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1 **Modern pollen-vegetation relationships within tropical marshes of Lopé National Park**
2 **(Central Gabon)**

3

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13

14

15 **Abstract**

16 In the Congo Basin, paleoenvironmental data are scarce, due to the lack of natural lakes. Using
17 marshes sedimentary deposits as alternative archives requires the calibration of modern
18 pollen assemblages, which are totally absent for these type of deposits. The aim of this study
19 is to understand and qualify how well surface marsh sediment pollen assemblages reflect the
20 contemporary vegetation. We compare pollen assemblages at the surface of 23 sedge
21 marshes disseminated in an enclave of savanna in the Gabonese forest and vegetation surveys
22 along transects from sampling areas. Very high diversity of forest pollen taxa is recorded, with
23 a gradient of diversity from most open environments to those where the forest is closer,
24 however savanna taxa remains low. The surface samples surprisingly reveal very weak

25 percentages of Poaceae pollen grains that never exceed 25%. The low proportion of Poaceae
26 is consistent with the deposition mode of pollen in these specific sites but challenges the
27 common interpretation of a straightforward relationship between this percentage and
28 savanna/forest balance.

29

30 **Keywords:** modern pollen assemblages; marshes; sediments; Congo Basin; savanna; lowland
31 rainforest

32

33 **1. Introduction**

34 The savannas on the edge of the forest block of the Congo Basin as well as those enclosed are
35 probably remnants of the “forest crisis” that occurred during the third millennium BP (Maley
36 2002) or relict of Last Glacial Maximum climate conditions (Oslisly et al. 2006). The causes of
37 forest destruction have been the under heavy debate recently, with arguments for a human
38 (Bayon et al. 2012; Garcin et al. 2018; Bayon et al. 2019) or climatic origin (Ngomanda et al.
39 2009; Maley et al. 2018). Increasing the number of fossil records and their spatiality is
40 necessary to better understand this event, but is made difficult due to the scarcity of lakes
41 with sediment accumulation spanning the last thousand years in the region. It is likely that the
42 basin’s geological and hydrological characteristics, combined with tropical forest ecological
43 dynamics, do not permit lake maintenance over several thousand years.

44 In Gabon, an enclave of savanna in the forest has the particularity of sheltering many lowlands
45 that have preserved organic matter in sedge marshes (White & Abernethy 1997),
46 disseminated in the savanna itself, as well as in the surrounding forest. This area lies in the
47 Lopé national Park (LNP), where the savanna is kept open by annual fires for decades by the
48 park managers (Jeffery et al. 2014) but also probably for centuries or millennia, as a

49 consequence of traditional landscape management (Oslisly 2001). The numerous marshes, of
50 few hundred square meters each, are not fed by rivers and preliminary studies showed that
51 they accumulated sediments for several thousand years (Oslisly & White 2000) and recorded
52 local deposition conditions (Obame et al. 2017). To our knowledge, no equivalent
53 environmental archives were ever used for paleoecological reconstructions in West or Central
54 Atlantic Africa nor in lowland tropical Africa. The most similar studies probably come from
55 marshes in the Brazilian Cerrados, where pollen assemblages have been analyzed over
56 sequences of several thousand years (Ledru 2002).

57 The purpose of this study is to assess the potential of the marshes for paleoecological
58 investigations, by comparing pollen assemblages at the surface of 23 marshes and vegetation
59 surveys along transects from sampling areas. On a larger scale, the spatial forest/savanna
60 structure is addressed using satellite data.

61 The main questions addressed in this article are:

- 62 1- What type of pollen signal do these small marshes record? Specifically, is it a local or
63 regional signal?
- 64 2- Is the forest-to-savanna ratio properly recorded by commonly used arboreal/non-
65 arboreal pollen ratio?
- 66 3- Are the floristic composition of the Guinean-Congolese forest and the subcategories
67 often used in pollen-based vegetation reconstructions such as "mature forest",
68 "secondary forest" or "pioneer forest" recorded?

69

70

71 **2. Material and methods**

72 *2.1 Geographical and botanical setting*

73 The study area is located in the northern part of the Lopé National Park (LNP), where a
74 savanna-forest mosaic stands as approximately 320 km² enclosed open area in the Guineo-
75 Congolian tropical moist forest formation (~1000km² for the savannas of the middle Ogooue
76 valley) (White 1983). The annual rainfall in this part of the park is around 1500 mm, with two
77 dry seasons: the longer spans about three/four months from mid-May to mid-September, the
78 shorter is about one/two-months long in January-February. The low tree cover of the savannas
79 is mainly composed by shrubs of *Crossopteryx febrifuga*, *Psidium guineense*, *Sarcocephalus*
80 *latifolius* and *Bridelia ferruginea*. Marshes occupying the topographical depressions are mainly
81 dominated by the tall Cyperaceae *Rhynchospora corymbosa* (White & Abernethy 1997). Most
82 marshes are permanent and fed by groundwater resurgences; the others are only rain fed and
83 dry out during the dry season. We selected 23 marshes, in an area of 45 km², along a gradient
84 from closed forest to plain savanna (Figure 1; names of the marshes in italic in the text).

85 **Table 1.** Characteristics of the marshes

Sample site	Latitude	Longitude	Elevation (m. asl)	Marsh length	Marsh width	Approx. Marsh Surface (m2)	% of Savanna vs Forest (radius of 200 m)	% of Savanna vs Forest (radius of 500 m)	Savanna	Forest- savanna	Forest	Permanent water
S01	-0.127985	11.605235	159	90	30	2121	100	94	*			
S02	-0.129767	11.607432	155	150	20	2356	95	95	*			
S03	-0.134325	11.607489	160	100	30	2356	100	90	*			
S16	-0.137195	11.613853	163	98	45	3464	97	83	*			
S04	-0.139689	11.606595	166	125	60	5890	89	88	*			
S05	-0.145851	11.60121	164	95	20	1492	89	83	*			
S06	-0.147283	11.605835	173	100	30	2356	100	82	*			
S14	-0.160535	11.608747	208	80	25	1571	98	88		*		
Vitex	-0.163246	11.585711	238	125	40	3927	81	79		*		*
S15	-0.164476	11.618837	219	99	30	2333	95	90	*			
Citron	-0.168619	11.587202	232	80	45	2827	49	52		*		*
Yao	-0.172074	11.58781	238	200	30	4712	69	51		*		*
S13	-0.176709	11.607833	248	170	50	6676	98	85		*		
S07	-0.178815	11.583223	255	100	10	785	64	44		*		*
S12	-0.182578	11.61105	262	150	50	5890	95	76	*			*
S11	-0.186315	11.622994	242	150	30	3534	92	77		*		
S08	-0.191981	11.590751	256	101	46	3649	69	51	*			
S10	-0.192216	11.613869	258	130	30	3063	54	41		*		
S09	-0.196182	11.597091	271	150	30	3534	86	71		*		*
Tortue-Foret	-0.213077	11.591333	275	50	20	785	63	51			*	*
Tortue-Savane	-0.213077	11.591333	275	150	60	7069	63	51	*			*
Paurosa	-0.213181	11.588708	279	150	64	7540	97	62		*		*
Lope2	-0.21781	11.58349	277	203	81	12914	28	30			*	*

86

87

88 **2.2. Vegetation survey**

89 Botanical nomenclature follows the International Code of Nomenclature for algae, fungi and
90 plants (Turland et al. 2018) and Family level is updated according to APG III (APG 2009) and
91 APG IV (Chase et al. 2016).

92 Botanical surveys were carried out around the 23 marshes in September 2016. Most plants
93 were identified to species, but some to genus and a few to family, due to the absence of
94 distinctive character at this period of the year. The selected marshes were either in an open
95 savanna environment, partially against the forest or entirely in the forest. We conducted two
96 different botanical survey protocols in savanna and forest.

97 In the savanna surrounding each marsh, three 100 m-long transects were defined in different
98 directions from the marsh margin. The margin was established visually based on the soil-
99 surface quality (from black in wet parts to brownish in the marsh border) and on the transition
100 from hydrophytic vegetation, with *Rhynchospora corymbosa*, to dry land vegetation. In seven
101 5 x 5 m quadrats placed every 15 m along each transects, botanical surveys were performed
102 according to Braun-Blanquet (1932), using abundance-dominance coefficient from 5 (plants
103 covering more than 75% of the surveyed area) to 1 (plants covering a small area of the
104 surveyed (<5%), R for rare specimens and + for specimens present one time. Abundance-
105 dominance is a general estimate of density and recovery rate (top-down projection of plant
106 air elements) of different species in the inventory square (Braun-Blanquet 1932). The semi-
107 quantitative values obtained were translated into quantitative data that can be used for
108 vegetation survey analysis. The median of each classes has been used to obtain a percentage
109 for each species (Class + (present) = 0.1%; R (rare)=1%; 1=2.5%;
110 2=15%;3=37.5%;4=62.5%;5=87.5%).

111 When forest patches were against the marsh area, three 250 m-long transects in forest
112 originating from marsh margin were performed. In three 50 x 10 m quadrats placed every

113 100 m in each transect, all trees with a diameter at breast height (dbh) greater than 10 cm
114 were identified and counted.

115 Two Correspondence Analyses (CA) were performed on the median of classes for the savanna
116 surveys and on the number of tree species for forest surveys. Due to the different protocols
117 used in savanna and forest, we were not able to make a single analysis of the whole dataset.
118 Analyses were done using the CA function in the FactoMineR package of R (Lê et al. 2008).

119

120 *2.3. Remote-sensing data analysis*

121 A 0.5 m resolution WorldView-2 images acquired on 07/13/2016 (id 10300100595CDA00 and
122 1030010058399300) downloaded from Esri Satellite available through Qgis. Relying on the
123 clear visual difference between forest and savanna in the image, we performed an automatic
124 pixel classification into “forest” and “savanna” with Qgis (QGIS Development Team 2015). We
125 then computed the proportion of savanna and forests in circular buffer zones centered on
126 each marsh with radii 20 m, 50 m, 100 m, 200 m, 300 m, 500 m and 700 m.

127

128 *2.4. Pollen sampling, extraction and counting*

129 Surface marsh sediment were sampled for pollen analysis in March 2015. Sampling method
130 was based on Wright (1967). In each of the 23 marshes, about 50 subsamples (the uppermost
131 centimeter of sediment) were randomly collected over the whole surface of the marsh.
132 Subsamples were homogenized and put in a plastic bag to obtain one sample per marsh.

133 Pollen extraction was conducted on 1 cm³ of sediment following Faegri and Iversen protocol
134 (Faegri & Iversen 1989). A minimum of 400 pollen grains (excluding Pteridophyte spores) was
135 counted per sample with an optical microscope at X630 magnification. The identification was
136 based on the pollen collection of Tropical Africa at the “Institut des Sciences de l'Evolution de

137 Montpellier (ISEM, Université Montpellier <https://data.oreme.org/observation/pollen>), and
138 on African atlases of pollen and spores (Bonnefille 1971; Ybert 1979; Sowunmi 1995; Gosling
139 et al. 2013). The nomenclature of pollen taxa was based on Vincens et al. (2007).
140 Pollen taxa were attributed to five ecological class according to the classification of Vincens et
141 al. (2007) for Africa, and locally specified according to White and Abernethy (1997): Marsh,
142 for pollen taxa corresponding to plants growing in waterlogged environments; Marsh border,
143 to plants growing in the vicinity of water but not in the submerged area; Savanna, to plants
144 characteristic of open environments; Forest front, to forest plants characteristic of forest
145 edge, generally fast-growing light-demanding forest species; Forest, to other forest plants.
146 For representation diagram, pollen percentages were calculated on the sum of all determined
147 pollen, including hydrophytic taxa (e.g. Cyperaceae) but excluding spores. The whole pollen
148 sum is used as in modern pollen-vegetation relationships studies (e.g. Vincens et al. 2000).
149 Pollen concentrations have been calculated by adding *Lycopodium* tablets during the chemical
150 treatment (Stockmarr 1971). Pollen diagrams were created with the Rioja package of R
151 (Juggins 2012). The most common taxa were defined as the taxa present in a minimum three
152 samples and with more than 2% of the pollen sum in at least one sample.
153 A Correspondence Analysis was performed on the total pollen sum (excluding undetermined
154 pollen and spores) and according to different options to refine interpretations: on the most
155 common taxa defined above, on pollen from terrestrial plants by excluding those attributed
156 to the Marsh class, and finally on Forest taxa only. Analyses were done using the CA function
157 in the FactoMineR package of R (Lê et al. 2008).

158

159 *2.5. Representation indices*

160 After establishing a correspondence between surveyed plants and identified pollen taxa, we
161 computed indices of Association (A), Under-representation (U) and Over-representation (O)
162 for the main taxa present in plant and pollen datasets (Davis 1984). These indices are based
163 on presence/absence data in vegetation and pollen from the 23 marshes and allow qualifying
164 the relationship between vegetation and pollen. They are defined as follows:

165

$$166 \quad A = \frac{B_0}{B_0 + P_0 + P_1}$$

$$167 \quad U = \frac{P_1}{B_0 + P_1}$$

$$168 \quad O = \frac{P_0}{B_0 + P_0}$$

169

170 and expressed as percentages, where: B_0 is the number of samples in which both the pollen
171 type and the associated plant are present; P_0 is the number of samples in which the pollen
172 type is present but not the associated plant; and P_1 is the number of samples in which the
173 pollen type is not present but the associated plant is. We also follow the classification used by
174 Amami et al. (2010) with Strongly-Associated taxa: $A > 65\%$; Associated taxa: $50\% < A < 65\%$;
175 Weakly Associated taxa: low A values and relatively high values for U (under-represented taxa)
176 or O (over-represented taxa).

177

178 **3. Results**

179 *3.1. Floristic distribution*

180 Canonical Analysis applied on the 439 botanical survey quadrats in savanna reflects a gradient
181 of plant distribution from quadrats closest to the marsh (Q1 and Q2; 0-30m) to the furthest in

182 the savanna (Figure 2; Panel A). The two first axes express 13.3% of the total dataset inertia.
183 In the species representation, the first axis opposes species from marshy areas with high
184 frequencies for species like *Aspilia africana*, *Hyparenia* sp., *Hypoxis angustifolia*, *Imperata*
185 *cylindrica*, *Ipomoea* sp1., *Ourenia lobata*, *Paspalum* sp., *Rhynchospora corymbosa*, *Sauvagesia*
186 *erecta* and *Schizachyrium platyphyllum*, and species more related to inland savanna zone such
187 as *Andropogon* sp., *Crossopteryx febrifuga* and *Kyllinga echinata*. The second axis also opposes
188 species from marshy areas, as Fern (unidentified), *Clappertonia ficifolia*, *Desmodium* sp.,
189 *Phyllanthus* sp. and *Triumfetta* sp., to more inland savanna species, as *Andropogon* sp.,
190 *Crossopteryx febrifuga* and *Kyllinga echinata*. The second lower panel (B) of Figure 2 where
191 Quadrat numbers are plotted reveals an opposition between Q1 plus Q2 and the other
192 quadrats presenting a higher homogeneity.

193 The two first axes of the Canonical Analysis applied on the 101 botanical survey quadrats in
194 forest are presented Figure 3. The axes express 28.3% of the total dataset inertia. They oppose
195 marshes close (*Citron*, *Paurosa*, S08) or within the forest (*Lopé2* and *Tortue-foret*) to others in
196 more open areas as *Vitex*, S06, S15 and S16 associated to gallery forest (Figure 3). The first
197 group is mainly explained by the frequency of *Aucoumea klaineana*, *Maprounea*
198 *membranacea*, *Variastrum* sp. and *Xylopia quintasii*, compared to *Ceiba pentandra*, *Elaeis*
199 *guineensis* and *Irvingia grandifolia* for the second group.

200

201 3.2. Pollen diagram

202 158 pollen taxa were identified in surface soil samples. Most of the pollen taxa (115 taxa) are
203 produced by forest trees. The “Savanna” vegetation is mainly represented by 27 taxa, the
204 “Marsh” by 8 taxa and the “Marsh Border” by 8 taxa.

205 The most common pollen taxa (>2%, present in more than 3 samples) of surface samples are
206 presented in a pollen diagram according to the five ecological classes and ranging according
207 to the first axis of a CA performed on the whole pollen assemblages (Figure 4; detailed pollen
208 diagram in supplementary file. Sup. X and CA in Sup x).

209 The pollen diagram shows that marshes with the highest degree of openness (marshes within
210 savanna) show low percentages of "Savanna" taxa in their pollen assemblages, with variation
211 between *ca.* 5 and 30%. The highest values of the "Savanna" taxa are obtained in marshes
212 within forest-savanna mosaic with values between *ca.* 20 and 40%, but do not exceed 50%.

213 "Forest front" pollen taxa are registered in all the 23 pollen assemblages with close values,
214 between *ca.* 1 and 5% and do not exceed 10%.

215 "Forest" pollen taxa are registered with the highest values in all marshes within savanna,
216 between *ca.* 70 and 80%, but do not exceed 90%. Their values vary between *ca.* 60 and 70%
217 and do not exceed 80% in the marshes within forest-savanna mosaic. The marshes within
218 forest (*Lopé 2* and *Tortue-foret*) have similar percentages to those respectively in forest-
219 savanna, and in savanna.

220 "Marsh" taxa are better registered in marshes within forest-savanna mosaic than those in
221 savanna or forest, with values between *ca.* 10 and 35%, without exceeding 40%.

222 In all marshes, pollen assemblages are dominated by Poaceae and Cyperaceae, with unusual
223 correlation of occurrence. The percentages remain low, respectively 4-27% and 1-33% for all
224 the marshes.

225

226 3.3. Pollen diversity

227 Several Correspondence Analysis (CA) were performed on the whole pollen assemblages,
228 marsh pollen excluded, on the forest taxa, on the forest taxa without rare taxa (superior to

229 2% in almost three samples) and with *Tortue-foret* excluded (because an over dominance of
230 *Uapaca* pollen in the assemblage) to refine the interpretation of the results. Figure 4 presents
231 selected CA with rare taxa and *Tortue-foret* excluded (A: all taxa and B: only forest taxa). The
232 distribution of marshes and taxon are quite the same for the two CA. Marshes in open areas
233 (S04, S08, S03, S12 and S01, S02) are opposed from those in more closed habitats (*Citron*,
234 *Paurosa*, *Vitex*, *Yao* and *Lopé2*, *Tortue-Savane*). The distribution is mainly explained by the
235 high frequency of *Cassia-type*, *Dialium*, Euphorbiaceae, Fabaceae Caesalpinioideae,
236 Flacourtiaceae, *Macaranga-type*, Olacaceae, Pontederiaceae, and for the second group by
237 Annonaceae, *Celtis*, Cyperaceae, *Laccosperma*, *Lophira alata-type*, Poaceae and *Uapaca*.
238 The gradient from marshes in open areas to closed habitats along the first axis is well visible
239 in the map of Figure 4C where value of the first axe of the CA (B) has been plotted with a color
240 scale.

241

242 3.4. Indices of vegetation representation in pollen assemblages

243 The Davis indices calculated for the 33 main pollen taxa indicate that 9 taxa are Strongly
244 Associated, 2 Associated, 0 Under-represented and the majority (20 taxa), Over-represented.
245

246 **Table 2.** Davis indices calculated for the main 33 pollen taxa: B_0 is the number of samples in
247 which both the pollen type and the associated plant is present; P_0 is the number of samples
248 in which the pollen type is present but not the associated plant; and P_1 is the number of
249 samples in which the pollen type is not present but the associated plant is associated (A),
250 under-represented (U) and over- represented (O).

		B0	P0	P1	A	U	O
Savanna	Poaceae	21	0	0	1	0	0
Forest	Cassia-type	21	0	0	1	0	0
Marsh	Cyperaceae	20	1	0	0.95	0	0.05
Forest	Annonaceae	18	1	0	0.95	0	0.05
Forest	Olacaceae	16	4	0	0.8	0	0.2
Forest Front	Lophira alata-type	15	2	3	0.75	0.17	0.12
Forest	Dialium	15	4	1	0.75	0.06	0.21
Forest	Uapaca	14	2	4	0.7	0.22	0.13
Forest	Moraceae	13	7	0	0.65	0	0.35
Forest Front	Elaeis guineensis	12	9	0	0.57	0	0.43
Forest	Diospyros	10	9	1	0.50	0.09	0.47
Marsh border	Ascolepis capensis	9	7	3	0.47	0.25	0.44
Forest	Anacardiaceae	8	9	1	0.44	0.11	0.53
Forest	Euphorbiaceae	8	13	0	0.38	0	0.62
Forest	Psychotria	6	13	0	0.32	0	0.68
Forest	Rubiaceae	5	16	0	0.24	0	0.76
Forest Front	Alchornea-type	4	15	0	0.21	0	0.79
Marsh border	Hypoxidaceae	4	17	0	0.19	0	0.81
Marsh border	Raphia	0	21	0	0	0	1
Forest	Caesalpiaceae	0	21	0	0	0	1
Forest	Flacourtiaceae	0	21	0	0	0	1
Forest	Sterculiaceae	0	20	0	0	0	1
Forest	Caloncoba-type	0	21	0	0	0	1
Forest	Fabaceae	0	21	0	0	0	1
Marsh	Pontederiaceae	0	18	0	0	0	1
Forest	Cnestis	0	21	0	0	0	1
Forest	Macaranga-type	0	19	0	0	0	1
Marsh border	Asteraceae	0	20	0	0	0	1
Forest	Laccosperma	0	20	0	0	0	1
Marsh	Crinum	0	19	0	0	0	1
Forest	Celtis	0	19	0	0	0	1
Forest	Mimosaceae	0	21	0	0	0	1
251 Savanna	Bridelia ferruginea-type	0	15	0	0	0	1

252 3.5. Pollen concentrations

253 Pollen concentrations were calculated first on the pollen sum (total concentration), second on
254 the regional pollen excluding Cyperaceae, Poaceae, other hydrophytes and spores (regional
255 concentration), and third on forest taxa only (forest concentration). Total concentration varies
256 from 36,996 (*Yao*) to 274,821 (*Vitex*), regional concentration from 16,288 (*Yao*) to 127,780
257 (*S05*), and forest concentration from 12,006 (*Yao*) to 94,173 (*S05*).

258 There is no trend in concentrations, either in terms of distance from the forest (forest
259 concentration), in terms of marsh size (regional concentration) or in terms of the permanent
260 or temporary nature of wetlands (total concentration). There is also no correlation with the

261 mean sediment accumulation rate calculated for 6 marshes, for which we have radiocarbon
262 dates (K. Henga-Botsikabobe & L. Bremond, unpublished data).

263

264 **4. Discussion**

265 *4.1. Savana pollen representation*

266 Arboreal Pollen grains versus Non-Arboreal Pollen grains (AP/NAP ratio) has long been used
267 to characterize the structure of the vegetation by simplifying complex pollen assemblages
268 (Faegri & Iversen 1964). In tropical areas, as in temperate regions, this ratio has been
269 confronted and discussed with quantified vegetation cover (Vincens et al. 2000; Favre et al.
270 2008). In fossil samples, the NAP grains are mainly Poaceae pollen and a common
271 interpretation is to link Poaceae pollen abundance and presence of savanna around the site
272 (e.g. Maley et al. 2018). In lake fossil records, the Poaceae that grow along the shoreline can
273 mask the regional forest signal and lead to a misinterpretation of the real openness of the
274 environment (Bush 2002), but it has never been observed that fossil sediments from a savanna
275 region contain very little Poaceae pollen grain. In lake Kamalété, in the South/East part of the
276 Lopé reserve, the study of Ngomanda et al. (2005) shows that Poaceae pollen grains were well
277 recorded and preserved (>60% of the pollen sum) in the sediments during the last 1400 years.
278 Also, Lebamba et al. (2009) observed that modern soil assemblages from the savanna
279 surrounding our studied marshes present more than 60% of Poaceae pollen grains in the
280 assemblages. These studies are consistent with previous works (Ybert 1975; El Ghazali &
281 Moore 1998; Vincens et al. 2000; Julier et al. 2018), which consider tropical savanna Poaceae
282 as strong pollen producers, and their wind-mediated pollen as well dispersed and usually over-
283 represented in pollen assemblages.

284 The surface samples of our study zone surprisingly reveal very weak percentages of Poaceae
285 pollen grains that never exceed 25%. The studies of Ngomanda et al. (2005) and Lebamba et
286 al. (2009) clearly prove that the very low proportions of Poaceae pollen found in our samples
287 are not due to low pollen production by Poaceae species from the savanna of La Lopé (mainly
288 *Anadelphia afzeliana*, *Hyparrhenia diplandra*, *Panicum nervatum* and *Schizachyrium*
289 *platyphyllum*; (Jeffery et al. 2014)). Moreover, in our surface samples, Poaceae are well
290 correlated with Cyperaceae (Pearson test: $r=0.78$; $p<0.01$), which suggests that they originate
291 from local helophytic vegetation, and not from savanna. The discrepancy between previous
292 results and our data should be due to both the marshy nature of our study sites and the spatial
293 scale of pollen trapping, inadequate to record the savanna vegetation. The spatial scale
294 represented by pollen assemblages has long been investigated. It is dependent on pollen
295 productivity and dispersion for each plant species, including its mode of primary and
296 secondary dispersal and its ability to be dispersed. Jacobson and Bradshaw (1981) proposed
297 that the relative weights of local (< 20 m), extra-local (< a few hundred meters) and regional
298 vegetation (from a few hundred meters to about 30 km) in the pollen assemblage strongly
299 vary with the size of the site. Here, the studied wetlands are small, very often less than 100 m
300 in diameter, which should reduce the proportion of the regional pollen influx. In addition, they
301 are not open water bodies, but herbaceous marshes without streams that feed them.
302 Herbaceous plants should block the runoff, further reducing extra-local supply. Pollen
303 assemblages will therefore be strongly influenced by local vegetation and partially by regional
304 one. The extra-local vegetation will therefore be masked by these two components. The study
305 of Jacobson and Bradshaw (1981) was quite theoretical, but later Sugita (1994) simulated
306 pollen loading in relation to distance-weighted plant abundance around the sedimentary
307 basin and specified that pollen loading and proportion in large lakes record the spatial

308 distribution pattern of vegetation as homogeneous rather than patchy. This confirms our
309 interpretation, especially since in Sugita's model the height of trees producing pollen grains is
310 not considered. Trees in the galleries in the savanna rarely exceed 25 m in height, while trees
311 in the mature forest can occasionally exceed 65 m (White & Abernethy 1997). The production
312 of pollen from tall trees against Poaceae pollen produced at less than one meter-high will
313 amplify the phenomenon of masking the recording of savanna Poaceae in the deposits. Our
314 samples therefore reflect a truncated composition of the extra-local vegetation. The regional
315 composition is represented by something like to 35-55% of the pollen count, which is
316 consistent with the estimates of Jacobson and Bradshaw (1981).

317

318 4.2. Pollen diversity: marshes, savanna, forest

319 Axis 1 of the CA indicates that there is a gradient from the most open environments to those
320 where the forest is closer. The assemblages that explain this distribution seem however to be
321 counter-intuitive when referring to the usual interpretations of pollen patterns in tropical
322 Africa (Maley & Brenac 1998). Indeed, Fabaceae Caesalpinioideae, usually considered as a
323 marker of mature forest, are better recorded far from the forest front, and pioneer taxa such
324 as Annonaceae and *Lophira alata* are more present in the sites close to the forest bloc. These
325 observations, based on pollen percentages, are confirmed by pollen concentrations of forest
326 trees that show no trend towards distance from the forest. This implies that the recorded
327 gradient clearly does not translate the nature of extra-local vegetation (savanna or forest). It
328 should be rather related to the mosaic nature of Lopé landscapes that include savannas,
329 gallery forests and forest stands. In the open part of the studied zone, there are tree species
330 associated to the presence of marshes and streams such as *Anthocleista* spp. (Loganiaceae),
331 *Berlinia* spp. (Fabaceae Caesalpinioideae), *Calancoba glauca* (Flacourtiaceae), *Mitragyna*

332 *ciliata* (Rubiaceae) and *Nauclea vanderguchtii* (Rubiaceae), found quite close to rivers and
333 streams, or *Homalium* (Flacourtiaceae) generally found in gallery forests close to savanna
334 (White et al. 1995). In the southern samples, closed to the forest, there are species of the
335 colonizing forest front, including *Aucoumea klaineana* (Burseraceae), a very weak pollen
336 producer, *Lophira alata* (Ochnaceae) and some species which are able to colonize savanna,
337 such as *Elaeis guineensis* (Arecaceae), *Klainedoxa gabonensis* (Irvingiaceae), *Uvariastrum*
338 *pierreanum* (Annonaceae) and *Xylopia* spp. (Annonaceae) (White et al. 1995).

339 The analysis of the botanical statement performed in the forested area closed to the studied
340 marshes is difficult to compare with the results of the pollen assemblages because the gallery
341 forest was not enough sampled. Statements are missing in open environments because
342 galleries and forest "bosquets" were not against the marsh area. However, we can note a
343 roughly similar distribution, with a distribution from swamps in open areas to those close to
344 the forest bloc. Vegetation in Lopé NP is complex due to the mosaic of forest types, 27
345 according to White et al. (1995), and the botanical surveys did not permit to differentiate
346 some of them.

347 In contrast, the botanical statements performed in the savanna surrounding the marshes
348 reflected a clear distribution of plants from the swamp border to further in the savanna.
349 Swampy species are opposed to inland savanna species. This distribution cannot be directly
350 recorded by the assemblages of surface pollen because of the sampling method which
351 consisted in obtaining a homogeneous assemblage over a surface area of several hundred
352 square meters and not a transect as Amami et al. (2010) done. Thus, it is important to identify
353 "indicator taxa" of the different environments and especially the presence of savanna around
354 the sites. Janssen (1967; 1970) and Amami et al. (2010) emphasized the importance of
355 "indicator taxa" to characterize a particular community. Our results, both quantitative, based

356 on Davis indices, and qualitative, based on pollen diagrams, indicate that no pollen correctly
357 records the main herbaceous and shrubby savanna species, namely *Crossopteryx febrifuga*,
358 *Sarcocephalus latifolius*, Poaceae, *Psidium guineense* and *Bridelia frerruginea*. Marsh border
359 species, such as *Ascolepis capensis* and Hypoxidaceae, are more sensitively recorded. These
360 taxa are associated with an opening of the environment around the marsh and probably a
361 lower annual permanent humidity condition.

362

363 4.3. Fossil assemblage interpretations

364 Our results from marsh surface sediments show that soil samples (e.g. Lebamba et al. 2009)
365 are not good analogues for marsh pollen records. Tropical savanna marshes are rare because
366 of the very strong evapotranspiration in these environments. A constant supply of water
367 during dry seasons is necessary to allow the accumulation of organic matter. To our
368 knowledge, there are no equivalent fossil deposits that have been studied in Africa. In Brazil,
369 some palm swamps, so-called “vereda”, are growing in the savanna-like vegetation commonly
370 known as “cerrado” and were studied for their pollen fossil contain (Salgado-Labouriau et al.
371 1997). This study do not really investigate the relationship between present vegetation and
372 pollen deposits, but the obtained results clearly do not show any distortion similar to the one
373 we observe in our sites, particularly with regard to Poaceae. In Ledru (2002), some surface
374 samples from cerrados can however register less than 20% of Poaceae, but the published data
375 does not allow identifying the exact environmental conditions of the study. Thus, the
376 interpretation of fossil data from the marshes where we studied the contemporary deposits
377 will have to be done very finely, considering these limitations. Fossil assemblages may have
378 to be analyzed by adding them to the Canonical Analyses performed on modern data in order

379 to differentiate riparian forest assemblages from those of mature forests as done by Montade
380 et al. (2019).

381

382 **5. Conclusion**

383 The results of the present work on pollen assemblages from Gabonese marsh surface
384 sediments are quite complex because they are often counter-intuitive. The low proportion of
385 Poaceae in the assemblages is explained but challenges the simplistic interpretation that
386 consists in considering this percentage as a degree of openness of the environment. These
387 results do not affect previous calibration results performed on soil surfaces and applicable to
388 lake sediments. However, they are essential for interpreting sedimentary sequences from
389 marshes.

390 The very high diversity of forest pollen taxa is not affected by the taphonomy of the deposits,
391 which nevertheless makes it possible to finely qualify the major changes in plant diversity that
392 may have occurred in the forests of the Congo Basin over the past few millennia.

393 To conclude, anywhere in the world “when you hear hoofbeats, think of horses not zebras”;
394 here, in Lopé, it is always the zebras you find.

395

396

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402

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- 535

Figure Captions

Figure 1. Study area and location of sampled marshes

Figure 2. Canonical Analysis applied on the 439 botanical survey quadrats in savanna.

Panel A: Distribution of the plant species according to axes 1 and 2 colored according to their ecology. Color gradient illustrate the contribution of each species to the CA according to the squared cosine (\cos^2).

Panel B: Distribution of the Quadrats according to axes 1 and 2. Q1 are the quadrats closest to the marsh and the other by incrementing by 15m.

Figure 3. Canonical Analysis applied on the 101 botanical survey quadrats in forest.

Panel A: Distribution of the plant species according to axes 1 and 2. Color gradient illustrate the contribution of each species to the CA according to the squared cosine (\cos^2).

Panel B: Distribution of the marsh where transects where performed according to axes 1 and 2.

Figure 4. Pollen diagram of the most common grains counted in the marsh surface samples.

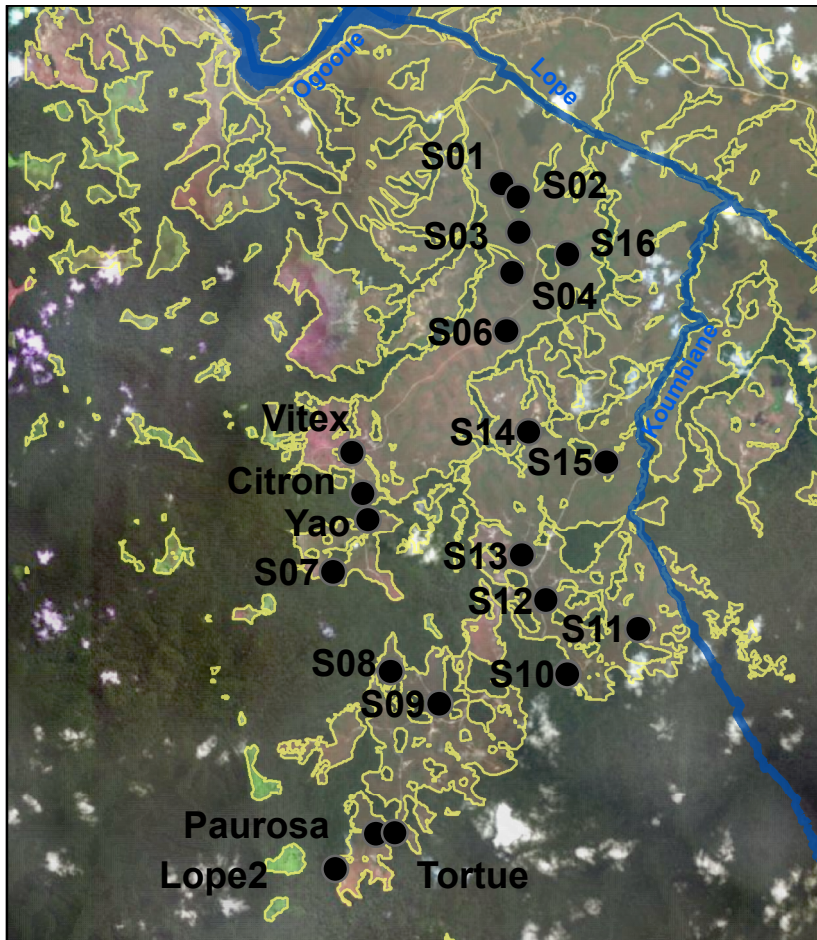
Samples are ranging according to the first axe of an CA performed on the whole pollen assemblages and taxa ranging according to their ecology affinity.

Figure 5. Canonical Analysis applied on the most common pollen grains.

Panel A: Distribution of the taxa according to axes 1 and 2. Color gradient illustrate the contribution of each taxa to the CA according to the squared cosine (\cos^2).

Panel B: Distribution of the sampled marshes according to axes 1 and 2.

Panel C: Mapping of Axe 1 of the CA with a color gradient for each marshes according to their location and position towards the forest-savanna mosaic.



● Studied marshes

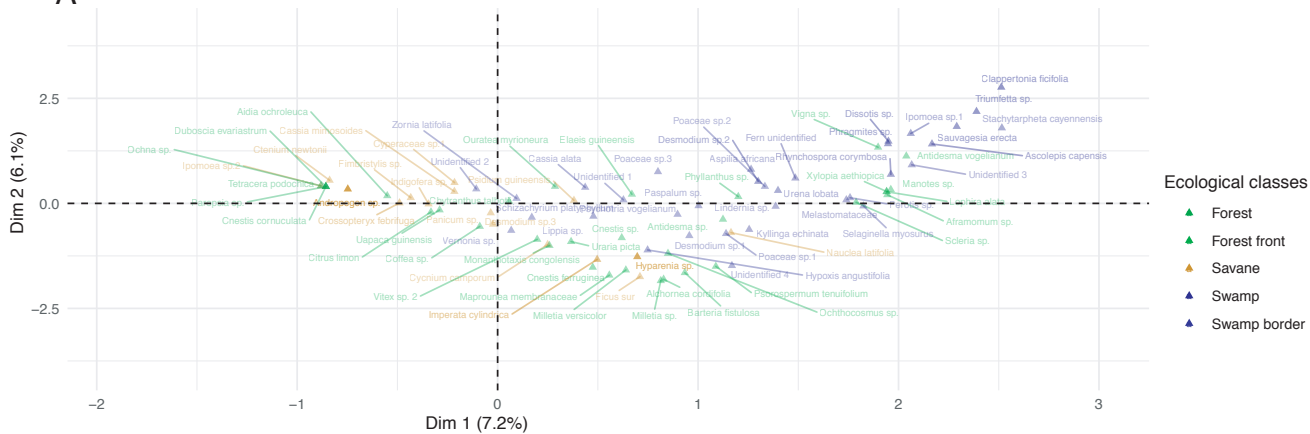
□ Savanna

■ River

0 1 2 Km

Origin data : Alos DSM (meters a.s.l.), Satellite imagery Esri et Sentinel 2A,
UMR 5554 ISEM (Land cover and river).
Data production and Design : L. Paradis, UMR 5554 ISEM, july 2019.

A



B

