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1 CLIMATE CHANGE, MIGRATIONS, AND THE PEOPLING OF SINE-SALOUM MANGROVES
2 (SENEGAL) IN THE PAST 6000 YEARS

3

4 Matthieu Carré^{1,2}, Louis Quichaud³, Abdoulaye Camara⁴, Moufok Azzoug⁵, Rachid Cheddadi⁶,
5 Diana Ochoa², Jorge Cardich², Alexander Pérez⁷, Rodolfo Salas-Gismondi², Julien Thébault⁸,
6 Yoann Thomas⁸

7

8 ¹ IPSL-LOCEAN laboratory, CNRS, IRD, MNHN, Sorbonne Université, 4 Place Jussieu, Paris,
9 France

10 ² Centro de Investigación para el Desarrollo Integral y Sostenible, Facultad de Ciencias y
11 Filosofía, Laboratorios de Investigación y Desarrollo, Universidad Peruana Cayetano Heredia,
12 Lima, Peru

13 ³ École normale supérieure de Lyon, Département de biologie, Lyon, France

14 ⁴ Laboratoire d'archéologie, Institut Fondamental d'Afrique Noire, Université Cheikh Anta
15 Diop de Dakar, Dakar, Sénégal

16 ⁵ Département de Génie des Procédés, Faculté de Technologie, Université de Bejaia, 06000,
17 Bejaïa, Algeria

18 ⁶ Institut de Sciences de l'Evolution de Montpellier, CNRS, IRD, Université de Montpellier,
19 France

20 ⁷ Departamento de Ingeniería, Facultad de Ciencias y Filosofía, Laboratorios de Investigación
21 y Desarrollo, Universidad Peruana Cayetano Heredia, Lima, Peru

22 ⁸ Univ Brest, CNRS, IRD, Ifremer, LEMAR, 29280 Plouzané, France

23

24 **Abstract**

25 We present a reconstruction of human demography and shell fishing activity in the Sine-
26 Saloum mangrove Delta (Senegal) in the past 6000 years using the summed probability
27 density (SPD) of radiocarbon dates in archaeological shell middens. We explore how this
28 local history relates to the climatic and political history of West Africa. We find that traces of
29 human presence were scarce from 6000 to 2000 yr BP, partly because the geomorphology of
30 the estuary was less favourable to human settlements at that time. A specialized shell fishing
31 population migrated massively to the Sine-Saloum around 2000 yr BP, at the end of the
32 aridification trend that followed the African humid period. This population, likely coming
33 from the northern coast in search of land and resources, fleeing from aridity and the
34 subsequent warfare, found refuge in the coastal mangroves and reached a maximum activity
35 at about 1700 yr BP. This period corresponds to the beginning of trans-Saharan trade, and to
36 a political complexification that would give rise to the Ghana empire. The incoming
37 migration may have occurred in two waves as suggested by two peaks in the SPD curve at
38 200-400 CE and 600-800 CE and by cultural differences within the Delta. Most sites in the
39 Sine-Saloum islands were abandoned in the early 15th century, before the arrival of
40 Europeans, possibly because intensive shell fishing was not sustainable anymore, or because
41 of the regional political destabilization associated to the fall of the Ghana empire and the
42 beginning of the Mali empire. Shortly after, in agreement with oral traditions, a new
43 population lead by the Manding Guelwars, moved to the Sine Saloum after a military defeat
44 and founded the modern towns. They had a reduced shellfishing activity compared to

45 previous inhabitants, possibly because activities were more oriented to the new trade with
46 Europeans or to a prosperous agriculture in more humid climatic conditions that prevailed
47 from 1500 to 1800 CE.

48

49

50

51 **1. Introduction**

52 The Sine-Saloum area in Senegal hosts one of the most radiocarbon dated archaeological
53 complex in West Africa, providing insights into the history of the demography and its
54 relationship with local and regional environmental and political context.

55 The Saloum Delta is a vast intertidal wetland covered by mangrove at the mouth of the Sine
56 and Saloum rivers in Senegal, today registered as a RAMSAR site and a UNESCO World
57 heritage site. One of the extraordinary features of this pristine maze of mangrove islands
58 and channels, is the presence of hundreds of archaeological shell mounds, including some of
59 monumental size (up to 15 m high over ~10 ha) which makes them among the largest in the
60 world (Thilmans and Descamps, 1982). These mounds, waste products of past human shell
61 fishing and processing, are evidence of a millennial activity that is still practiced by Serer-
62 Niominka people who live today in the Saloum Delta (Camara et al., 2017; Cormier-Salem,
63 2014; Descamps, 1994; Hardy et al., 2016). Little is known, however, about the history of the
64 shell-collecting populations that inhabited the Delta during the last thousands of years.

65 Historical documents from European travellers or traders, and oral tradition provide
66 some information on people migrations, their economy, and the succession of local and
67 regional political changes over the last five centuries. During his travel to the Saloum islands

68 in the 15th century, the Portuguese Valentim Fernandes described in the village of Diofandor
69 a population dedicated to shell fishing, pottery, and agriculture (Monod et al., 1951). Trade
70 with Europeans, which included gold, salt, leather and slaves, rapidly grew and transformed
71 the economy and political relationships in the region (Barry, 1998; Cormier-Salem et al.,
72 1999). Before the first contact with Portuguese travellers, sources are limited to oral
73 tradition, archaeological evidence, and to Arab travellers' texts who documented the
74 regional context. Mangrove swamps in west African estuaries are thought to have been a
75 refuge in the past millennia for populations running away from wars, kingdom authorities, or
76 climate change (Cormier-Salem, 2014). The Sine-Saloum population in particular has been
77 likely influenced by several migrations related to the rise and fall of west African empires,
78 islam expansion, and trans-Atlantic trade (Barry, 1998; Pélissier, 1966). However, the impact
79 of those events on the Sine-Saloum population cannot be fully assessed without indications
80 about the demographic evolution in the Saloum Delta.

81 Climate variability likely had also a determinant influence on past human activities and
82 migrations in West Africa. After the African humid period (AHP), which lasted approximately
83 from 12,000 to 5,500 years before the present (yr BP), the aridification of the Sahara and the
84 Sahel from 6000 to 3000 yr BP is now well documented, in particular by the sedimentological
85 records of Lake Yoa (Kröpelin et al., 2008), Lake Bosumtwi (Shanahan et al., 2009) and Lake
86 Tislit (Cheddadi et al., 2021), and by a series of marine sediment cores off West Africa
87 (deMenocal et al., 2000; Shanahan et al., 2015; Tierney et al., 2017). The climate variability
88 in the Sahel in the past two millennia has only been recently reconstructed using the isotopic
89 record of the Saloum Delta shell middens (Azzoug et al., 2012a, 2012b; Carré et al., 2019).
90 Saloum shell middens indicate that the climate in the Sahel is more arid today than in any
91 other period, as a consequence of an abrupt decrease of precipitation in the past 200 years

92 (Carré et al., 2019; Gallego et al., 2015). The climate conditions of the past two millennia
93 have therefore always been more favourable than today, with the most humid period
94 recorded in the pre-colonial time from ca. 1500 to 1800 C.E., within the little ice age (LIA)
95 (Carré et al., 2019). This paleoclimate reconstruction brings new key elements to understand
96 the history of civilizations in western Sahel.

97 In this study, changes in the frequency of radiocarbon dates in archaeological shell mounds
98 are estimated and used to reconstruct the evolution of the intensity of shell fishing activities
99 and human occupation in the Sine-Saloum mangrove Delta since the first occurrence
100 recorded at 5849 yr BP. Radiocarbon datings from archaeology and paleoclimatology
101 research projects together yield a database of 103 radiocarbon dates from 21 archaeological
102 sites from across the Delta and an opportunity to estimate past human occupation through
103 time. Summed probability density (SPD) of radiocarbon dates has been shown to be a
104 powerful tool to explore past population changes provided potential biases (related to
105 sampling, preservation...etc) are taken into account (Chamberlain, 2006; Contreras and
106 Meadows, 2014; Rick, 1987; Shennan et al., 2013; Surovell and Brantingham, 2007; Williams,
107 2012). The large changes observed in the shell fishing population over the past millennia in
108 the Delta are discussed in the context of climatic and political changes in the region.

109

110 **2. Material and Methods:**

111 2.1. The shell middens

112

113 Most shell middens in the Sine-Saloum mangroves are almost exclusively composed of *Senilia*
114 *senilis* shells (bloody cockle), while some are composed of *Crassostrea gasar* (mangrove

115 oysters) shells, or a succession of layers of these species. Pores are mainly filled with sand,
116 charcoal and ashes. The scarcity of artefacts supports the idea that the middens were not
117 permanent villages but working places, possibly seasonally used, and dedicated to the
118 collecting and processing of mollusks. However, the numerous burials mounds found on top
119 of the largest middens (Descamps and Thilmans, 1979) suggest that they played a more
120 complex role in past Saloum societies (Hardy et al., 2016).

121 The archaeological shell middens of the Sine-Saloum Delta have been extensively surveyed by
122 Thilmans and Descamps (1982) who reported 96 sites (Figure 1). These authors studied and
123 dated the stratigraphy of three large shell middens, Dioron Boumak (Descamps et al., 1974),
124 Faboura (Descamps et al., 1977), and Bangaler (Elouard et al., 1974). These two latter sites do
125 not exist anymore, used up for construction material. Only a few sites have been dated besides
126 those until 2011 when a new research project started with the aim of reconstructing past
127 climate conditions using shell middens (Azzoug et al., 2012b, 2012a). Eleven additional shell
128 middens were sampled and 65 new radiocarbon dates were produced. In this more recent
129 work, shell middens from most areas of the estuary were randomly sampled, although a
130 preference was given to larger accumulations. Sites are distributed across the whole
131 mangrove area. Since no particular period was targeted and shell middens do not show any
132 visual evidence of their age, sampling biases are minimized. In large shell middens cut by tidal
133 erosion or by human exploitation, several samples were collected for radiocarbon dates along
134 the outcropping stratigraphy. In Dioron Boumak, for instance, samples were collected every
135 meter along the ~11 m high cliff (Azzoug et al., 2012a). Unlike most archaeological shell

136 middens, these sites show little mixing and fast stratified accumulation, as evidenced by the
137 depth-age models obtained in three of those sites (Carré et al., 2019).

138

139 2.1. Radiocarbon dates

140

141 We completed the synthesis published by Hardy et al. (2016) with 41 new radiocarbon dates,
142 reaching a total number of 103 radiocarbon datings of samples collected from the surface or
143 the stratigraphy of 21 shell middens. Samples are composed of either terrestrial material
144 (mostly charcoal and one bone) or marine material (otolith or mollusc shells including *S. senilis*
145 and *C. gasar*). The concentration of ^{14}C was measured using β radioactivity in the earlier
146 studies, and later exclusively with Atomic Mass Spectrometry (AMS) which yields higher
147 precision and allows for the analysis of small charcoal fragments. New radiocarbon dates of *S.*
148 *senilis* were measured on the shell hinge, a part that is best preserved from recrystallization
149 and integrates several years of growth. All dates are reported in [Supplementary Table 1](#).

150

151 2.2. Calibration

152

153 Radiocarbon dates were all calibrated using the R package rcarbon (Crema and Bevan, 2020)
154 with the calibration curves [IntCal20 \(Reimer et al., 2020\)](#) and [Marine20 \(Heaton et al., 2020\)](#).

155 For otolith and mollusk shell samples, it must be considered that the conditions in the estuary
156 are not fully marine. Today, the Saloum Delta is an inverse estuary during the dry season: the
157 sea water enters the Delta with tides and becomes hypersaline landward because of
158 evaporation (Pagès and Citeau, 1990; Savenije and Pagès, 1992; Mikhailov and Isupova, 2008;

159 Carré et al., 2019). The estuary recovers a normal salinity gradient during the rainy season
160 (July-September) with salinities ranging approximately from 15 to 30 in the mangrove area
161 where mollusc live (Carré et al., 2019). Oxygen isotopic values in archaeological shells showed
162 that the salinity was lower in the past, especially from 1500 to 1800 C.E. (Carré et al., 2019).
163 Shell calcium carbonate was thus precipitated from dissolved inorganic carbon (DIC) that is
164 partly marine and partly terrestrial. As marine and terrestrial carbon have different carbon
165 isotopic composition ($\delta^{13}\text{C}$), their proportions were [estimated](#) from the $\delta^{13}\text{C}$ values measured
166 in [shell samples \(Supplementary Table 1\)](#), since *S. senilis* shells precipitate aragonite in isotopic
167 [equilibrium with DIC \$\delta^{13}\text{C}\$ without significant fractionation as observed from modern \$\delta^{13}\text{C}\$ DIC](#)
168 [and shell measurements \(Carré et al., 2019\)](#). The ratio of marine carbon versus terrestrial
169 carbon was calculated assuming a $\delta^{13}\text{C}$ value of 0‰ (V-PDB) [for marine carbon](#) and a $\delta^{13}\text{C}$
170 [value of -22‰ \(V-PDB\) for terrestrial carbon issued from the degradation of mangrove organic](#)
171 [matter. This latter \$\delta^{13}\text{C}\$ value was estimated considering a value of -31‰ for dissolved organic](#)
172 [matter of mangrove \(Dittmar et al., 2006\) and a fractionation of 9‰ between dissolved \$\text{CO}_2\$](#)
173 [and carbonate ions \$\text{HCO}_3^-\$ \(Zeebe and Wolf-Gladrow, 2001\) used in shell aragonite](#)
174 [precipitation](#). The contribution of terrestrial carbon was generally less than 20%, with a
175 maximum value of 54% (Supplementary Table 1). [When a \$\delta^{13}\text{C}\$ value was available](#), the
176 calibration of mollusk shells was thus performed using a mix of [IntCal20 and Marine20 \(\$\Delta R=0\$](#)
177 [± 50\)](#) calibration curves in the R package rcarbon. Throughout the text, yr BP ages refer to

178 calibrated years before present (using conventionally 1950 CE as the present). For the more
179 recent period (the last 2000 years), the Current Era (CE) scale is used.

180

181 2.3. Summed Probability Distribution (SPD)

182

183 Summed Probability Distribution (SPD) have been widely used to estimate past changes in
184 human demography through time and space (Rick, 1987; Chamberlain, 2006; Williams, 2012;
185 Shennan et al., 2013). One of the most important bias that may arise from this technique is
186 the overrepresentation of some periods or sites where archaeological efforts were
187 concentrated (Chamberlain, 2006; Surovell and Brantingham, 2007; Contreras and Meadows,
188 2014). [To minimize this bias](#), some radiocarbon dates have been excluded from the SPD
189 calculation using the following criteria. For each site, samples with close radiocarbon dates
190 and similar depths were considered redundant and only one of the replicates was kept, with
191 a preference for terrestrial carbon source and/or better precision. The SPD was finally built
192 from [73](#) radiocarbon dates (50 terrestrial and [23](#) marine). Probability distributions from
193 radiocarbon date calibration were calculated and summed using the rcarbon package (Crema
194 and Bevan, 2020). SPDs were first calculated separately for marine and terrestrial samples and
195 then summed. A 100-yr moving average of the total SPD was calculated. The confidence
196 interval was defined by the 0.025 and 0.975 quantiles of values in the 100-yr windows. Three
197 additional SPD curves were built to evaluate the effect of sample selection and of the use of
198 mixed curve calibration of marine samples: (1) all the dates available were included (no
199 sorting) and only the Marine13 calibration curve was used for marine samples (no mixing)
200 (Figure S1a), (2) only the selected subset of dates was included (sorting) and only the Marine13

201 calibration curve was used for marine samples (no mixing) (Figure S1b), and (3) all dates were
202 included (no sorting) but mixed [Marine20 and IntCal20](#) curves were used for marine samples
203 when [possible](#) (mixing) (Figure S1c).

204

205 **3. Results**

206

207 The oldest human presence in the Sine-Saloum was evidenced [ca. 5800 Cal. yr. BP](#) in the site
208 Sipo, a ~2 m thick shell midden on top of a sandy beach ridge in the southern area (Figure 1).

209 After this first occurrence, dates are scarce until the beginning of the Current Era, and mainly
210 concentrate between 0 and 1500 CE (Figure 2). A sharp decline is observed in the 15th century.

211 This decline is also accompanied by a strong turnover in the sites that cannot be seen in the
212 SPD curve. A large number of sites are abandoned in the 13th and 14th century. The last five
213 centuries are only represented by one site, Diofandor, in our record (Figure S2). These main
214 features are robust regardless the data selection or the calibration method (Figure S1).

215 Redundant datings have been identified mainly in Dioron Boumak, Faboura, Guior and NDiar.

216 Since most dates excluded as redundant were from obtained marine material, this process
217 mainly affected the SPD derived from marine samples. The most prominent effect is to
218 drastically reduce the peak between ca. 700 CE and 1300 CE (Figure S1). Using mixed
219 calibration curves for shell samples yields better defined peaks in the marine SPD curve. The
220 use of the mixed calibration is *a posteriori* supported by a better agreement between the
221 terrestrial and the marine SPD curves, especially when using the selected dates (Figure S1).

222 The high frequency variability in the SPD curve is not considered as a significant signal. Only
223 the changes observed in the 100-year smoothed SPD curve are thus discussed here (Figure 2).

224 Within the main occupation period (200-1500 CE), the SPD curve shows two peaks at 200- 400
225 CE and at 600-800 CE, followed by an intermediate level plateau from ~900 to ~1400 CE. Sites
226 are distributed in the whole mangrove area, with a higher concentration around the central
227 axis of the Diomboss (Figure 1, S2). Joal Fadiouth, at the northern end of the Sine-Saloum, is
228 one of the oldest occupation and is still inhabited today by a shellfishing community (Hardy et
229 al., 2016), suggesting a possible 3000 years long occupation in this area.

230

231 **4. Discussion**

232 *4.1. Radiocarbon dates, shellfishing, and population density*

233 Summed probability density of ^{14}C dates from archaeological sites may yield powerful
234 insights into the past dynamics of human population but is also prone to several potential
235 biases (Williams, 2012). All the archaeological sites known in the Sine-Saloum mangroves are
236 shell middens, the age of which cannot be estimated before dating. Since the first objective
237 of the sampling was to build a long paleoclimatic record, the sampling effort was not focused
238 on a specific period but rather intended to cover a period as large as possible, so that sites
239 were chosen as diverse and disperse as possible, with a preference for long sequences. A
240 bias related to the site selection process is thus not considered significant here. For diverse
241 reasons, some sites have been more dated than others. This overrepresentation has been
242 corrected for (see section 2.3) so that sampling bias would be minimum in the final SPD.

243 The record might be also possibly biased by the destruction of some shell middens used up
244 for construction material during the 20th century. This exploitation preferentially affected
245 sites accessible by roads on the periphery of the Mangrove, while sites in the core of the
246 mangrove area were better preserved. Faboura and Bangalère for instance, dated in the

247 1970s, do no longer exist. Only sites within the mangrove could thus be sampled during the
248 more recent dating campaign. This selective destruction would create a bias in the SPD if
249 shell mounds from outside or within the mangrove had a different age, which is not
250 supported by dates from Faboura and Bangalère.

251 The total sample size determines the uncertainty of the SPD and the reliability of its
252 variations. The 21 sites dated here are only a fraction of the 96 shell middens reported by
253 Thilmans and Descamps (1982). Some of these sites were dated in their stratigraphy and
254 showed different occupation periods, yielding also a diachronic dimension that adds to the
255 SPD. Using a Monte Carlo statistical resampling approach, Michczyńska and Pazdur (2004)
256 determined that a minimum number of 14 dates per millennium is required to have a
257 meaningful signal, and 56 dates per millennium are required for statistical variability to be
258 less than 20% (considering a mean ^{14}C dating error of 115 years). Williams (2012) reached a
259 similar result finding that a minimum of 500 dates is needed over a period of 40,000 years
260 (i.e. ~ 13 dates per millennium). In our record, radiocarbon dates are very scarce before the
261 Current Era. Although ancient sites may have been more subject to erosion or human
262 exploitation, this scarcity can only be interpreted as a period of very low human activity.
263 Detailed changes within this period cannot be resolved with this dataset. Radiocarbon dates
264 are here concentrated in the past 2000 years, with ~ 30 dates per millennium (~ 50 dates per
265 millennium before selection), above the minimum suggested by these earlier statistical
266 studies. In addition, the 100-year moving average removes a large part of the variability
267 related to stochastic sampling. The 95% confidence interval associated to the moving
268 average curve provides an indication of the statistical significance of the SPD variations
269 (Figure 2). We thus conclude that the broad phases observed in the SPD in the last 2000
270 years are statistically robust.

271 4.2. Shellfish exploitation and population size

272 *Senilia senilis* is still very abundant today, has a high growth rate, and is the main mollusk
273 species collected in the Sine-Saloum. The species lives in the first centimetres of the
274 sediment on intertidal mudflats, where it is manually collected by women during low tides.
275 *Crassostrea gasar*, an oyster species that lives attached to mangrove roots is also easily
276 collected from a small boat at low tide, and is the second most used species. Mollusks are
277 such an easy and reliable protein source in the Sine-Saloum, that it seems very likely that this
278 resource has been part of the economy of any human group living in or close to the
279 mangrove area. Inhabitants of the mangrove today collect mollusks for their own
280 consumption and accumulate shells in temporary fishing sites as well as in their villages
281 (Camara et al., 2017; Hardy et al., 2016).

282 The density of radiocarbon dates in shell middens primarily reflects the intensity of the
283 shellfishing activity in the Sine-Saloum, and indirectly the size of the population living in the
284 area, assuming that shellfishing intensity and population size are linked. Because of the
285 multiple use of the mangrove ecosystem (Piqué et al., 2016), the abundance and easy access
286 of *Senilia senilis*, and the economic importance of this resource, it can be reasonably
287 assumed that changes in shellfishing intensity are linked on a first order to population size,
288 but it also depends on the economic strategies chosen by the groups. Those strategies may
289 change through time with climatic conditions or cultural evolution. Hence, shellfishing
290 intensity may overestimate population size in periods when the mollusk extraction effort is
291 intensified for trade, or underestimate it when efforts are reallocated in other kinds of
292 resources or activities.

293 Ancient shell middens in the Sine-Saloum are almost exclusively composed of shells. Because
294 remains of artifacts or settlements are scarce, these sites have been considered as work site
295 dedicated to the processing of shells, the flesh of which is dried or smoked and then
296 transported to be consumed elsewhere (Camara et al., 2017; Descamps, 1994; Hardy et al.,
297 2016). The monumental size and the fast accumulation rate of some middens such as Dioron
298 Boumak suggest an industrial activity aimed for trade rather than for domestic consumption
299 (Descamps et al., 1974; Descamps and Thilmans, 1979). This hypothesis, however, also bears
300 uncertainty. First, these very large mounds are only a handful among the 96 reported sites
301 and the possibly hundreds of unreported ones (Thilmans and Descamps, 1982). It also must
302 be noted that these very large sites generally bear numerous funeral tumuli sometimes
303 containing rich artefacts (Descamps and Thilmans, 1979), which suggest an intermediate
304 type of use in between the temporary fishing sites and the permanent villages observed
305 today. Finally, the hypothesis is fundamentally based on the idea that the shell production
306 exceeded the needs of the local population, based on an analogy with the modern
307 population size rather than on archaeological evidence of past population size. Additional
308 quantitative evidence on traded products and past food production strategies including fish,
309 cattle, and crops, are required to test this hypothesis.

310 Although no simple relationship exists between shellfishing intensity and population size due
311 to changing practices, we consider here, based on the available information, that they are
312 broadly positively linked, so that the SPD can be considered as a reliable qualitative indicator
313 of population presence, activity and size in the Sine-Saloum mangrove area. While possibly
314 amplified by trade-oriented extraction, the broad SPD peak observed between ~200 and
315 ~1400 CE, very likely represents a maximum population size. This is supported by the larger

316 number of sites (not only the number of datings) and the larger spatial coverage during this
317 period (Figure S2).

318 *4.3. The influence of sea level and coastal geomorphology*

319 The availability of land for shell middens and of mollusk resources depends on the
320 geomorphology of the Sine-Saloum, which has strongly evolved during the Holocene. The
321 relative sea level was about 1 to 2m higher than today during the Nouakchottian marine
322 transgression period from approximately 6500 to 4000 yr BP. This event has been well dated
323 and described in Mauritania and Senegal (Ausseil-Badie et al., 1991; Barousseau et al., 1995;
324 Elouard, 1968; Faure et al., 1980). For the combined effect of high sea level and a stronger
325 flow of the Saloum River in the African humid period (AHP), the Sine-Saloum was a
326 macrotidal estuary, with large shallow and intertidal areas and relatively open and high
327 energy environments (Ausseil-Badie et al., 1991). Some early beach barriers, like the one in
328 Sipo where the oldest shell midden was found, created protected area where *Senilia senilis*
329 could grow and be gathered. However, the absence of mangrove islands and channels
330 reduced greatly the availability of the mollusk banks and the terrain to build shell middens.
331 After sea level reached its modern value 4-3ka (Faure et al., 1980; Nizou et al., 2010) and
332 after the AHP, new beach barriers and a littoral spit formed *ca.* 3.5 to 2.5ka. Fluvial and
333 aeolian sediments then accumulated in the barred estuary to progressively form the islands
334 and channels that constitute the modern mangrove Delta (Ausseil-Badie et al., 1991; Diara
335 and Barousseau, 2006). The Delta geomorphology was similar to the modern one *ca.* 1500 BP.
336 Although the geomorphological and ecological conditions were more favorable to
337 shellfishing in the past 2000 years than before, these changes cannot fully explain the SPD.
338 Dense *S. senilis* banks were present from 6000 to 2000 yr BP as attested by vast natural

339 Nouakchottian deposits (Debenay and Bellion, 1983), by their presence in beach barrier sand
340 (Ausseil-Badie et al., 1991), and by a few archaeological shell middens. Although mangrove
341 islands were not available in early times to establish camp sites, these islands were not
342 indispensable for human to use mollusks. Numerous mid-Holocene *S. senilis* shell middens
343 were found around the Banc D'Arguin in Mauritania (Barusseau et al., 2007; Vernet and
344 Tous, 2004). The large shell middens of Faboura and Bangalère, accumulated between 1900
345 and 600 yr BP, were built respectively on substrate dated of 4700 yr BP (Ausseil-Badie et al.,
346 1991), and on pre-Holocene substrate (Barusseau et al., 1995; Elouard et al., 1974). If
347 geomorphological conditions were the primary factor determining the presence of
348 shellfishing people in the Sine-Saloum, we would expect a progressive increase of
349 radiocarbon date frequency in the past 6000 years, following the progressive formation of
350 the Delta. Instead, human presence and shell fishing abruptly increases from insignificant
351 level before 2000 yr BP to an absolute maximum 300 years later. This pattern could only be
352 explained by the sudden arrival of a large human population who migrated and settled in the
353 Sine-Saloum approximately 2000 years ago.

354 *4.4. The influence of climate change*

355 In the Sahel and the close-by Sahara, climate largely determines the availability of resources
356 and agriculture productivity and is therefore a primary driver of human societies' strategies,
357 success, and movements (Brooks et al., 2005; Magadza, 2000). In this section, we examine
358 how past climate and environmental changes in west Africa in the past 6000 years may be
359 related to the peopling of the Sine-Saloum reflected by shell middens SPD.

360 The early to mid-Holocene in Africa is known as the African humid period. In response to
361 seasonal insolation changes, the west African monsoon was intensified and shifted north

362 (Braconnot et al., 2000; Jousaume et al., 1999; Kutzbach and Liu, 1997) while the
363 mediterranean winter rainfall system was also intensified and shifted south (Cheddadi et
364 al., 2021). As a consequence, rainfall was increased from the Gulf of Guinea to the
365 Mediterranean coast, lakes and watersheds were active, and the Sahara was covered by
366 vegetation (Bartlein et al., 2011; Jolly et al., 1998; Kröpelin et al., 2008; Watrin et al., 2009).
367 The end of the AHP, once thought to have occurred abruptly *ca.* 5500 cal yr BP (deMenocal
368 et al., 2000), was more likely progressive as shown by a broad range of indicators including
369 pollen records (Cheddadi et al., 2021; Kröpelin et al., 2008), wetland radiocarbon dates
370 (Lézine et al., 2011), and leaf wax deuterium records (Niedermeyer et al., 2010; Shanahan et
371 al., 2015; Tierney et al., 2017). These records indicate an aridification trend approximately
372 from 6000 to 3000 yr BP (Figure 3). This transition from a productive environment to the
373 extreme aridity of the Sahara Desert represents the largest Holocene environmental change
374 on Earth (Jansen et al., 2008; Wanner et al., 2008).

375 Human societies have been profoundly affected by this environmental change across all
376 northern Africa. The Sahara, widely occupied by diverse human groups living from hunting,
377 fishing, and pastoralism during the AHP (Holl, 2004; Lhote, 1970; Paris, 1993; Smith, 1980;
378 Sutton, 1977), was progressively abandoned as aridity increased (Brooks, 2006; Maley and
379 Vernet, 2015; Manning and Timpson, 2014; McIntosh and McIntosh, 1983; Vernet, 2002).
380 While in the eastern Sahara, people found refuge in the Nile valley, possibly giving rise to the
381 ancient Egypt civilization (Kuper and Kröpelin, 2006), in central Sahara, pastoralists migrated
382 to the Sahel, following the southward migration of Savanna and pasturage (McIntosh and
383 McIntosh, 1983; Smith, 1979). The progressive decline of the Saharan population at the end
384 of the AHP has been well demonstrated by radiocarbon dates density in all the regions of the
385 Sahara (Manning and Timpson, 2014; Vernet, 2002). Interestingly, the population of the

386 West African Atlantic coast has an opposite dynamics and tend to grow at the end of the
387 AHP to reach a maximum 3.5 to 3ka (Manning and Timpson, 2014; Vernet and Tous, 2004).
388 The reliability of marine resources was likely a factor of resilience and the Mauritanian coast
389 may have become a momentary refuge. Between 3 and 2ka, the shellfishing groups of
390 Mauritania abandoned also their sites and seem to move south towards Senegal, as aridity
391 kept increasing (Vernet and Tous, 2004). A final abrupt aridification occurred in the Sahel
392 around 2 ka to reach the modern semi-arid landscape (Lézine, 1989).

393 The abrupt rise of shellfishing population in the Sine-Saloum around 2ka coincides with the
394 end of the aridification after the African humid period (Figure 3), and the end of shellfishing
395 activities in Mauritania. Human occupation patterns in West Africa suggest that
396 environmental changes forced large migrations in search of vegetal resources in the Sahel
397 and marine resources on the Atlantic coast. We hypothesize that a human group migrated
398 and found refuge in the Sine-Saloum around 2ka as a consequence of the increasing scarcity
399 of land in the Sahara and Sahel [and the subsequent increasing competition for resources](#).

400 They immediately organized an intensive exploitation of *S. senilis*, which is evidenced by the
401 high accumulation rate of the middens (Azzoug et al., 2012a; Descamps et al., 1977, 1974)
402 and by the rapidly decreasing size of the shells (personal observation) which indicates a
403 strong gathering pressure on the species. This observation suggests that they were already
404 specialized or at least knowledgeable in this activity, and testifies therefore a possible origin
405 from northern Senegal and Mauritanian coast (Vernet and Tous, 2004). [An ancient](#)
406 [shellfishing population collecting *S. senilis* was also present in the estuary of the Senegal](#)
407 [River since at least 5ka](#) (Mbow, 1997; Michel et al., 1967). [Potteries found in middens of the](#)
408 [first millennium BCE were decorated with impressed cord-wrapped stick](#) (Mbow, 1997), a
409 [technique observed soon after in the Sine-Saloum sites](#) (Thilmans and Descamps, 1982),

410 suggesting a cultural filiation. Shellfishing activity did not end *ca.* 2ka in the Senegal River
411 Delta as it did in Mauritania. It seems thus that the shellfishing Mauritanian population,
412 moving South, may have triggered also a migration from the Senegal River Delta to the Sine-
413 Saloum.

414 The arrival of people in the Sine-Saloum also roughly coincides with the spread of rice
415 cultivation in West Africa (Linares de Sapia, 1971; Linares, 2002; McIntosh and McIntosh,
416 1981). It is thus possible as well that the new settlers came in search of fields for rice
417 cultivation since West African mangroves have long been a highly productive environment
418 for rice (Cormier-Salem et al., 1999; Linares, 2002; Pélissier, 1966), and collected mollusks as
419 a complement during the dry season. Determining who these people were, where they came
420 from, and the exact cause of their migration will, however, require a more detailed
421 archaeological characterization of the shell middens in the Sine-Saloum.

422 In the past 2000 years, the changes in the SPD does not present any clear relationship with
423 climate variability (Figure 4). Soil erosion related to agriculture intensity in the region, as
424 indicated by the dust fraction in marine sediments, constantly increases during the past
425 2000 years, with a strong acceleration with recent industrial agriculture (Mulitza et al.,
426 2010). The two large peaks in radiocarbon dates density around 300 and 700 CE are not
427 related to any climatic event. Aridity conditions reconstructed by mollusk shell oxygen
428 isotopes show instead little variations until approximately 1500 CE when precipitations
429 increased and the environment became less saline (Carré et al., 2019). The Sine-Saloum was
430 much less occupied during the humid period that lasted from ~1500 to 1800 CE (Figure 4).
431 We could expect people to invest more in agriculture during a wet period and rely less on
432 shellfishing. Combined with overexploitation of *S. senilis*, indicated by the small size of shells

433 in the middens (pres. obs.), the benefit-cost balance of shellfishing may have become too
434 low for this activity to be pursued, especially in a context of higher crop productivity. It is
435 however difficult to draw a causal relationship between these circumstances because of the
436 chronological uncertainty. Most shell middens were abandoned in the 14th century, when
437 climate was starting to improve, but before rainfall had reached its optimum. This abrupt
438 decrease in shellfishing population in the 14th century (it artificially appears in the 15th
439 century in figure 4 because of the effect of the 100-yr smoothing, but is better seen in
440 Figures 2, S1, and S2) may therefore rather be related to local or regional political troubles.

441

442 *4.5. The influence of regional conflicts*

443 The decreasing water resources across the Holocene and the subsequent migrations likely
444 triggered conflicts, warfare and political evolution in the whole region. Evidence of these
445 conflicts are however hard to identify in the archaeological record. Changes in the structure
446 of villages in the sequence of the Tichitt tradition in southern Mauritania seem to indicate a
447 period of warfare in the middle of the first millennium CE (Munson, 1980). Shortly after,
448 trans-Saharan trade would start and become progressively a essential element of West
449 African economy (Fauvelle-Aymar, 2013). From -300 to 500 CE, the trade favoured a socio-
450 economic transformation in the Sahara and the Sahel with the apparition of cities, increasing
451 exchanges and political complexity, that would lead to the rise of the Ghana Empire (Holl,
452 1985; McIntosh and McIntosh, 1983; Munson, 1980). The shellfishing people settled in the
453 Sine-Saloum during this phase of regional scale transformation, and likely took part to these
454 new trade relationships using dried mollusks, as attested by the industrial scale of
455 shellfishing, and possibly crops.

456 The second peak in the SPD from 600 to 800 CE might correspond to a second migratory
457 movement possibly in relation to the foundation of the Ghana Empire but the archaeological
458 information about the Sine-Saloum and the regional context is scarce in this period. The
459 hypothesis of a second migratory arrival is supported by cultural differences observed
460 between Faboura, which started with the first SPD peak, and Dioron Boumak which started
461 with the second peak. While ceramics at Faboura are similar to those found further North,
462 Dioron Boumak ceramics seem related to those from Casamance (Descamps et al., 1977).

463 It has been proposed that the Serer population living in the Sine-Saloum today came from
464 the north pushed by the expansion of Islam through the influence of Almoravids, and
465 especially from the kingdom of Tukrur in northern Senegal (Sarr and Becker, 1986), one of
466 the first that officially adopted Islam in the 11th century (Niane, 1985). Almoravids
467 eventually destabilized and accelerated the collapse of the Ghana Empire in the 12th
468 century, which was followed by a regional scale political reorganization. With the rise of the
469 Mali Empire, West African Manding population expanded to the Senegambian coast, and the
470 Sine-Saloum mangroves were likely incorporated in the new empire in the 13th century
471 (Meideros, 1980; Niane, 1985). Shortly after, during the 13th and 14th century, most of the
472 main sites of the islands were abandoned, including Dioron Boumak, Faboura, Tioupane.

473 Although the causes of this abandonment are not clear, we speculate it was somehow
474 related to a period of strong political instability in West Africa (Figure 4).

475 New settlements were dated in the 15th century. They were fewer and smaller. Shells were
476 large again, indicating that *S. senilis* populations were less exploited during a time and could
477 recover. This peopling turnover is strikingly coherent with the oral tradition of the Sine-
478 Saloum. According to the oral record, the ancestors of the current inhabitants found the

479 islands deserted when they arrived in the Sine-Saloum and the population who had built the
480 large shell middens had disappeared (Cormier-Salem et al., 1999; Pélissier, 1966). After the
481 battle of Troubang (1335 CE) in the civil war of the Kaabu kingdom, the Manding Guelwar
482 aristocratic elite found refuge in the Sine-Saloum area and initiated a dynasty who ruled over
483 the Sine and Saloum kingdoms until the 20th century (Cormier-Salem et al., 1999; Richard,
484 2012; Sarr and Becker, 1986), first as vassals of the Wolof kingdom, then within the French
485 colony. The alliance and mixing of the Guelwars and the local Serer seems at the origin of
486 the Niominkas, the actual inhabitants of the Sine-Saloum islands.

487 The first contact with European travellers was likely around 1446 CE (Cormier-Salem et al.,
488 1999; Person, 1985; Thiaw, 2012), after the settling of the Guelwars (i.e. after they had been
489 abandoned and reoccupied). Fernandes visited the Saloum Delta where ships found a safe
490 anchoring site, mentioned the village of Diofandor, and described a population living from
491 shellfishing and agriculture (Monod et al., 1951). In the following period, the trade of salt,
492 iron, spices, ivory and slaves with Europeans deeply affected the economic and political
493 relationships in West Africa (Person, 1985), but the trade routes were still controlled by the
494 Niominkas (Cormier-Salem et al., 1999). The intense trade with Europeans may have
495 contributed to reduce the need of shell fishing. For the last 300 years, the peopling of the
496 Sine- Saloum would be likely better documented by the history of the modern villages, which
497 has not been documented by archaeological methods so far.

498

499 **5. Conclusions**

500 The millennial history of the Sine-Saloum peopling, as revealed by radiocarbon dates
501 frequency in archaeological shell middens, is closely related to the climatic, environmental

502 and political evolution of West Africa since the middle Holocene. The geomorphology of the
503 estuary was less favorable to human settlement and shellfishing in the mid-Holocene when
504 sea level was higher and mangrove islands had not formed yet. However, traces of human
505 occupation were still scarce between 3000 and 2000 BP, when beach ridges were formed
506 and the Delta islands were close to their modern morphology. The population arrived
507 massively around 2000 BP and reached a maximum shellfishing activity at about 1700 BP.
508 This abrupt increase indicates the settlement of a migrating population in search of
509 resources and land at the end of the aridification trend that followed the African humid
510 period. The Sine-Saloum seems to have been a refuge for people fleeing the Saharan
511 desertification and the subsequent warfare. This period corresponds to the beginning of
512 trans-Saharan trade, and to a political complexification that would give rise to the Ghana
513 empire. The incoming migration may have occurred in two waves as suggested by the
514 double SPD peak at 200-400 CE and 600-800 CE and by cultural differences within the Delta.
515 After that time, the Sine-Saloum peopling seemed primarily driven by political changes,
516 conflicts and the subsequent migrations than by climate change. Most sites in the Sine-
517 Saloum islands were abandoned in the 13th and 14th century, before the arrival of
518 Europeans, likely in relation to the regional political destabilization that followed the fall of
519 the Ghana empire and the beginning of the Mali empire. The Manding Guelwars, defeated in
520 the Trandang battle in 1335 CE, moved and founded the modern towns of the Sine-Saloum
521 in the 14th century. They had a reduced shellfishing activity compared to previous
522 inhabitants, possibly because of a more prosperous agriculture in humid climatic conditions,
523 and maintained their dynasty at the head of the Sine and Saloum kingdoms until the 20th
524 century.

525

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533

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796 **FIGURE CAPTIONS**

797

798 **Figure 1.** (A) Map of the Sine-Saloum study area, Senegal. Location of the shell middens
799 dated and listed in [Supplementary Table 1](#) (white circles). Pictures of some representative
800 shell middens: Site 85 (B), Bossinka (C), and Tioupane (D). Numbers used in some site names
801 are from Thilmans and Descamps (1982).

802

803 **Figure 2.** SPD curve of selected radiocarbon dates from shell middens of the Sine-Saloum
804 Delta. The SPD of terrestrial samples (dark grey) is added to the SPD of marine samples (light
805 grey) calibrated using mixed IntCal13 and Marine13 calibration curves. 100-yr moving
806 average is shown (black line) with the 95% confidence interval (dotted lines).

807

808 **Figure 3.** Sine-Saloum peopling and regional climate in the past 6000 years. (a) SPD 100-yr
809 moving average of the Sine-Saloum. Indicated below are the evolution of the Sine-Saloum
810 Delta (BR indicates the formation of Beach Ridges), the intensity of the African Humid Period
811 (AHP), and the period of pastoralism in the Sahara. The precipitation trend in West Africa is
812 indicated by (b) the record of Deuterium of precipitation in GC68 marine core collected off
813 Mauritania (Tierney et al., 2017), (c) the leaf wax deuterium record from GeoB9508 marine
814 core off the Senegal River (Niedermeyer et al., 2010), (d) the leaf wax deuterium record of
815 the Bosumtwi Lake, Ghana (Shanahan et al., 2015).

816

817 **Figure 4.** Sine-Saloum peopling and regional context in the past 2000 years. (a) Schematic
818 chronology of main political structures in Senegal and West Africa. (b) SPD 100-yr moving
819 average of the Sine-Saloum. (c) Precipitation changes in the Saloum basin reconstructed

820 from shell oxygen isotopes (Carré et al., 2019). (d) Dust fraction in GeoB9501 marine core
821 collected off the Senegal River, related to soil erosion and agriculture practice (Mulitza et al.,
822 2010)

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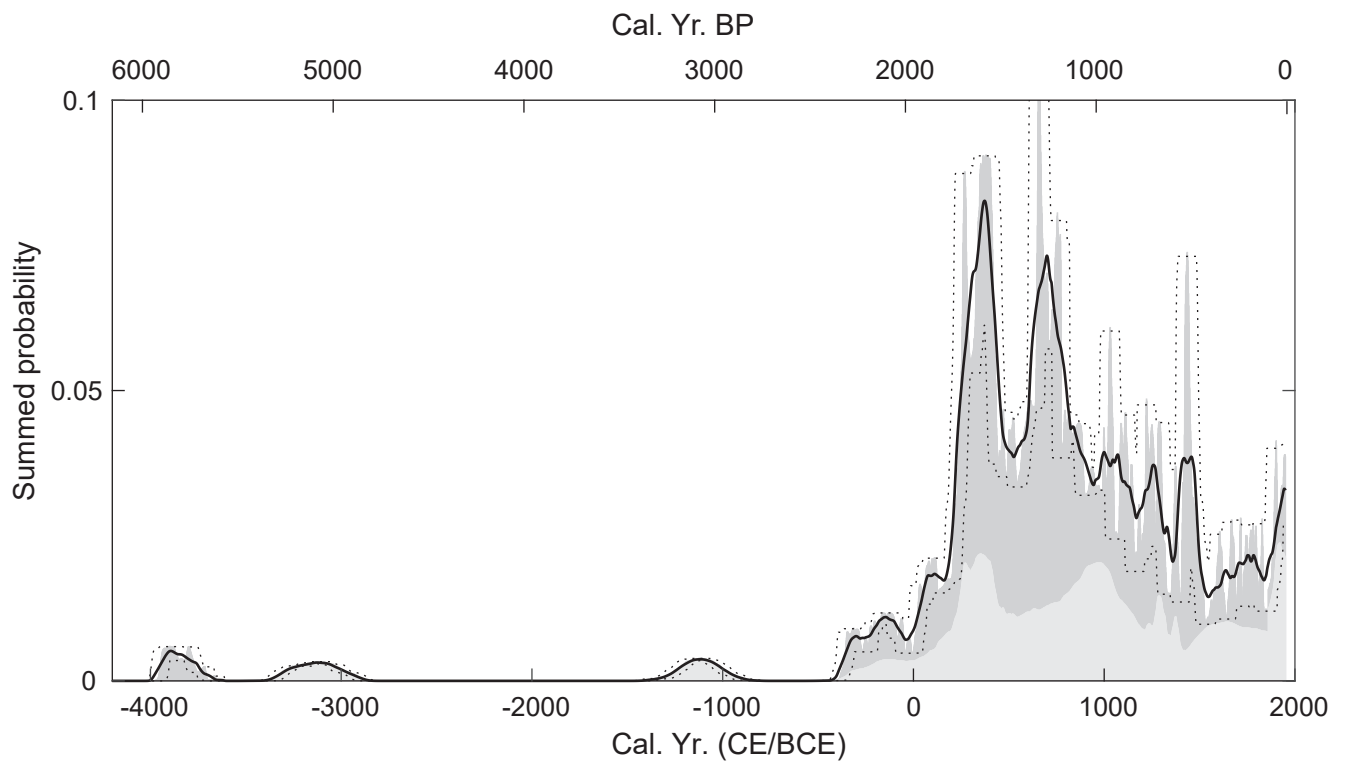
826 SUPPLEMENTARY INFORMATION

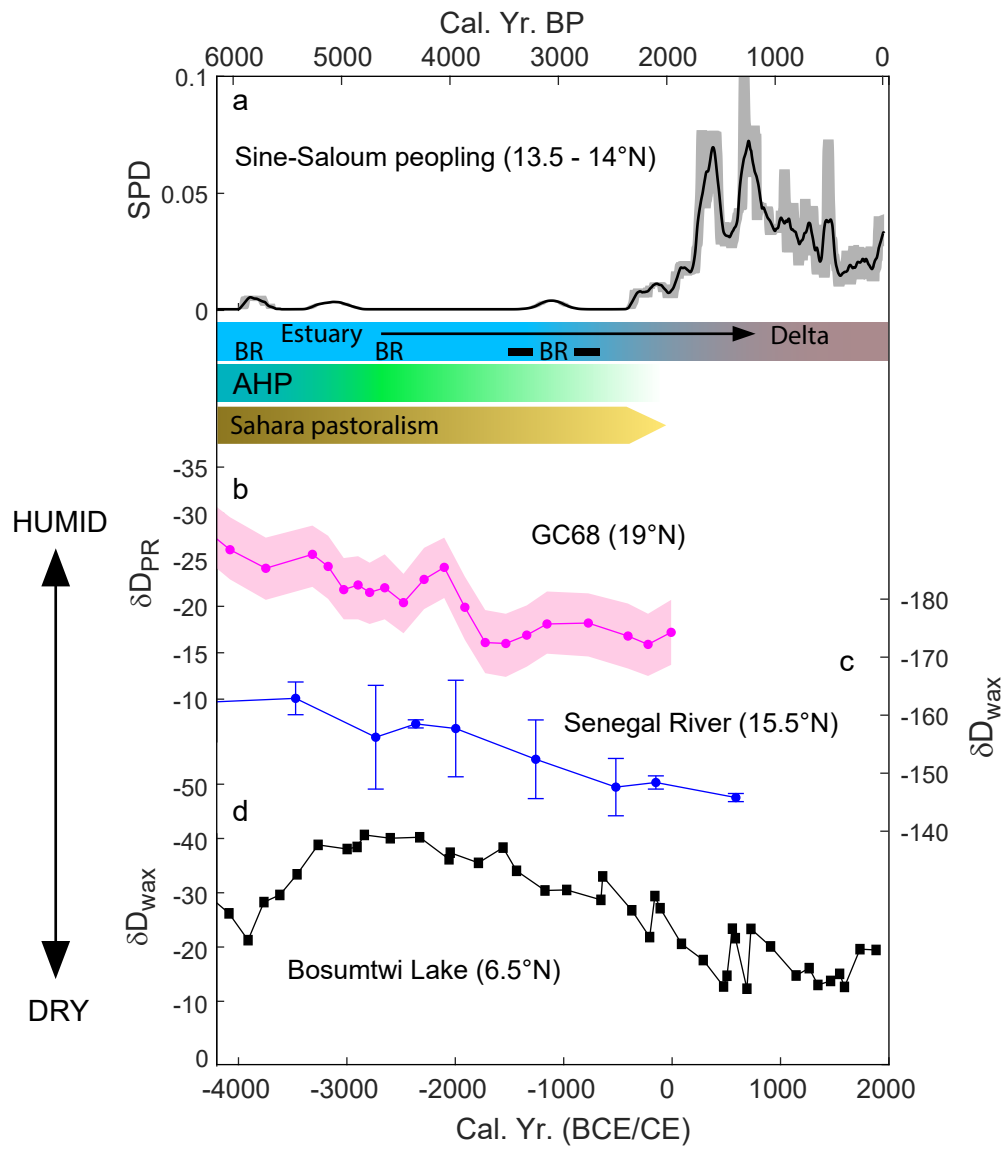
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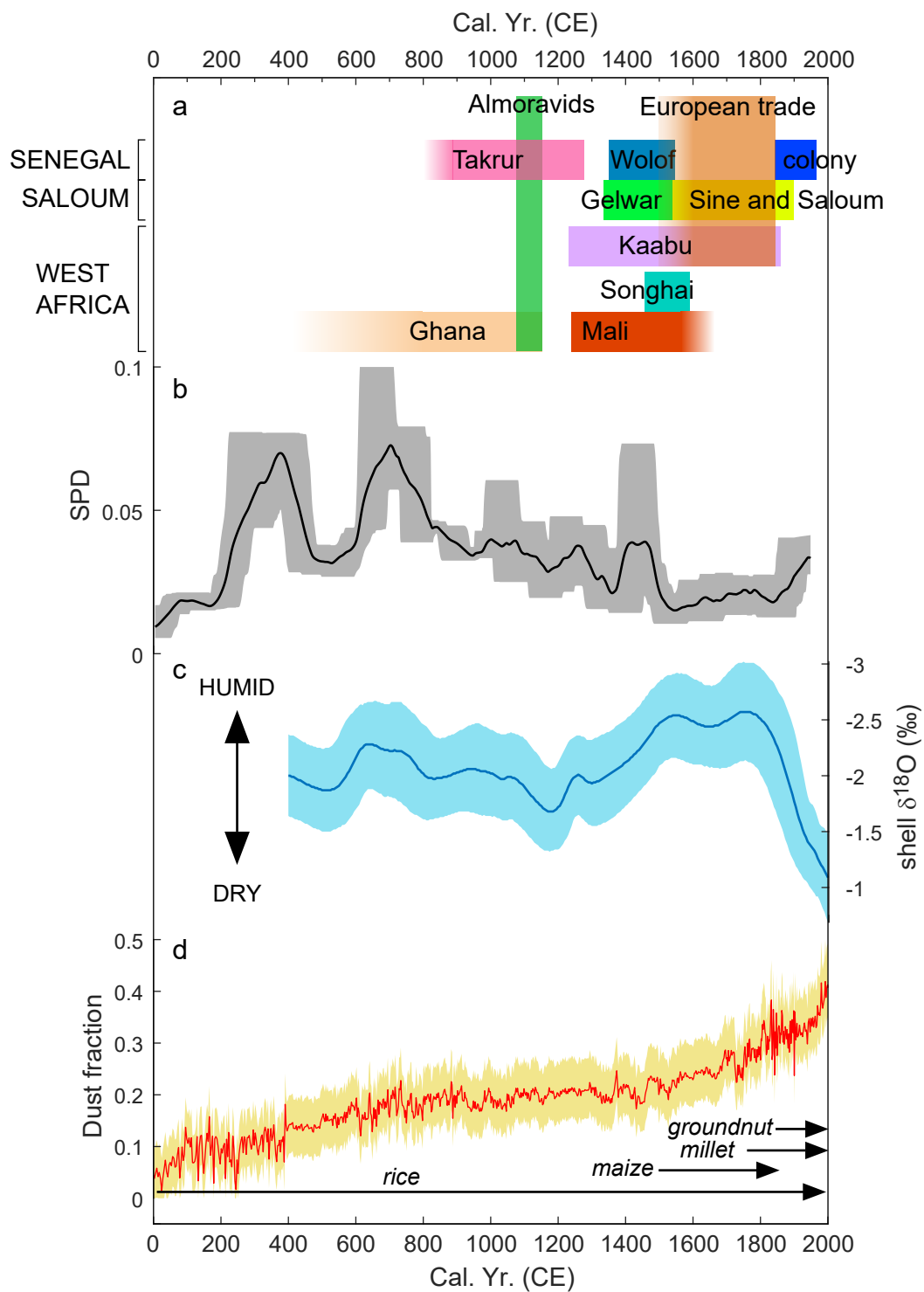
828 **Figure S1.** SPD curves S1 (a), S2 (b), and S3 (c). See methods for details. SPD from marine
829 samples only (blue), from terrestrial samples only (red), and the sum shown in light grey. The
830 summed SPD curve in panel (d) is the same as in Figure 2.

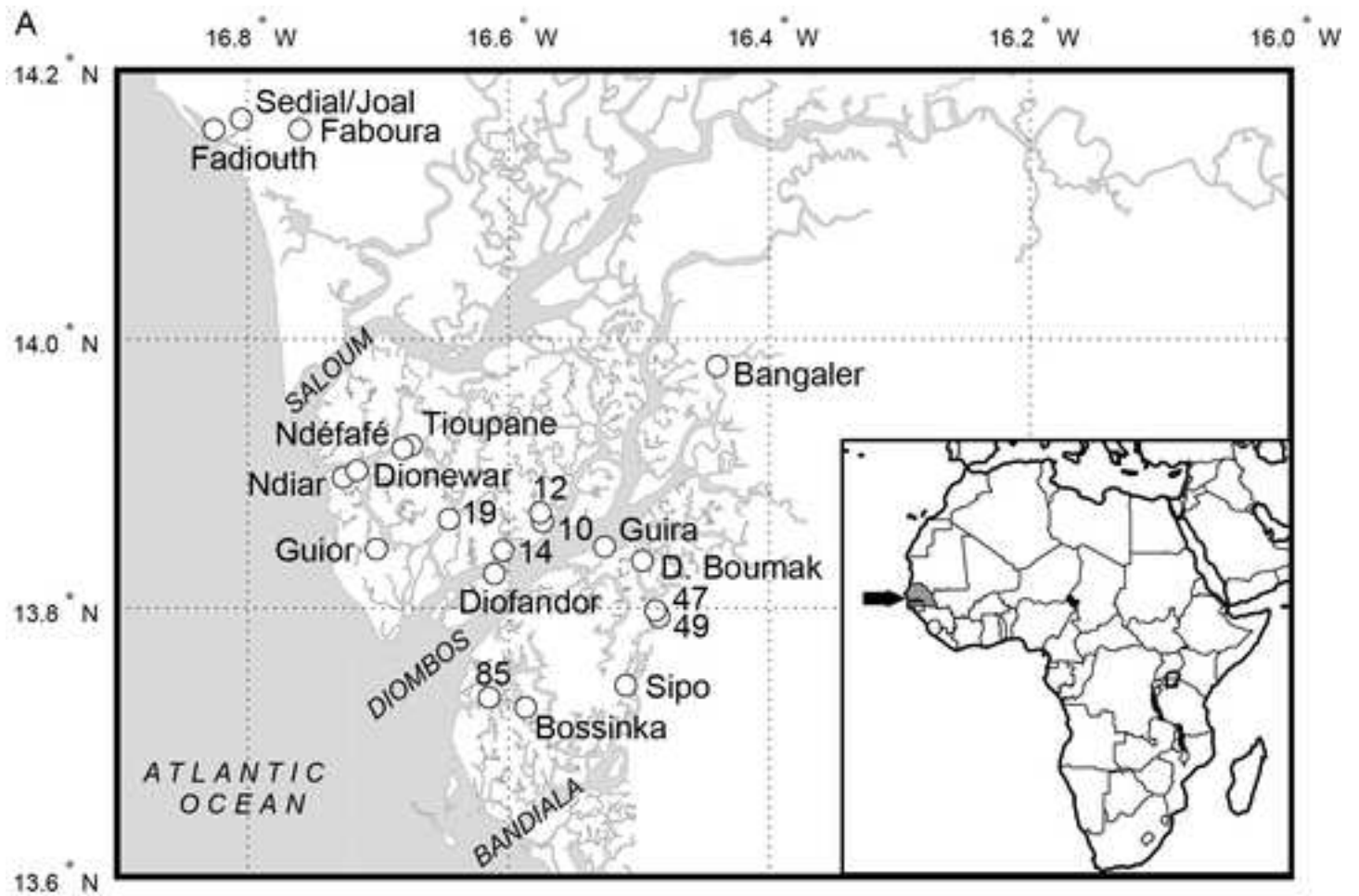
831

832 **Figure S2.** Distribution of radiocarbon dates through time and space across the Saloum
833 Delta. The size of the circles is related to the number of dates in the time interval. All dates
834 were considered.










Declaration of interests

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

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Author Statement

Matthieu Carré conceptualized the study, Matthieu Carré, Moufok Azzoug, Abdoulaye Camara, and Rachid Cheddadi participated to field work, Louis Quichaud did the radiocarbon calibrations and the SPD, Diana Ochoa, Jorge Cardich helped with statistics, Matthieu Carré, Abdoulaye Camara, Moufok Azzoug, Alexander Pérez and Rodolfo Salas contributed to the bibliographical synthesis, Matthieu Carré, Julien Thébault, Yoann Thomas, and Jorge Cardich contributed to funding acquisition. All authors commented on the methodology, read the manuscript and contributed to its preparation.



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