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New evidence on the role of past human activities and edaphic factors on the fine-scale distribution of an important timber species: *Cylicodiscus gabunensis* Harms

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ABSTRACT

Despite the implementation of management plans, commercial tree species densities are declining in the forests of Central Africa. In the region, *Cylicodiscus gabunensis* Harms (Fabaceae-Caesalpinioideae; common name 'okan'), is one such species most exploited, but its ecology remains poorly understood. The rarity of its regeneration in evergreen forest suggests that, like other commercial light-demanding species, the conditions that allowed populations to become established are no longer present. Using a combined archaeobotanical and pedological approach, the aim of this study is to identify the factors explaining the current distribution of *C. gabunensis* individuals at local scale. Within a plot of 1050 ha in a forest concession in south-eastern Gabon, we installed 40 archaeological pits equally divided between sites with and without *C. gabunensis*. The artefacts encountered were collected and analysed. Charcoal masses were quantified and 18 charcoals were dated. These ages were compared with the average age of the tree population, using growth data from 50 individuals and heartwood dating from 4 individuals. An analysis of the physico-chemical properties of the soil was carried out on composite samples from each archaeological pit. Pottery sherds were found in two pits while charcoal was present in all pits, suggesting widespread human occupation and fire throughout the study area. Human occupation occurred in two phases: between 2480 and 1010 BP and from 590 to 80 BP. The abandonment of agricultural land at the end of this second phase could coincide with the establishment of the *C. gabunensis* cohort whose average age has been estimated at between 90 and 148 years. Soil analyses showed that *C. gabunensis* individuals were located on soils that were comparatively richer in element potentially toxic (Fe) and in some plant nutrients (K, P) and total nitrogen. The current scarcity of young trees argues for the implementation of a silviculture that integrates the light requirements of the species as well as the chemical fertility of the soil.

1. Introduction

Logging in Central Africa is based on the implementation of management plans. These plans define a set of parameters, including cutting cycle and minimum harvesting diameter, which are set based on the calculation of recovery rates for harvested populations (Durrieu De Madron et al., 2000; Fargeot et al., 2004; Umunay et al., 2019). Despite the existence of these standards, which have given Central Africa a pioneering role in sustainable forest management, populations of key timber species are declining over time (Kalema and Kasenene, 2007).

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The rarity of their regeneration is thought to be the cause (Karsenty and Gourlet-Fleury, 2006; Vleminckx et al., 2014). These species are mostly light-demanding and are characterised by Gaussian population structures that reflect low natural regeneration and aging of the tree population (Doucet, 2003; Kouadio, 2009; Bourland, 2013; Morin-Rivat et al., 2017).

Many commercial species are light-demanding, and their current abundance in the canopy of Central African forests can be explained by anthropogenic disturbances dating back to the end of the 19th century. According Morin-Rivat et al. (2017), several of these species have regenerated in fields abandoned by human populations following European colonisation. This is evident from the frequency of charcoal and pottery sherds found in stands where these species are abundant (Biwolé et al., 2015a; Bourland et al., 2015), and a correspondence between the age of the charcoal and the average age of the tree populations studied was validated for four commercial species: *Triplochyton scleroxylon* K. Schum, *Terminalia superba* Engl. & Diels, *Erythrophleum suaveolens* Brenan and *Pericopsis elata* (Harms) Meeuwen (Morin-Rivat et al., 2017).

The physico-chemical characteristics of the soils can also play a determining role in the composition of forest stands, both on a large scale (5–100 km) (Swaine, 1996; Fayolle et al., 2012) and on a local scale (<5 km) (Vleminckx et al., 2017). This seems to be the case particularly for light-demanding species, which have higher acquisition strategies and growth rates on fertile soils than shade-tolerant species (Ashton and Hall, 1992). For example Ouédraogo et al. (2016) showed that nutrient-rich substrates support more physiologically light-demanding species. However, soil fertility is thought to have little effect on the growth of most Fabaceae due to their ability to produce bacterial nodules, which facilitate the acquisition of phosphorus from the soil by producing more nitrogen-rich enzymes (phosphatases) that mineralise organic phosphorus (Nasto et al., 2014). However, the role of soil fertility in the growth of the few leguminous species without bacterial nodules, such as *Cylicodiscus gabunensis* Harms, is not known (Tedersoo et al., 2018).

Mainly known by the commercial name 'okan', *C. gabunensis* is the sixth-most exploited species in Central Africa (FRM, 2018) and is the most exploited timber after *Aucoumea klaineana* Pierre in Gabon (ATIBT, 2010; FRM, 2018). Its very dense and durable wood is used for heavy outdoor construction (Meunier et al., 2015). Due to a regeneration deficit in evergreen forest, the species is assumed to be light-demanding, but its ecology remains poorly understood (Ndonda Makemba et al., 2019). Understanding the ecological factors behind the spatial distribution of tree species is a requirement for the sustainable management of their populations (Réjou-Méchain et al., 2021).

Using both archaeobotany and pedology, the present study aims to determine the factors explaining the distribution of *C. gabunensis* on a local scale. Two hypotheses are tested: (i) like other species with a Gaussian distribution of stem numbers per diameter class, *C. gabunensis* may have regenerated mainly in the 19th century in agricultural fallow land, (ii) because of the absence of bacterial nodules, the species may prefer nutrient-rich soils.

2. Materials and methods

2.1. Species studied

Cylicodiscus gabunensis (Fabaceae-Caesalpinioideae) is a large tree reaching 60 m in height (Meunier et al., 2015) found in rainforests from the Ivory Coast to the Republic of Congo (Ndonda Makemba et al., 2019). Its fruit is a long pod (60–100 cm long and 4.5–5 cm wide) that contains numerous winged seeds (7.5 cm long) dispersed by the wind (Meunier et al., 2015). The roots of the seedlings are often covered with ectotrophic mycorrhizae for a relatively short period (De La Mensbruge, 1966). These ectotrophic mycorrhizae probably disappear and are replaced by arbuscular endomycorrhizae during later tree growth (Onguene and Kuyper, 2001).

2.2. Study site and population characterisation of C. gabunensis

The study was carried out in the sustainably managed concession granted to Precious Woods CEB, a FSC (Forest Stewardship Council) certified forestry company. The concession is located in the Lastoursville region of Gabon between 0°30′–1°00′ S and 12°30′–14°00′ E. It is composed of three forest management units (FMU 1, FMU 2 and FMU 3; Fig. 1a) covering an area of 596823 ha. The present study was carried out in FMU 2, specifically within the DynAfFor plot (https://www.dynafac.org) (1050 ha; Fig. 1b). The forest in which the concession and this plot are located is evergreen and rich in Fabaceae and Burseraceae (White, 1986). According to Réjou-Méchain et al. (2021), these forests are divided between the Atlantic inland evergreen (27%, 15% and 14% of species are Fabaceae, Burseraceae and Myristicaceae respectively) and mixed evergreen (30%, 10% and 8% of species are Fabaceae, Olacaceae and Myristicaceae respectively) forest types. The soil is ferralitic on Francevillian sandstone. Elevations range between 300 and 700 m above sea level and some areas have significant slopes (TEREA, 2015). The climate is equatorial (Martin et al., 1981) with two rainy seasons (March to May and October to December) alternating with two dry seasons (Cabaillé and Fontès, 1978). The average annual temperature is 25.3 °C (Martin et al., 1981; Olivry, 1986) and annual rainfall is 1700 mm (Moupela et al., 2014). In the study area, densities of *C. gabunensis* (diameter at breast height, DBH ≥ 20 cm) decrease overall from West to East and from North to South, with extreme mean values per FMU of 0.370 and 0.004 stems/ha. The diameter-class distribution of *C. gabunensis* is quite similar in the three FMUs, with a general Gaussian distribution pattern characterised by a relatively greater number of large-diameter trees (Fig. 1a; TEREA, 2015).

2.3. Anthraco-archaeological excavations

In order to explore the impact of past anthropic activities on the *C. gabunensis* populations, anthraco-archaeological excavations were performed. Within the DynAfFor plot 50 *C. gabunensis* individuals of DBH ≥ 10 cm were inventoried and mapped. This mapping made it possible to define two main types of zone according to the presence or absence of the species (control zone). In each zone, 20 archaeobotanical excavation sites were carried out, evenly distributed according to a toposequence (lower, middle and upper slopes). In the site with *C. gabunensis*, pits of 60 cm × 60 cm × 60 cm were dug under the crown of each tree, while in the control sites, pits of the same dimensions were randomly positioned.

The soil of each pit was searched for charred plant material (charcoal, charred seeds) and pottery sherds. The excavations were removed in 10 cm layers. Each 10 cm layer of soil was sieved with a 1 mm mesh screen. After sieving, the remnants were dried and carefully sorted, distinguishing charcoal from charred seed pieces. They were then weighed to a precision of 0.01 mg following Talon et al. (2005) and Talon (2010). All other human artefacts were separated and described following the recommendations of Meister and Eggert (2008).

2.3.1. Radiocarbon dating of charcoal

Radiocarbon dating was conducted to compare the average age of the tree population with that of the charcoal collected by the anthraco-archaeological excavations. This dating was carried out on 18 charcoal samples, 9 of which were collected from sites with *C. gabunensis* and 9 from control sites. The dated charcoal samples were selected from hilltop pits according to the recommendations of Oslisly and White (2003). The dated charcoal samples were collected from the different soil layers in order to assess the relationship between soil depth and charcoal age. We favoured charcoals close to pieces of pottery sherds, assuming that the ages were close. The Beta Analytic Testing Laboratory (BETA) (USA) dated the charcoal samples using National Electrostatics Corporation 250 kV single stage accelerator mass spectrometers (SSAMS). The calibration of dates was achieved using one of the databases (SHCAL13) of

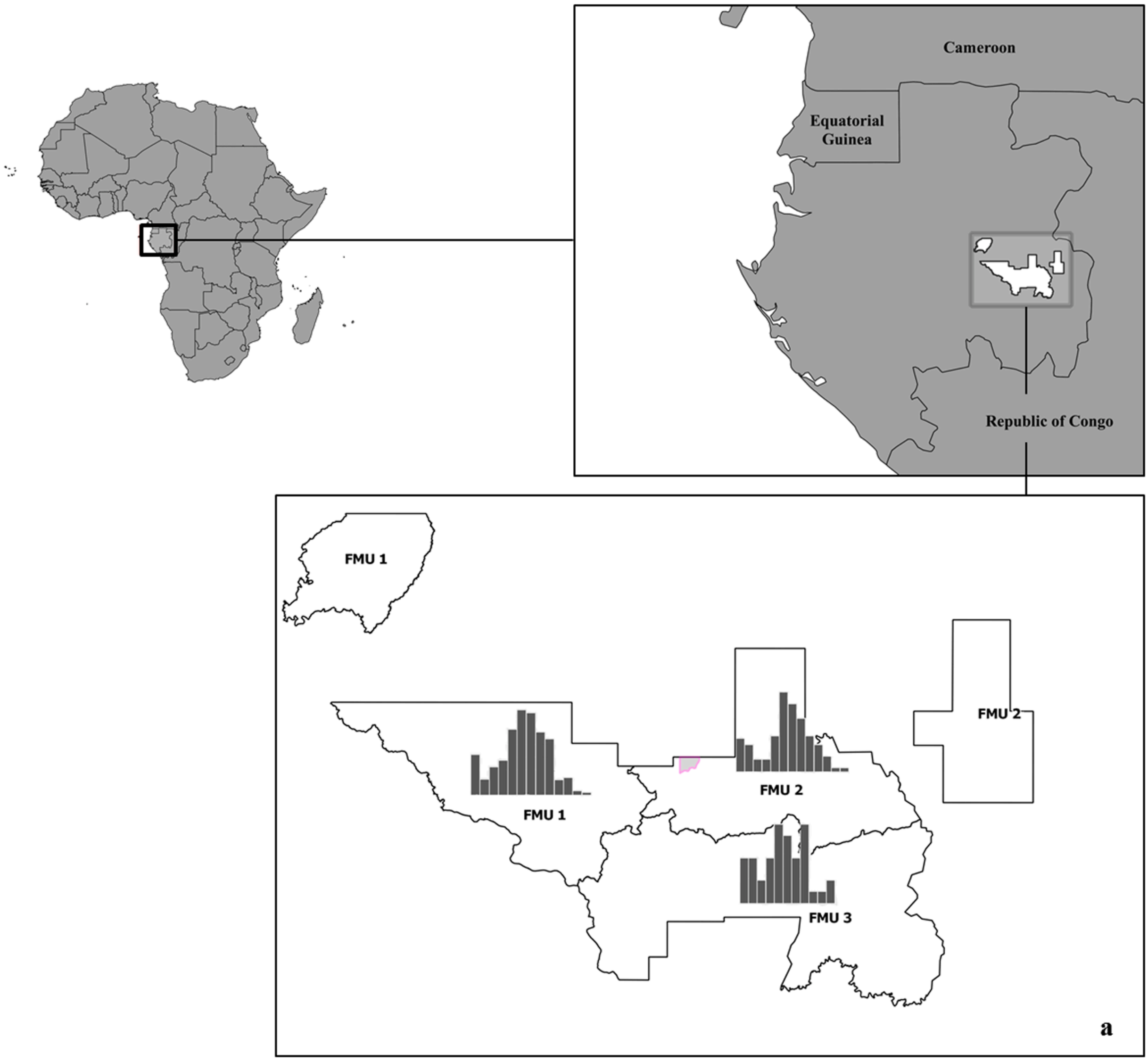


Fig. 1. a. Representation of Precious Woods CEB's three FMUs and associated diameter-class distribution; location of the DynAfFor plot (in pink) **b.** DynAfFor plot and control sampling sites, without *C. gabunensis* (squares in black; T1 to T20, continuous numbering) and with *C. gabunensis* (green circles; C.g2 to C.g45, non-continuous numbering). Yellow circles represent unsampled *C. gabunensis* trees. The base map corresponds to the topography over a high (white) to low (grey) relief spectrum (data from Alaska Satellite Facility at 10 m resolution; ASF, 2018).

the INTCAL 2013 programme (Ramsey, 2009; Hogg et al., 2013).

2.4. Average age of the C. gabunensis population studied

In order to calculate the age of *C. gabunensis* trees, the growth of a sample of 50 individuals from the DynAfFor plot was measured annually from January 2015 to February 2017, following the proposed protocol of Tosso et al. (2020).

As growth conditions may have varied over the last decades, the estimates obtained were compared to ages obtained by heartwood dating of four individuals of *C. gabunensis* whose growth was studied in the field (DBH; 80, 90, 100 and 110 cm). The samples were dated using the same methodology as the charcoal. They were randomly collected from individuals harvested by the logging company in the study area in 2017.

2.5. Soil sampling and analysis

Physico-chemical soil properties were analysed to determine the contribution of soil characteristics to the distribution pattern of *C. gabunensis* in the study area. Soil cores from the top 20 cm were taken from the 40 excavation sites (20 sites with *C. gabunensis* and 20 control sites). Four soil samples were taken systematically along the four cardinal directions (North, South, East and West) at 3 m around the target trees in the sites with *C. gabunensis*. The same sampling protocol was followed in the control sites. A composite sample was then drawn for each sample site. Samples were air-dried at room temperature and analysed using standard protocols (Pansu and Gautheyrou, 2006). Details on the methods used for soil physical and chemical analyses can be found in Appendix A.

3. Data analysis

To test whether sites with and without *C. gabunensis* experienced similar anthropogenic disturbances, the cumulative total charred plant material masses per pit and per depth (0–20, 20–40 and 40–60 cm) were compared with an analysis of variance (ANOVA). A log transformation was performed on charcoal abundance to meet the normality and

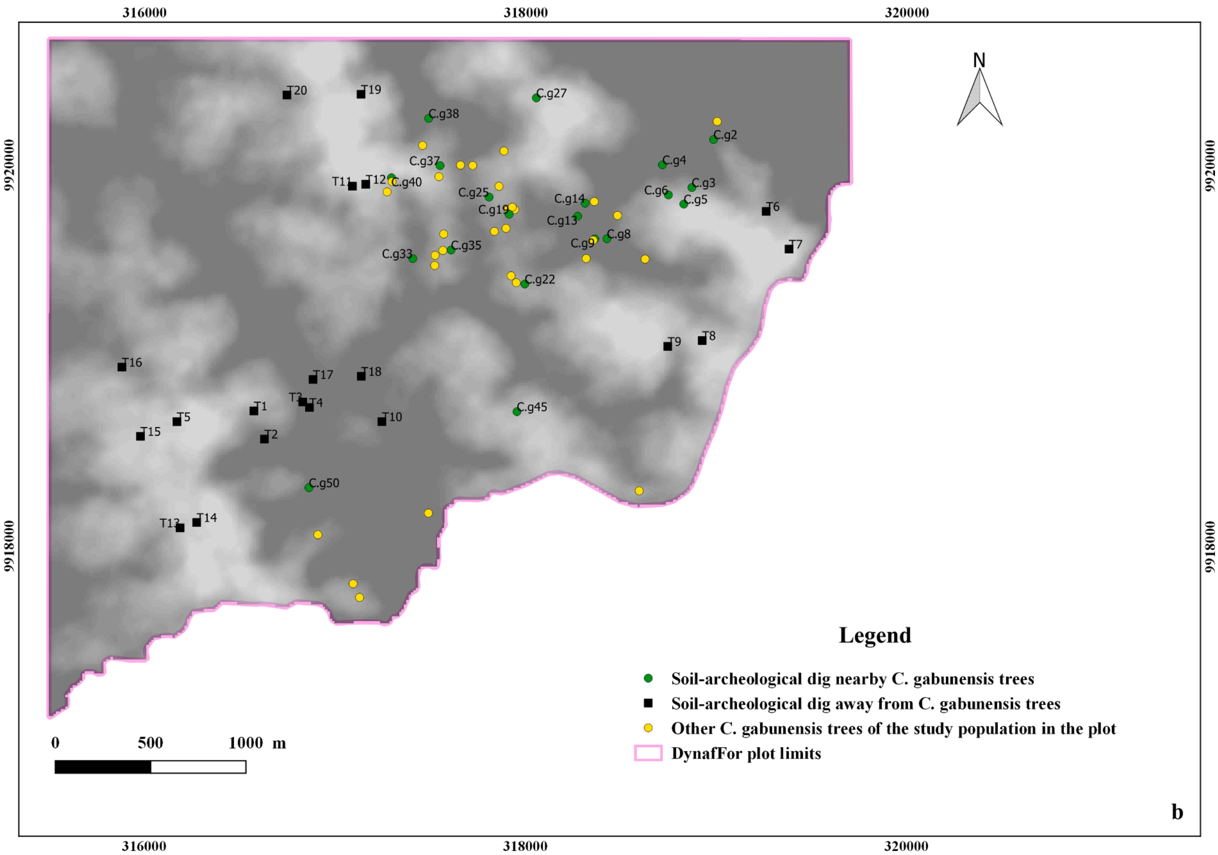


Fig. 1. (*continued*).

homoscedasticity assumptions.

The inventory of *C. gabunensis* individuals made it possible to draw up the population structure of the species and to compare it to the diameter-class distribution described within the three FMUs of Precious Woods CEB.

Growth monitoring data were used to calculate the average annual growth in diameter (*AAGD*). It was calculated with equation (1).

$$AAGD = (Df - D0)/nd \times 365,25 \quad (1)$$

Where:

Df = final diameter (cm);

$D0$ = initial diameter (cm);

nd = number of days between the two measurements.

AAGD was used to estimate the mean age per diameter class of the *C. gabunensis* population in the study site. This age (*AG*) was obtained with equation (2):

$$AG = Dm/AAGD \quad (2)$$

with Dm representing the diameter obtained in the population structure mode. The mode was estimated after fitting a normal distribution function to the diametric-class distribution.

Data on the physico-chemical properties of the soil, associated with the total charcoal masses of the soil sampling sites, were processed via Principal Component Analysis (PCA). The influence of environmental factors on the distribution of *C. gabunensis* populations was determined by projecting sites with and without *C. gabunensis* in the first factorial plane. Subsequently, we executed a Kruskal-Wallis test to compare the soil properties between the control area and the area with *C. gabunensis* and corrected p values for multiple comparisons using the false discovery rate (FDR) method (Benjamini and Hochberg, 1995). Additionally, we performed a correlation matrix analysis of the variables to identify which variables were correlated with each other and linear discriminant analysis (LDA) to find the most important variables to discriminate between the two groups (controls and with *C. gabunensis*). Prior to LDA, we performed a standardization of the variables, and then we excluded collinear variables at the threshold of 0.70 (function “vifcor” of the usdm package). The probability of assignment of the sampling sites to the two predefined groups (controls and with *C. gabunensis*) was calculated using LDA. Finally, significance of predefined groups was determined using a Welch two-sample *t*-test on the scores of the first linear discriminant (LD1). The Shapiro test was used to test the normality of the distribution of the score data, and the Levene test was employed to check the homoscedasticity of the groups.

All analyses were carried out in the R statistical environment version 4.1.2 (R Core Team, 2021) using mainly the packages “modeest” (Poncet and Poncet, 2019), “FactoMineR” (Husson et al., 2016) and “MASS” (Ripley et al., 2013).

4. Results

4.1. Charred plant remains and pottery sherds

The charcoal represented the totality of the masses, since no charred seeds were identified. Charred plant macroremains were found in all soil pits to a depth of 60 cm. However, these quantities were not significantly different between the sites with *C. gabunensis* and the control sites; the same trend was observed between soil layers (Table 1).

Pottery sherds were found in two pits in the control site, between 0 and 20 cm depth. The pottery sherds did not show any specific decoration and their small size (between 5 and 17 cm^2) did not allow the establishment of a ceramic typo-chronology (Fig. 2a). Pieces of reddened soil and charcoal-associated soil were found in the pits near the stems of *C. gabunensis*, indicating repeated fires in the study area (Fig. 2b; Table 2). These pottery sherds, pieces of reddened soil and

Table 1
Summary of charcoal mass (average ± SD) as a function of vegetation (*C. gabunensis* vs control) and ANOVA test values after log transformation, as a function of depth in cm.

Depth (cm)	*C. gabunensis* (g)	Control (g)	Charcoal	
			F	P
0–20	10.5 ± 21.6	12.4 ± 25.7	0.364	0.55
20–40	20.7 ± 53.9	2.9 ± 4.0	2.473	0.124
40–60	10.8 ± 34.0	2 ± 4.3	0.72	0.401
Total	42 ± 73.9	17.4 ± 27.2	0.522	0.474

Fig. 2. Artefacts and fragments of reddened soil found in the study area: **a.** Pottery sherds found between 0 and 20 cm depth in the control sites; **b.** From top to bottom, the first three lines represent fragments of reddened soil, the last two lines represent lumps of soil associated with charcoal, found between 20 and 40 cm and 30–40 cm depth respectively in sites with *C. gabunensis*.

lumps of soil were found in the vicinity of the charcoal (Table 2).

4.2. Temporal distribution of radiocarbon ages of wood charcoal

The radiocarbon ages obtained for the 18 charcoals were in the Late Holocene. The dates range from 2480 ^{14}C yr BP (control date) to 2330 BP (*C. gabunensis* date) and from 150 to 80 BP, respectively for the *C. gabunensis* and control dates (Table 2). The age of remains was divided into two phases. A first phase with 22% of the dates between 2480 and 1010 BP (phase A), and a second phase with 78% of the dates between 590 and 80 BP (phase B). These two phases were separated by a hiatus. Dates after 1010 cal. BP were concentrated in the first 30 cm of depth, except for three that were between 30 and 50 cm (Table 2), while the older dates were obtained at depths of 40 to 60 cm (Table 2). The charcoals associated with pottery sherds, reddened earth and charcoal-associated soil were aged between 590 and 80 BP, and between 400 and 230 BP respectively, and were from the pre-colonial period.

4.3. Growth and age of the C. gabunensis population studied

The average annual diameter growth obtained for the study population was 0.64 ± 0.27 cm yr^{-1} (95% CI). Considering the distribution mode obtained at 94.67 cm (Fig. 3.a), the average age of the cohort can be estimated to be 148 years old.

C^{14} dating of four wood samples taken from the heartwood of *C. gabunensis* trees of varying diameters (80, 90, 100 and 110 cm) gave slightly lower ages (Table 3).

Table 2
Raw dates in BP years with BetaCal 3.21 calibration.

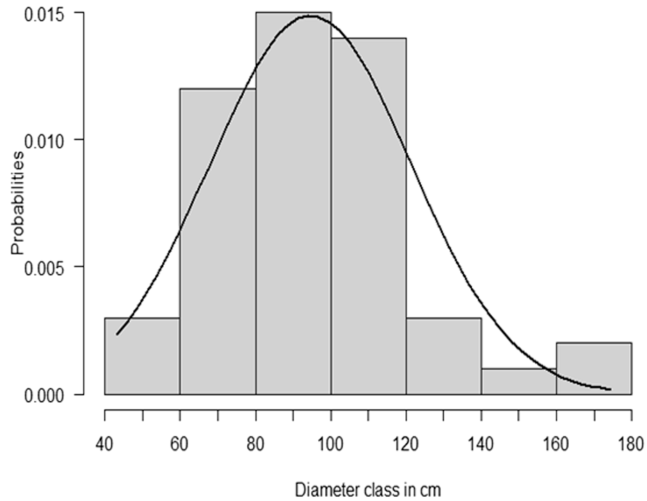
Map code	Sample code	Depth (cm)	Ages (^{14}C yr BP, 1σ)	Ages (cal yr BP, 1σ)	Archaeology
T17	Beta-545202	40–50	2480 ± 30	2622/2514	–
T10	Beta-545203	50–60	2420 ± 30	2595/2525	–
C.g5	Beta-545190	50–60	2330 ± 30	2308/2239	–
T14	Beta-545200	20–30	1010 ± 30	929/798	–
T6	Beta-545204	0–10	590 ± 30	597/556	Pot.
C.g37	Beta-545194	30–40	570 ± 30	592/558	–
T13	Beta-545206	20–30	440 ± 30	444/384	–
C.g4	Beta-545196	10–20	410 ± 30	456/379	–
C.g14	Beta-545193	20–30	400 ± 30	455/376	RS
T15	Beta-545201	30–40	310 ± 30	393/319	–
T16	Beta-545198	0–10	260 ± 30	271/208	–
C.g27	Beta-545189	40–50	240 ± 30	267/201	CS
C.g25	Beta-545195	20–30	230 ± 30	204/156	RS
C.g4	Beta-545191	0–10	200 ± 30	222/144	–
C.g50	Beta-545197	0–10	190 ± 30	144/64	–
T19	Beta-545199	10–20	160 ± 30	215/105	–
C.g22	Beta-545192	10–20	150 ± 30	211/108	–
T7	Beta-545205	10–20	80 ± 30	156/103	Pot.

“Map code” refers to the sample codes shown in Fig. 1b (T = control, C.g = number of studied *C. gabunensis*). Pot. = pottery sherds; RS = reddened soil and CS = charcoal-associated soil.

4.4. Influence of edaphic factors on the distribution of C. gabunensis stems

In a first step, possible associations between sampling sites and soil variables were explored with a PCA. The eigenvalue graph (screeplot) allowed us to retain four PCA axes (Appendix B). The first four axes, respectively, explained 41.5, 23.3, 10.4 and 6.0 % of the total variance of 81.16%. On the first four axes and in descending order, the variables contributing most to the axes were: (i) cationic exchange capacity (CEC), total nitrogen (N) and Al (axis 1); (ii) electrical conductivity (EC), pH-H_2O and Fe (axis 2); (iii) Ca, Mn and Mg (axis 3) and (iv) K, pH-H_2O and OM (axis 4) (Appendix C). PCA indicated a separation of the sites into two groups (control and *C. gabunensis*) on the factorial plane formed by the first two axes (Fig. 4). The graphical representation on the factorial plane formed by axes 1 and 3 did not provide any additional information. Several soil properties varied significantly between control and *C. gabunensis*. When corrected for multiple comparisons with the FDR method, the results remained significantly the same. The pH-H_2O, pH-Cohex and Mn were significantly higher in the control sites than in the *C. gabunensis* sites. While EC, CEC, OM, Al, Fe, K, P and N were significantly higher in the sites with *C. gabunensis*. Soil texture, Ca, Mg and Zn did not show significant differences between the two types of areas (Appendix D).

Prior to LDA analysis, 8 of the 18 standardised variables were excluded due to collinearity (CEC, Sand, pH-H_2O, EC, N, Al, Silt and Mg): CEC covaried positively with N and Clay. EC covaried with Fe, while N covaried positively with OM and Al. Finally, Mg covaried



a

Diameter classes	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Number	0	0	0	1	2	5	7	10	5	10	4	2	1	1	0	1	1

b

Fig. 3. a. Diameter distribution of *Cylicodiscus gabunensis* stems obtained from the inventory of the study site and fitted with a curve for mode determination: (i) the x-axis shows 7 diameter classes ([40–60[, [60–80[, …, [160–180[cm), (ii) the y-axis represents the probabilities of the normal distribution for each diameter class; **b.** Distribution of *C. gabunensis* stem numbers by diameter class in the DynAfFor plot. Diameter class (1 = 10 to 19.9 cm; 2 = 20 to 29.9 cm; …; 17 = 170 to 179.9 cm).

Table 3
Raw dates in BP years of *C. gabunensis* trees. The dates are ordered from the most recent to the oldest. C.g = number of studied *C. gabunensis*.

Sample code	Trees	Diameter (cm)	Years BP ± SD
Beta-591249	C.g36	100	90 ± 30
Beta-591247	C.g19	110	100 ± 30
Beta-591250	C.g14	80	110 ± 30
Beta-591248	C.g27	90	110 ± 30

positively with Ca (Appendix E). The LDA showed discrimination between the different groups. The a posteriori probabilities of belonging to the different groups allowed 87.5% of the sites to be correctly classified. Three sites with *C. gabunensis* were reclassified as control sites and two control sites as sites with *C. gabunensis* (Fig. 5). The probabilities of assignment of the sampling sites to the groups formed are shown in Appendix F. Negative values of LD1 are associated with the control group, while positive values are more related to the group with *C. gabunensis*. Subsequently, we investigated the correlations of each variable with LD1. The strongest correlations are with Mn (−0.68), Fe (0.61) and OM (0.46). The negative values of the correlation between the variables and LD1 indicate the variables associated with the control group (Mn, Ca and Zn), while LD1 was positively correlated with the variables Fe, OM, Charcoal, K, Clay and P (Appendix G). The two categories of groups differed significantly on LD1 (Welch two-sample *t*-test: $t = -7.05$, $df = 34.76$, $p < 0.001$).

5. Discussion

5.1. *Cylicodiscus gabunensis occurs in formerly cultivated areas*

In this study, we aimed to characterise the timing and evidence of past human activities in relation to *C. gabunensis* populations at the local scale in the rain forests of south-eastern Gabon. We found evidence of human activity and settlement, which was mainly dated to the late Holocene. Variations in charcoal abundance obtained in sites with *C. gabunensis* were similar to those found by Biwolé et al. (2015a). Charcoal was found in all pits, suggesting that man had a major impact throughout the study area. The large quantities of charcoal associated with pottery sherds, pieces of fire-reddened soil and lumps of burnt soil suggest a significant past human occupation in the study area. In this regard, Vleminckx et al. (2014) assume that the lack of significance between control and sites with *C. gabunensis* could be related to homogeneous past anthropogenic disturbances, thus blurring the signal of human disturbances. However, with a similar method, Bourland et al. (2015) found significantly higher charcoal masses in soils collected in stands of another timber light-demanding species (*Pericopsis elata*).

Dates of human occupation found in several studies in central Africa correspond to the dates we found at in our study area (Fig. 6). Radiocarbon dating of selected charcoals showed that human occupation occurred in two phases: between 2480 and 1010 BP, and from 590 and 80 BP. The chronological phases obtained go back more than two thousand years (2480 ± 30 BP) reflecting a succession of human disturbances. By dating 10 organic pieces, Biwolé et al. (2015a) established a chronology of ancient fires in forests of south-western Cameroon. The authors identified two main periods of human occupancy: one from 2200 to 1500 BP and a second from three centuries. Excluding a charcoal sample taken at 110 cm and dated to 9400 BP, Vleminckx et al. (2014) also obtain two periods of human occupation based on 59 dates. A first period between 2745 and 1495 BP, and a second more recent period between 860 and 80 BP. By dating 43 charcoals Morin-Rivat et al. (2014) established a chronology of ancient fires that spans three periods of anthropogenic impacts in the forests of south-eastern Cameroon and northern Republic of Congo. The three periods were divided into two more recent periods and a third older period (with two dates 12620 and 4610 BP). The two recent periods of human expansion ranged from 2300 to 1300 BP and the other from below 670 BP. The third older period could be explained by deeper trenches in their study. Indeed, these dates were obtained respectively at 120 and 145 cm depth. The two recent periods in our study were obtained at a maximum depth of 60 cm,

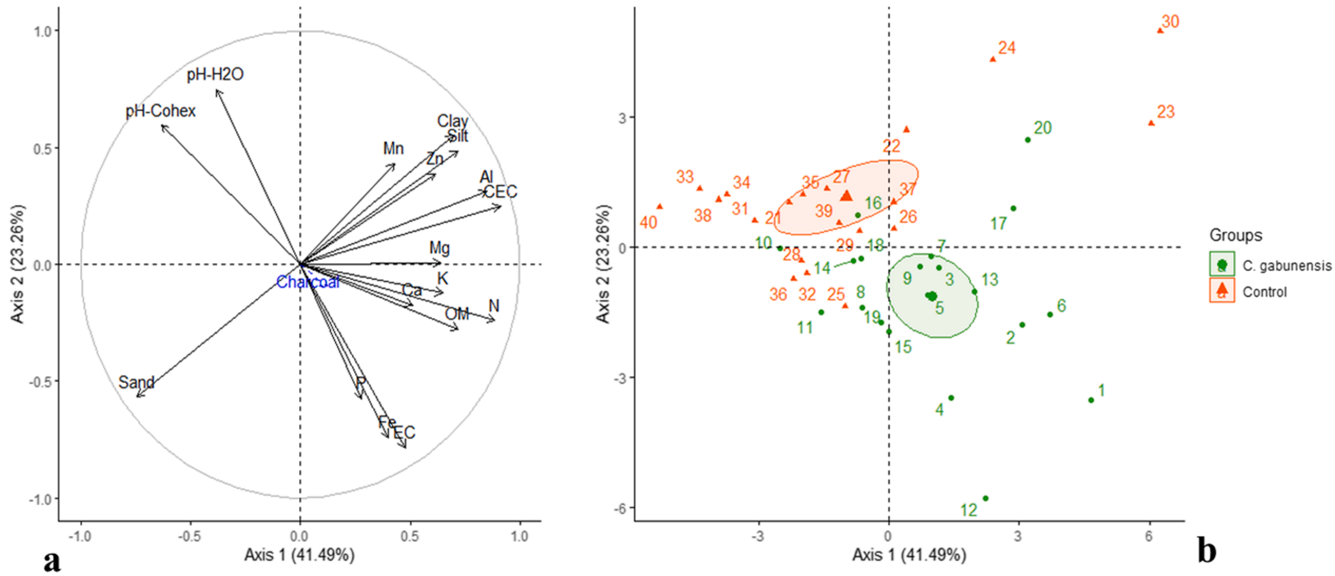


Fig. 4. Representation in the first factorial plane of the principal component analysis carried out on the environmental variables of the sites with (in green) and without (in orange) *C. gabunensis*. **a.** The correlation circle resulting from the PCA on quantitative variables with coefficients of charcoal added as supplementary variable (in blue). **b.** Score projections are colored according to areas with and without *C. gabunensis*. Confidence ellipses describing the differentiation pattern of the two zones. See Appendix 1 for the meaning of the codes of the explanatory variables.

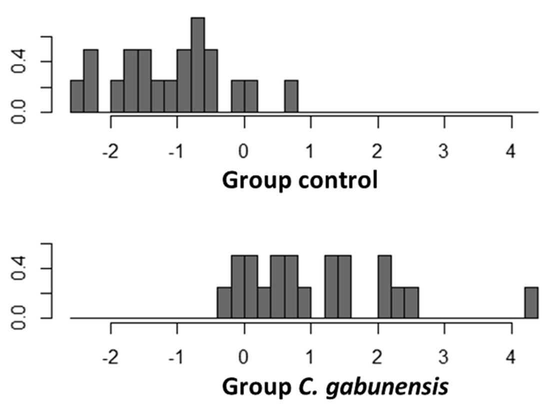


Fig. 5. Graphical representation of the separation of sites with and without *C. gabunensis*. The x-axis represents the discriminant axis (LD1) and the y-axis represents the scores of the sample sites.

whereas in Morin-Rivat et al. (2014) the maximum depth was 75 cm for the same recent periods except for one sample located at 210 cm and dated to 195 BP.

During the Holocene around 3000 BP, the climate change that occurred in Central Africa (Schwartz, 1992; Assi Kaudjhis et al., 2010) is thought to have modified forest cover and favoured the expansion of Bantu populations (Schwartz, 1992; Ngomanda et al., 2009; Oslisly et al., 2013a). The first phase of expansion of the Bantu populations has been estimated between 2300 and 1400 BP and corresponds to a massive arrival of human populations from the northwest of Cameroon. A second phase of expansion took place between 670 and 20 BP, separated by a phase of depopulation (Wotzka, 2006; Oslisly et al., 2013b; Morin-Rivat et al., 2016). The Bantu people roamed the forests and practised shifting cultivation on bushland, then left former agricultural land fallow. Many authors have demonstrated agricultural impacts on forests, through the observation of charcoal and artefacts (Willis et al., 2004; Oslisly et al., 2013a; Morin-Rivat et al., 2014; Biwolé et al., 2015a). Metallurgical needs could also explain the abundance of charcoal (Schwartz, 1992; Maley, 2003; Neumann et al., 2012). Indeed, to obtain fuel for smelting iron ore, the Bantu populations cleared large areas of forest around their homes or forge sites (Clist, 1990). However, we did not find any slag or old smelting furnaces which are a direct sign of metallurgy as indicated by Assoko Ndong (2002). Also, in this study, we did not find carbonised seeds, compared to other studies (Gillet and Doucet, 2013; Morin-Rivat et al., 2014; Biwolé et al., 2015a). In their studies, the latter authors found mainly carbonised seeds of *Elaeis guineensis* Jacq. and *Canarium schweinfurthii* Engl. Two species known for their capacity to provide subsistence to ancient populations and which favoured their sedentarisation (Oslisly et al., 2000; Clist, 2006). Moreover, Gillet and Doucet (2013) and Biwolé et al. (2015a) highlighted that the presence of charred seeds was linked to intensive human activities. It is therefore likely that our study area was considered a transient camp area where agricultural activities were practiced as reported by Oslisly et al. (2000).

The presence of pottery sherds in the study site constitutes irrefutable evidence of human presence, confirming other observations made

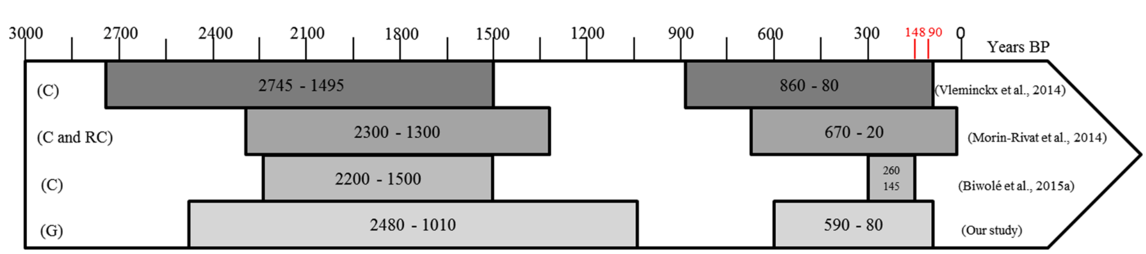


Fig. 6. Timeline based on uncalibrated ages of the two recent periods of human expansion, adapted from, Vleminckx et al. (2014), Morin-Rivat et al. (2014), Biwolé et al. (2015a) and the tree ages of *C. gabunensis* (in red). Letters in brackets represent countries: C = Cameroon; RC = Republic of Congo and G = Gabon.

in central Gabon (Oslisly, 1999; Assoko Ndong, 2002), the Republic of Congo (Morin-Rivat et al., 2014) and southwest Cameroon (Biwolé et al., 2015a). The hypothesis of a past anthropisation of the study area culminating two or three centuries ago is therefore well supported by our observations.

5.2. Cylicodiscus gabunensis, a species that regenerates in fallow land

The Gaussian population structure obtained in our study area could be explained by a regeneration dating back between one and two centuries depending on the estimation method used. Heartwood dating of the dominant trees gives an estimate of between 90 and 110 years, while the estimate based on the average annual growth of the population is 148 years. Lower values obtained by the first method are not surprising. Indeed Ligot et al. (2019) have shown that analysis of data from harvested individuals tends to overestimate growth rate because the trees selected by foresters are generally the most vigorous and therefore grew faster than the rest of the cohort.

By comparing the age of charcoal and trees, it is likely that *C. gabunensis* regenerated in fallow land after agricultural abandonment, like other species now dominating the canopy and exploited for their wood (Gillet and Doucet, 2013; Morin-Rivat et al., 2017). According to Morin-Rivat et al. (2016), the charred botanical remains indicate two types of land use: (i) domestic, with oil palm endocarps most often associated with pottery sherds (villages) and (ii) agricultural, with charcoal as a remnant of slash-and-burn agriculture (fields). The fact that the pottery sherds were found in areas without *C. gabunensis* is therefore not surprising. A similar distribution pattern has been observed for *Lophira alata* Banks ex C.F. Gaertn by Biwolé et al. (2015a) in Cameroon. Like this species, *C. gabunensis* may have regenerated in fallow land rather than on bare soils in former villages (Biwolé et al., 2015b). Several authors have shown that this anthropogenic impact on the establishment of light-demanding species dates back about two centuries (Gillet and Doucet, 2013; Biwolé et al., 2015a; Bourland et al., 2015).

5.3. Cylicodiscus gabunensis prefers soils rich in Fe, K, p and N

We assumed that *C. gabunensis* may prefer nutrient-rich soils. Our results show that soils from sites with *C. gabunensis* have significantly higher values of: EC, CEC, OM, Al, Fe, K, P and N. While pH-H_2O, pH-Cohex and Mn were significantly higher in control sites than in sites with *C. gabunensis* (Appendix D). According to LDA, the species seems to be preferentially present on soils characterised by relatively high levels of Clay, OM, Fe, K and P. Clay had a strong positive correlation with CEC, and Al which differed significantly between the two types of sites. Similarly, OM had a strong positive correlation with N. As these variables were excluded from LDA analysis we can therefore assume that: CEC, Al, N and EC are also part of the soil properties that can explain the presence of *C. gabunensis* in our study area. Although we obtained significant differences in pH between control and *C. gabunensis* sites, tropical soils are generally low pH (Sanchez, 1976). And less fertile and toxic soils are often characterised by deficiencies in plant-available nutrients (e.g. Ca, Mg and P) (Sanchez, 1976). This is not the case in our study. For Ca and Mg, levels did not differ significantly between control and *C. gabunensis* sites, while available phosphorus levels were significantly higher in *C. gabunensis* sites than in control sites. This confirms our second hypothesis that *C. gabunensis* might prefer nutrient-rich soils. Other studies in Central Africa have also demonstrated the influence of chemical soil properties on the likelihood of establishment and abundance of commercial upper canopy species (Hall et al., 2004; Medjibe et al., 2011; Vleminckx et al., 2020). In West Africa and the Amazon, the link between soil nutrients and the presence of tree species confirms the crucial role played by soil nutrients in the distribution of plant species (Swaine, 1996; Wieringa and Poorter, 2004; Svenning et al., 2004 and 2006; Paoli et al., 2006). The establishment of *C. gabunensis* seedlings on relatively fertile soils could give a competitive advantage to this species, which does not withstand well competition with other woody species in its first years of growth (Doucet et al., 2016).

6. Conclusion

The combination of anthropogenic disturbance and chemical fertility of the soil seems to explain the establishment of *C. gabunensis* in the evergreen forests of south-eastern Gabon. Today, the regeneration deficit observed for this species is potentially due to the forest closure and absence of large-scale anthropogenic disturbance. The scarcity of *C. gabunensis* seedlings and saplings in evergreen forests (Duah-Gyamfi et al., 2014; Ada et al., 2020) suggests that the canopy openings created for slash-and-burn cultivation, followed by a long recovery period, no longer occur, following the sedentarisation of agriculture (Van Gemerden et al., 2003). The impact of selective logging as carried out in managed forests on seedling establishment should be investigated, as well as a finer quantification of light requirements so that a silviculture adapted to the species can allow the maintenance of production capacity in the long term.

Declaration of Competing Interest

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.

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Appendix A. . Table of physico-chemical properties and associated methods (adapted from Pansu and Gautheyrou, 2006).

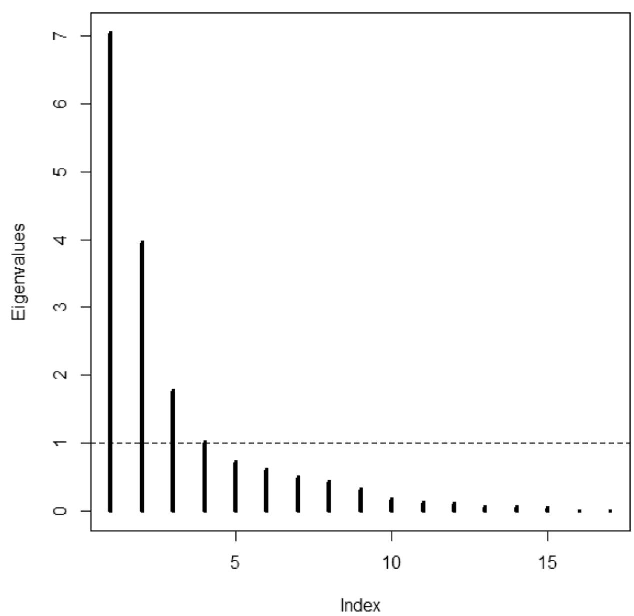
Variables	Methods
Clay (%) Sand (%) Silt (%) pH-H_2O	Wet sieving, pipette method after destruction of the organic matter by hydrogen peroxide (H_2O_2) and dispersion of the clay by sodium citrate.

(continued on next page)

(*continued*)

Variables	Methods
Electrical conductivity (EC) [μS.cm^{-1}]	pH-H_2O and electrical conductivity were measured with glass electrodes (Mettler-Toledo) and a conductivity meter (VWR EC300) respectively on a soil: deionised water 1:5 suspension.
pH-Cohex	pH obtained by extraction of a cobaltihexamine salt solution
Plant-available elements: Ca, Mg, K, Al, Fe, Mn, P and Zn (μg.g^{-1})	The available elements (Ca, Mg, K, Al, Fe, Mn, P and Zn) were extracted with 0.5 M EDTA 0.03 M ammonium acetate at pH 4.65 and measured by Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) with a CCD detector (Varian, Vista MPX).
Cation exchange capacity (CEC) [cmolc.kg^{-1}]	The cation exchange capacity (CEC) was determined by molar ammonium acetate at pH 7 and was calculated as the sum of the concentrations of exchangeable Ca, K, Mg and titrated Al (Alexch).
Total nitrogen (N)	Measured by flash combustion at 1350 °C in a CN elemental analyser (Dumas method, ISO 10694).
Organic matter (OM) [%]	The organic matter content was calculated by the mass loss of a sample from an ash dried at 550 °C.
Charcoal (g)	Total mass of charcoal from each dig site.

Appendix B. . The eigenvalue graph (screeplot); the x-axis represents the number of axes (Index) and the y-axis the eigenvalues. The axes with an eigenvalue above the mean (equal to 1 in the case of a standardized value analysis) were retained.



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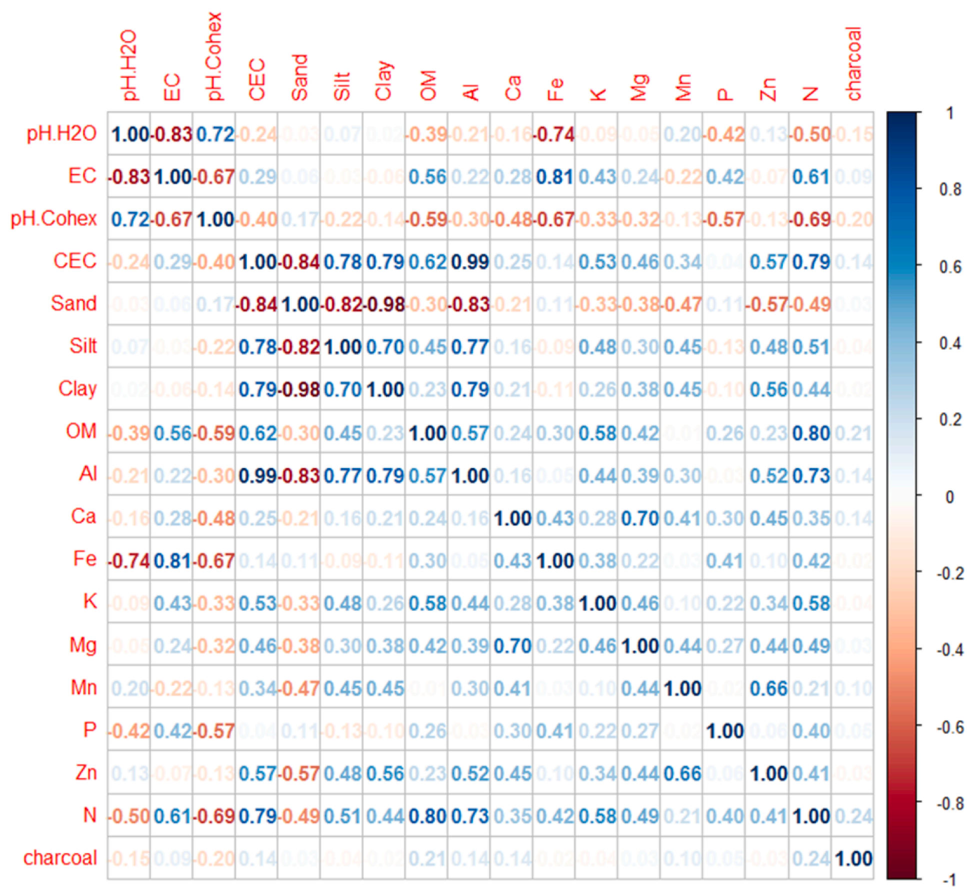
Appendix C. . Contribution of soil variables on the PCA axes.

Variables	Axis.1	Axis.2	Axis.3	Axis.4
pH-H2O	2.1	14.2	3.1	17.7
Electrical conductivity (EC)	3.2	15.6	1.6	0.0
pH-Cohex	5.7	9.0	0.2	4.6
CEC	11.8	1.6	3.8	0.2
Sand	7.8	8.2	1.0	4.0
Silt	7.3	6.0	2.3	0.3
Clay	6.9	7.7	0.6	6.9
OM	7.3	1.9	4.1	13.5
Al	10.2	2.4	6.2	0.5
Ca	3.7	0.8	27.7	0.0
Fe	2.3	13.9	1.8	3.5
K	6.0	0.4	0.1	33.6
Mg	5.8	0.0	14.5	8.4
Mn	2.6	4.7	18.7	6.1
P	1.1	8.4	3.7	0.1
Zn	5.4	3.8	9.3	0.2
N	11.1	1.5	1.4	0.6

Appendix D. . Summary of physical and chemical properties (averages ± SD) as a function of sites (with *C. gabunensis* vs control) for the 0 – 20 cm layer.

Soil properties	*C. gabunensis*	Control	P values Kruskal-Wallis test
pH-H2O	3.87 ± 0.09	4.05 ± 0.15	p < 0.05
EC (μS.cm^{-1})	76.75 ± 16.08	52.05 ± 11.60	p < 0.05
pH-Cohex	3.16 ± 0.12	3.25 ± 0.09	p < 0.05
CEC (cmolc.kg^{-1})	3.75 ± 0.93	2.80 ± 1.58	p < 0.05
Sand (%)	69.45 ± 6.82	70.15 ± 12.24	p > 0.05
Silt (%)	7.30 ± 1.56	6.55 ± 3.27	p > 0.05
Clay (%)	23.5 ± 6.24	23.01 ± 9.30	p > 0.05
OM (%)	2.90 ± 0.97	1.70 ± 0.98	p < 0.05
Al (μg.g^{-1})	261 ± 71.81	196.5 ± 114.53	p < 0.05
Ca (μg.g^{-1})	11.05 ± 5.65	10.40 ± 4.56	p > 0.05
Fe (μg.g^{-1})	9.45 ± 3.04	6.05 ± 2.55	p < 0.05
K (μg.g^{-1})	52.25 ± 21.56	32.20 ± 23.11	p < 0.05
Mg (μg.g^{-1})	7.15 ± 2.58	6.90 ± 2.11	p > 0.05
Mn (μg.g^{-1})	0.41 ± 0.49	0.99 ± 0.60	p < 0.05
P (μg.g^{-1})	0.24 ± 0.11	0.16 ± 0.09	p < 0.05
Zn (μg.g^{-1})	0.25 ± 0.11	0.90 ± 0.15	p > 0.05
N	0.14 ± 0.03	0.09 ± 0.04	p < 0.05

Appendix E. . Correlation matrix of environmental variables.



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Appendix F. . Table of posterior probabilities of membership of the sample sites according to the two groups formed from the LDA.

ID	Probability of Control	Probability of *C. gabunensis*
C.g2	3.191049e-03	0.996808951
C.g3	5.544686e-03	0.994455314
C.g4	1.095549e-02	0.989044515
C.g5	2.773297e-02	0.972267031
C.g6	5.431429e-02	0.945685706
C.g8	1.145275e-02	0.988547253
C.g9	1.616860e-01	0.838313951
C.g13	4.141010e-01	0.585898961
C.g14	1.439339e-01	0.856066105
C.g19	4.211462e-01	0.578853845
C.g22	5.740191e-01	0.425980907
C.g25	6.100498e-05	0.999938995
C.g27	5.600344e-01	0.439965610
C.g33	3.344969e-01	0.665503118
C.g35	5.780943e-02	0.942190574
C.g37	2.760346e-01	0.723965403
C.g38	6.277792e-01	0.372220794
C.g40	2.003781e-01	0.799621930
C.g45	2.973803e-02	0.970261973
C.g50	2.105659e-01	0.789434098
T1	9.948559e-01	0.005144092
T2	9.802731e-01	0.019726935
T3	7.717902e-01	0.228209832
T4	5.042571e-01	0.495742871
T5	8.558252e-01	0.144174777
T6	9.956926e-01	0.004307383
T7	9.688848e-01	0.031115233
T8	8.727353e-01	0.127264707
T9	7.699795e-01	0.230020466
T10	9.931042e-01	0.006895751
T11	9.782979e-01	0.021702110
T12	4.764739e-01	0.523526081
T13	9.601498e-01	0.039850158
T14	9.881275e-01	0.011872542
T15	9.560959e-01	0.043904126
T16	1.990767e-01	0.800923347
T17	8.503377e-01	0.149662268
T18	8.230522e-01	0.176947756
T19	9.119999e-01	0.088000115
T20	8.684147e-01	0.131585337

Appendix G. . Correlation of LD1 with the variables.

Variable	Correlation Coefficient
pH-Cohex	0.02
Clay	0.18
OM	0.46
Ca	−0.27
Fe	0.61
K	0.34
Mn	−0.68
P	0.48
Zn	−0.08
Charcoal	0.46

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