Plantago maritima/P. alpina	
Geranium	Plantago media	
Geranium-type	Plantago media-type	
Hemaria	Plantago sp.	
Hemaria-type	Plantago undiff.	
Malva sylvestris-type	Plantago-type	
Malva-type	Secale cereale	
Malvaceae	Trifolium	
Portulaca oleracea	Trifolium undiff.	
Solanum nigrum-type	Trifolium-type	

API = Anthropogenic Pollen Index; RPI = regional pastoral indicators; ANH = Anthropogenic nitrophilous herbs; CC = cultures and crops; OJCV: *Olea-Juglans-Castanea-Vitis*.

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540 **Table 3.** Pollen taxa grouped in the four natural vegetation groups

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Conifer trees	Deciduous Trees	Steppe	Evergreen shrubs and trees
Abies	Acer	Aster-type	Acacia
Cedrus	Alnus	Artemisia	Adenocarpus
Cupressaceae	Carpinus	Asphodeline	Buxus
Juniperus	Carpinus betulus-type	Asphodelus	Ceratonia
Taxus baccata	Castanea	Asteraceae subf. Asteroideae	Ceratonia siliqua
Tetraclinis articulata	Celtis	Asteraceae subf. Cichorioideae	Cistus ladanifer-type
	Corylus	Centaurea	Cistaceae
	Fraxinus	Centaurea cyanus	Coniferae (vesiculate)
	Juglans	Centaurea cyanus-type	Cupressus
	Ostrya	Centaurea nigra-type	Cytisus-type
	Ostrya/Carpinus orientalis-type	Chenopodiaceae	Erica arborea-type
	Populus	Compositae subf. Cichorioideae	Genista-type
	Prunus-type	Cyperaceae	Ilex
	Quercus canariensis	Dipsacaceae	Laurus
	Quercus canariensis-type	Dipsacus	Lavandula stoechas-type
	Quercus cf. Q. canariensis	Ephedra	Ligustrum
	Quercus faginea	Ephedra distachya	Myrtaceae
	Quercus pyrenaica	Ephedra distachya-type	Myrtus communis
	Quercus robur-type	Ephedra fragilis	Olea
	Salix	Ephedra fragilis-type	Oleaceae
	Tilia	Poaceae	Phillyrea
	Ulmus	Sanguisorba minor	Phillyrea latifolia
		Scabiosa	Pinus
		Thymelaeaceae	Pinus halepensis
			Pinus halepensis/P. Pinea-type
			Pinus pinaster
			Pistacia
			Quercus
			Quercus coccifera
			Quercus ilex
			Quercus ilex-type
			Quercus rotundifolia
			Quercus suber
			Rhamnaceae
			Rhamnus
			Rhamnus alaternus-type
			Ribes
			Ruscus
			Tamarix
			Viburnum
			Vitis
			Ziziphus
			Ziziphus lotus

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Table 4. Demographic peaks or troughs with statistically significant deviation from null model (see Fig. 5). The dates summarise the duration of these events:

Event	Start (cal BP)	End (cal BP)	Duration (years)
1	9220	9030	190
2	8450	8370	80
3	8210	8030	180
4	7180	6740	440
5	6330	6240	90
6	4820	4530	290

Table 5. Spearman's correlation coefficients between the pollen percentages of different anthropogenic markers (ANH, API, CC, OJCV, RPI), vegetation groups and arboreal pollen (AP) from fossil pollen records and archaeo-demographic datasets (SPD) by region and elevation for the period 10000-3000 cal BP. Statistical significance: green: 0.05>P value>0.001; red: P value <0.001

	Morocco	Atlas	Rif	Low elevation
AP	0,26	0,4	0,3	-0,09
ANH	0,63	-0,12	0,22	0,59
API	0,61	0,05	0,13	0,61
CC	0,7	0,16	0,03	0,74
OJCV	0,24	0,5	0,11	0,1
RPI	-0,17	-0,23	0,61	0,06
Taxa diversity	0,26	-0,19	0,31	0,51
Conifers	0,48			
Deciduous	-0,16			
Evergreen	-0,13			
Steppe	-0,33			

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570 **References**

- 571 Abel-Schaad D, Iriarte E, López-Sáez JA et al. (2018) Are *Cedrus Atlantica* forests in the Rif
572 Mountains of Morocco heading towards local extinction? *The Holocene*, 28(6): 1023–1037
- 573 Arredi B, Poloni ES, Paracchini S et al. (2004) A predominantly neolithic origin for Y-
574 chromosomal DNA variation in North Africa. *The American Journal of Human Genetics*
575 75(2): 338-345.
- 576 Ballouche A and Marinval P (2003) Données palynologiques et carpologiques sur la
577 domestication des plantes et l'agriculture dans le Néolithique ancien du Maroc
578 septentrional. Le site de Kaf Taht el-Ghar. *Revue d'archéométrie* 27: 49-54.
- 579 Balsera V, Bernabeu Aubán J, Costa Caramé, M et al. (2015) The Radiocarbon Chronology of
580 Southern Spain's Late Prehistory (5600–1000 Cal BC): a Comparative Review. Oxford.
581 *Journal of Archaeology* 34(2): 139-156.
- 582 Behre KE (1981) The interpretation of anthropogenic indicators in pollen diagrams. *Pollen et*
583 *Spores* 23(2): 225–245.
- 584 Bentayebi K, Abada F, Izhmad H et al. (2014) Genetic ancestry of a Moroccan population as
585 inferred from autosomal STRs. *Meta Gene* 2: 427–38.
- 586 Bevan A and Crema ER (2018) rcarbon v1.2.0: Methods for calibrating and analysing
587 radiocarbon dates. URL: <https://CRAN.R-project.org/package=rcarbon>
- 588 Bevan A, Colledge S, Fuller D et al. (2017) Holocene fluctuations in human population
589 demonstrate repeated links to food production and climate. *Proceedings of the National*
590 *Academy of Sciences* 201709190.
- 591 Birks HJB and Line JM (1992) The use of rarefaction analysis for estimating palynological
592 richness from Quaternary pollen-analytical data. *The Holocene* 2(1): 1–10.
- 593 Bocquet-Appel J-P, Naji S, Linden MV, Kozłowski JK (2009) Detection of diffusion and contact
594 zones of early farming in Europe from the space-time distribution of 14C dates. *Journal of*
595 *Archaeological Science* 36: 807-820.
- 596 Bosch E, Calafell F, Perez-Lezaun A et al. (1997) Population history of North Africa: evi dence
597 from classical genetic markers. *Human Biology* 69: 295–311.
- 598 Brakez Z, Bosch E, Izaabel H et al. (2001) Human mitochondrial DNA sequence variation in the
599 Moroccan population of the Souss area. *Annals of human biology* 28(3): 295–307.
- 600 Brockerhoff EG, Jactel H, Parrotta JA et al. (2008) Plantation forests and biodiversity: Oxymoron
601 or opportunity? *Biodiversity & Conservation* 17(5):925–51.
- 602 Campbell JFE, Fletcher WJ, Joannin S et al. (2017) Environmental drivers of Holocene forest
603 development in the Middle Atlas, Morocco. *Frontiers in Ecology and Evolution* 5: 113.
- 604 Capuzzo G, Zanon M, Dal Corso M, Kirleis W and Barceló JA (2018) Highly diverse Bronze Age
605 population dynamics in Central-Southern Europe and their response to regional climatic
606 patterns. *PloS one* 13(8): p.e0200709.
- 607 Carrión JS, Fernández S, González-Sampériz P et al. (2010) Expected trends and surprises in the
608 Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands.
609 *Review of Palaeobotany and Palynology* 162(3): 458-475.
- 610 Cavalli-Sforza LL, Menozzi P and Piazza A (1993) Demic expansions and human evolution.
611 *Science* 259(5095): 639-646.
- 612 Cheddadi R, Bouaissa O, Rhoujjati A et al. (2016) Environmental changes in the Moroccan
613 western Rif mountains over the last 9,000 years. *Quaternaire* 27(1): 15-25.
- 614 Cheddadi R, Fady B, François L et al. (2009) Putative glacial refugia of *Cedrus atlantica* from
615 Quaternary pollen records and modern genetic diversity. *Journal of Biogeography* 36:
616 1361-1371.
- 617 Cheddadi R, Henrot AI, François L et al. (2017) Microrefugia, Climate Change, and Conservation
618 of *Cedrus atlantica* in the Rif Mountains, Morocco. *Frontiers in Ecology and Evolution* 5:114.

- 619 Cheddadi R, Nourelbait M, Bouaissa O et al. (2015) A history of human impact on Moroccan
620 mountain landscapes. *African Archaeological Review* 32(2): 233-248.
- 621 Cincotta RP, Wisnewski J and Engleman R. (2000) Human population in the biodiversity
622 hotspots. *Nature* 404: 990-992.
- 623 Crema ER, Habu J, Kobayashi K et al. (2016) Summed Probability Distribution of 14C Dates
624 Suggests Regional Divergences in the Population Dynamics of the Jomon Period in Eastern
625 Japan. *PLoS One* 11(4):1-18.
- 626 Daugas JP, Raynal JP, El Idrissi A et al. (1998). Synthèse radiochronométrique concernant la
627 séquence néolithique au Maroc. In Actes du colloque "14C et Archéologie": 349-353.
- 628 Desanges J (1981) The proto-Berbers J. *General history of Africa II*. 423-440.
- 629 El Baït MN, Rhoujjati A, Eynaud F et al. (2014) An 18 000-year pollen and sedimentary record
630 from the cedar forests of the Middle Atlas, Morocco. *Journal of Quaternary Science* 29(5):
631 423-432.
- 632 Fox JW (2013) The intermediate disturbance hypothesis should be abandoned. *Trends in
633 ecology & evolution*, 28(2): 86-92.
- 634 Fyfe RM, Woodbridge J and Roberts CN (2018) Trajectories of change in Mediterranean
635 Holocene vegetation through classification of pollen data. *Vegetation History and
636 Archaeobotany*: 27: 351-364.
- 637 Gamble C, Davies W, Pettitt P et al. (2004) Climate change and evolving human diversity in
638 Europe during the last glacial. *Philosophical Transactions of the Royal Society of London B:
639 Biological Sciences* 359(1442): 243-254.
- 640 Görsdorf J and Eiwanger J (1999) Radiocarbon datings of late Palaeolithic, Epipalaeolithic and
641 Neolithic sites in northeastern Morocco. *Mémoires de la Société préhistorique française* 26:
642 365-369.
- 643 Hajar L, Haïdar-Boustani M, Khater C et al. (2010) Environmental changes in Lebanon during
644 the Holocene: Man vs. climate impacts. *Journal of Arid Environments* 74(7): 746-755.
- 645 Hays JD, Imbrie J and Shackleton NJ (1976) Variations in the Earth's Orbit: Pacemaker of the Ice
646 Ages. *Washington, DC: American Association for the Advancement of Science* 194(4270):
647 1121-1132.
- 648 Hewitt GM (2000) The genetic legacy of the Quaternary ice ages. *Nature* 22, 405(6789): 907-
649 13.
- 650 Hublin JJ, Ben-Ncer A, Bailey SE et al. (2017) New fossils from Jebel Irhoud, Morocco and the
651 pan-African origin of Homo sapiens. *Nature* 546(7657): 289.
- 652 Hughes PD, Fenton CR and Gibbard PL (2011) Quaternary glaciations of the Atlas Mountains,
653 North Africa. *Developments in Quaternary Sciences*. Elsevier 15: 1065-1074.
- 654 Hughes PD, Woodward JC and Gibbard PL (2006) Quaternary glacial history of the
655 Mediterranean mountains. *Progress in physical geography* 30(3): 334-364.
- 656 Hughes PD, Fink D, Rodés Á et al. (2018) Timing of Pleistocene glaciations in the High Atlas,
657 Morocco: New 10 Be and 36 Cl exposure ages. *Quaternary Science Reviews* 180: 193-213.
- 658 Ibouhouten H, Zielhofer C, Mahjoubi R et al. (2010) Archives alluviales holocènes et occupation
659 humaine en Basse Moulouya (Maroc nord oriental). *Géomorphologie: Relief, Processus,
660 Environnement* 16 (1): 41-56.
- 661 IUCN (2018) The IUCN Red List of Threatened Species. Version 2018-1.
- 662 Jalut G, Dedoubat JJ, Fontugne M et al. (2009) Holocene circum-Mediterranean vegetation
663 changes: climate forcing and human impact. *Quaternary international* 200(1-2): 4-18.
- 664 Kaplan JO, Krumhardt KM and Zimmermann N (2009) The prehistoric and preindustrial
665 deforestation of Europe. *Quaternary Science Reviews* 28: 3016-3034.
- 666 Lamb HF, Damblon F and Maxted RW (1991) Human impact on the vegetation of the Middle
667 Atlas, Morocco, during the last 5000 years. *Journal of Biogeography* 18: 519-532.

- 668 Lavorel S. Ecological diversity and resilience of Mediterranean vegetation to disturbance.
669 *Diversity and Distributions* 1999;5:3–13.
- 670 Leydet, M. (2007–2018). The European pollen database. [http://www.eu](http://www.europeanpollendatabase.net/)
671 [ropeanpollendatabase.net/](http://www.europeanpollendatabase.net/)
- 672 Linstädter J, Aschrafi M, Ibouhouten H et al (2012) Flussarchäologie der Moulouya-
673 Hochflutebene, NO-Marokko. *Madriider Mitteilungen* 53: 1-84.
- 674 Linstädter J, Broich M and Weninger B (2018) Defining the Early Neolithic of the Eastern Rif,
675 Morocco - Spatial distribution, chronological framework and impact of environmental
676 changes. *Quaternary International* 472: 272-282.
- 677 Linstädter J, Kehl M, Broich M et al. (2016) Chronostratigraphy, site formation processes and
678 pollen record of Ifri n'Etsedda, NE Morocco. *Quaternary International* 410: 6-29.
- 679 López-Sáez JA and López-Merino L (2008) Antropización y neolitización durante el Holoceno
680 en Marruecos: Una aproximación paleopalinológica. In *Act. IV Congreso del Neolítico*
681 *Peninsular I. Museo Arqueol Alicante, Alicante* 438-444.
- 682 López-Sáez JA, Abel D, Bokbot Y et al (2013) Paisajes neolíticos del noroeste de Marruecos:
683 Análisis arqueopalinológico de la Cueva de Boussaria. In: Goncalves VS, Diniz M and Sousa
684 AC (eds) 5° Congresso do Neolítico Peninsular. Lisboa: Universidade de Lisboa, pp. 92–97.
- 685 Lotter AF (1998) Late-glacial and Holocene vegetation history and dynamics as shown by
686 pollen and plant macrofossil analyses in annually laminated sediments from Soppensee,
687 central Switzerland. *Vegetation History and Archaeobotany* 8(3): 165-184.
- 688 Manning K, Timpson A, Colledge S et al. (2014) The chronology of culture: a comparative
689 assessment of European Neolithic dating approaches. *Antiquity* 88(342): 1065-1080.
- 690 Mercuri AM (2008) Human influence, plant landscape evolution and climate inferences from
691 the archaeobotanical records of the Wadi Teshuinat area (Libyan Sahara). *Journal of Arid*
692 *Environments* 72(10): 1950–1967.
- 693 Mercuri AM and Sadori L (2012) Climate changes and human settlements since the Bronze age
694 period in central Italy. *Rendiconti Online della Società Geologica Italiana* 18: 32–34.
- 695 Mercuri AM, Mazzanti MB, Florenzano A et al (2013a) Anthropogenic pollen indicators (API)
696 from archaeological sites as local evidence of human-induced environments in the Italian
697 Peninsula. *Annali Di Botanica* 3: 143-153.
- 698 Mercuri AM, Mazzanti MB, Florenzano A et al (2013b) *Olea, Juglans* and *Castanea*: The OJC group
699 as pollen evidence of the development of human-induced environments in the Italian
700 peninsula. *Quaternary International* 303: 24-42.
- 701 Mercuri AM, Sadori L and Uzquiano OP (2011) Mediterranean and North-African cultural
702 adaptations to mid-Holocene environmental and climatic changes. *The Holocene* 21(1):
703 189-206.
- 704 Michczyńska DJ and Pazdur A (2004) Shape analysis of cumulative probability density function
705 of radiocarbon dates set in the study of climate change in late glacial and holocene.
706 *Radiocarbon* 46 (2): 733-744.
- 707 Michczyńska DJ, Michczyński A, Pazdur A (2007) Frequency distribution of radiocarbon dates
708 as a tool for reconstructing environmental changes. *Radiocarbon* 49 (2): 799-806.
- 709 Mikdad A, Eiwanger J, Atki H et al. (2000) Recherches préhistoriques et protohistoriques dans
710 le Rif oriental (Maroc): rapport préliminaire. *Beiträge zur Allgemeinen und Vergleichenden*
711 *Archäologie* 20: 109-167.
- 712 Mikdad A, Nekkal F, Nami M et al. (2012) Recherches sur le peuplement humain et l'évolution
713 paléoenvironnementale durant le Pléistocène et l'Holocène au Moyen Atlas central:
714 résultats préliminaires. *Bulletin d'Archéologie Marocaine* 22: 53-71.
- 715 Morales J, Pérez-Jordà G, Peña-Chocarro L et al. (2013) The origins of agriculture in North-West
716 Africa: macro-botanical remains from Epipalaeolithic and Early Neolithic levels of Ifri

- 717 Oudadane (Morocco). *Journal of Archaeological Science* 40(6): 2659-2669.
- 718 Myers N, Mittermeier RA, Mittermeier CG et al. (2000) Biodiversity hotspots for conservation
719 priorities. *Nature* 403(6772): 853.
- 720 Palmisano A, Bevan A and Shennan S (2017) Comparing archaeological proxies for long-term
721 population patterns: An example from central Italy. *Journal of Archaeological Science* 87:
722 59-72.
- 723 Palmisano A, Woodbridge J, Roberts N et al. (2019, in press) Holocene Landscape Dynamics and
724 Long-term Population Trends in the southern Levant. *The Holocene*.
- 725 Pausas JG, Llovet J, Anselm R, Vallejo R (2008) Are wildfires a disaster in the Mediterranean
726 basin? A review Vegetation changes Shrublands dominated by resprouting species.
727 *International Journal of Wildland Fire* 17:1-22.
- 728 Pearson RG, Dawson TP 2003. Predicting the impacts of climate change on the distribution of
729 species: are bioclimate envelope models useful? *Global Ecology & Biogeography* 12(5):
730 361-71.
- 731 Quézel P and Médail F (2003) *Ecologie et biogéographie des forêts du bassin méditerranéen*.
732 *Paris : Elsevier* 572.
- 733 Rando JC, Pinto F, González AM et al. (1998) Mitochondrial DNA analysis of Northwest African
734 populations reveals genetic exchanges with European, Near Eastern, and sub Saharan
735 populations. *Annals of human genetics* 62(6): 531-50.
- 736 Rankou H, Culham A, Jury SL et al. (2013) The endemic flora of Morocco. *Phytotaxa*, 78(1): 1-
737 69.
- 738 Reille M (1976) Analyse pollinique de sédiments postglaciaires dans le Moyen Atlas et le Haut
739 Atlas marocains : premiers résultats. *Ecologia Mediterranea* 2: 155-170.
- 740 Reille M (1977) Contribution pollenanalytique a l'histoire holocène de la végétation des
741 montagnes du rif (Maroc septentrional). *Recherches françaises sur le Quaternaire INQUA*
742 50: 53-76.
- 743 Reille M (1979) Analyse pollinique du lac de Sidi Bou Rhaba, littoral atlantique (Maroc).
744 *Ecologia Mediterranea* 4: 61-65.
- 745 Reimer PJ, Bard E, Bayliss A et al. (2013) IntCal13 and Marine13 radiocarbon age calibration
746 curves 0-50,000 Years cal BP. *Radiocarbon* 55(4): 1869-1887.
- 747 Rick JW (1987) Dates as Data: An examination of the Peruvian radiocarbon record. *American*
748 *Anitquity* 52: 55-73.
- 749 Roberts N, Woodbridge J, Bevan A et al. (2018) Human responses and non-responses to climatic
750 variations during the last glacial-interglacial transition in the eastern Mediterranean.
751 *Quaternary Science Reviews* 184: 47-67.
- 752 Saadi F and Bernard J (1991) Rapport entre la pluie pollinique actuelle, le climat et la végétation
753 dans les steppes à *Artemisia* et les milieux limitrophes au Maroc. *Palaeoecology of Africa*
754 *and the Surrounding Islands* 22: 67-86.
- 755 Sadori L, Jahns S and Peyron O (2011) Mid-Holocene vegetation history of the central
756 Mediterranean. *The Holocene* 21(1): 117-129.
- 757 Shennan, S. 2018 *The first farmers of Europe. An evolutionary perspective*. Cambridge UP.
- 758 Shennan S, Edinborough K (2007) Prehistoric population history: from the late Glacial to the
759 late Neolithic in Central and Northern Europe. *Journal of Archaeological Science* 34: 1339-
760 1345.
- 761 Shennan S, Downey SS, Timpson A et al. (2013) Regional population collapse followed initial
762 agriculture booms in mid-Holocene Europe. *Nature Communications* 4: 2486.
- 763 Tabel J, Khater C, Rhoujjati A et al. (2016) Environmental changes over the past 25 000 years in
764 the southern Middle Atlas, Morocco. *Journal of Quaternary Science* 31(2): 93-102.
- 765 Thuiller W, Richardson DM, Pysek P et al. (2005) Niche-based modelling as a tool for predicting

766 the risk of alien plant invasions at a global scale. *Global Change Biology* 11: 2234–50.

767 Timpson A, Colledge S, Crema E et al. (2014) Reconstructing regional population fluctuations
768 in the European Neolithic using radiocarbon dates: a new case-study using an improved
769 method. *Journal of Archaeological Science* 52: 549-557.

770 Turchin, P. 2001. Does population ecology have general laws? *Oikos* 94 (1), 17-26.

771 Van Der Plicht J, Bruins HJ and Nijboer AJ (2009) The Iron Age around the Mediterranean: a
772 High Chronology perspective from the Groningen radiocarbon database. *Radiocarbon*,
773 51(1), 213-242.

774 van de Loosdrecht M, Bouzouggar A, Humphrey L et al (2018) Pleistocene North African
775 genomes link Near Eastern and sub-Saharan African human populations. *Science*
776 360(6388), 548-552.

777 Vitousek PM, Mooney HA, Lubchenco J et al. (1997) Human domination of Earth's ecosystems.
778 *Science* 277(5325): 494-499.

779 Weninger B, Clare L, Jöris O et al. (2015) Quantum theory of radiocarbon calibration. *World*
780 *Archaeology* 47(4): 543-566.

781 Weninger B, Clare L, Rohling E et al. (2009) The Impact of Rapid Climate Change on Prehistoric
782 Societies during the Holocene in the Eastern Mediterranean. *Documenta Praehistorica*
783 *Ljubljana* 36: 7-59.

784 Williams AN (2012) The use of summed radiocarbon probability distributions in archaeology:
785 a review of methods. *Journal of Archaeological Science* 39(3): 578–589.

786 Woodbridge J, Roberts CN and Fyfe RM (2018) Holocene vegetation and land-cover dynamics
787 in the Mediterranean from pollen data. *Journal of Biogeography* 45: 2159-2174.

788 Zapata L, López-Sáez JA, Ruiz-Alonso M (2013) Holocene environmental change and human
789 impact in NE Morocco: Palaeobotanical evidence from Ifri Oudadane. *The Holocene* 23(9):
790 1286-1296.

791 Zielhofer C, Faust D, Linstädter J (2008) Late Pleistocene and Holocene fluvial records in the
792 Western Mediterranean: hydroclimatical changes and past human response. *Quaternary*
793 *International* 181: 39-54.

794 Zielhofer C, Fletcher WJ, Mischke S et al. (2017) Atlantic forcing of Western Mediterranean
795 winter rain minima during the last 12,000 years. *Quaternary Science Reviews* 157: 29-51.

796