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REGULAR PAPER

New data on the recent history of the littoral forests of southern Cameroon: an insight into the role of historical human disturbances on the current forest composition

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Background and aims – Prior to European colonisation of Central Africa, human populations were dispersed through the forests, where they practiced slash-and-burn cultivation. From the 19th century they were progressively concentrated in villages along roads, leaving large areas of forest derelict. In south-western Cameroon, and elsewhere in Central Africa, forest canopy is dominated by long-lived light-demanding tree species, suggesting a possible role of human disturbance. The aim of this study was to bring new insights into the possible effect of historical human disturbances in terms of timing and spatial extent on the current forest composition.
Location – Wet evergreen littoral forest in south-western Cameroon.
Methods and key results – A combined vegetation sampling and archaeobotanical survey were conducted. Potsherds, oil-palm endocarps, and charcoal were found throughout the study area, suggesting generalised human occupation and anthropogenic fire. Human occupancy occurred in two periods: between 2200 and 1500 BP, and, more recently, beginning three centuries ago. High frequency of fire and the presence of *Elaeis guineensis* both dated recently (between 260 and 145 BP) suggest slash-and-burn shifting cultivation practices. These human-induced disturbances may coincide with the age of the current emergent light-demanding species, the age of which can be estimated around 200 years, or with the phases of drying climate recorded in the Central African forest in the early 18th century.
Conclusions – These results support the idea that historical human disturbances are one of the major factors that shaped the current forest composition in Central Africa.

Key words – Charcoal, forest composition, human disturbances, long-lived light-demanding tree species, oil-palm endocarps, potsherds, slash-and-burn cultivation, southern Cameroon.

INTRODUCTION

For several millennia, tropical forests were inhabited by groups of hunter-gatherers and farmers. Presently, archaeological and palaeoecological data suggest that these ecosystems, which have long been regarded as pristine, in fact underwent substantial historical human disturbances (Willis et al. 2004, Barton et al. 2012).

In Central Africa, the oldest evidence of human presence is dated to 40,000 BP and points to small groups of hunter-gatherers in Gabon (Clist 1996). During the late Holocene, between 3000 and 2000 BP, a massive forest regression was recorded throughout Central Africa: at Ossa (Reynaud-Farrera et al. 1996), Barombi Mbo (Maley & Brenac 1998), Nyabessan (Ngomanda et al. 2009b) and Mbalang (Vincens et al. 2010) in Cameroon ; Kamalété, Nguéné, and Maridor

(Ngomanda et al. 2007, 2009a) in Gabon; and Sinnda, Kitina, and Songolo (Elenga et al. 1996, Vincens et al. 1999) in the Republic of Congo. The forest regression coincided with the arrival of Bantu populations from north-western Cameroon (Schwartz 1992). Whether this event was due to human activities or climate-induced disturbance is still hotly debated, however. Some authors argue that past Central African forest regression have been due to human activities, while others attribute this event to regional climate change caused by an increase of seasonality (Bayon et al. 2012a, 2012b, Maley et al. 2012, Neumann et al. 2012b).

The expansion of Bantu populations into the rainforest happened in two phases – between 2500 and 1400 BP and between 1000 and 100 BP – separated by a depopulation phase (Wotzka 2006, Oslisly et al. 2013b, Morin-Rivat et al. 2014). These populations practised slash-and-burn agriculture and iron smelting, two activities that required the felling of trees and produced large amount of charcoal (Clist 1997, Neumann et al. 2012a, Oslisly et al. 2013b). The discovery of banana phytoliths (*Musa* sp.) and pearl millet seeds [*Pennisetum glaucum* (L.) R.Br.] in southern Cameroon dated to 2500 and to 2200 BP, respectively (Mbida et al. 2000, Kahlheber et al. 2009), clearly attests to cultivation practices. Many remaining metallurgy slags have been found throughout Central Africa (Clist 1990, Oslisly & Peyrot 1992, Lanfranchi et al. 1997). The oldest, dated to 2800 BP, are iron-working furnaces in southern Cameroon (Essomba 1998). Bantu migrants also used fire for hunting (Oslisly et al. 2013b) and practiced an arboriculture based on oil-palm trees (*Elaeis guineensis* Jacq.) (Maley 1999). This latter aspect is frequently highlighted in archaeological sites through the presence of oil-palm endocarps (Clist 1997, Mbida 1998). More recently (in the 19th century), movements of human populations due to European colonisation and inter-ethnic conflicts could have significantly impacted forest composition (Oslisly et al. 2013b). These are probably still noticeable today because of the long life-span of some emergent trees (White & Oates 1999).

In general, tree species distribution is partially linked to climatic, geological, and edaphic factors (Swaine 1996, Newbery et al. 1998, Réjou-Méchain et al. 2008, Fayolle et al. 2012). Nevertheless, a major part of the variability observed remains unexplained. In south-western Cameroon, the wet evergreen littoral forest is characterised by two emergent light-demanding long-lived tree species: *Lophira alata* Banks ex Gaertn. and *Sacoglottis gabonensis* (Baill.) Urb. (Letouzey 1985). Based on the lack of *L. alata* regeneration, Letouzey (1985) hypothesised that past human disturbances may have favoured the regeneration of this light-demanding tree species a few centuries ago (prior to the colonisation). Jones (1956) described similar trends in south-western Nigerian forests. Assessing human-induced disturbances in terms of timing and spatial extent is difficult to achieve in Central African forests because of the difficulties of prospecting in dense and structurally complex ecosystem (Oslisly 1998, Brncic et al. 2007). Of all the archaeological sites studied in Central Africa, only one-third was located in the forest zone, with most investigations performed in open areas along roadsides, agricultural lands, villages, and mining and logging zones (Oslisly et al. 2013b). There is therefore an urgent need to understand the impacts of historical human activities on current vegetation in the deepest forests.

The aim of this study was to bring new insights into the possible effect of historical human disturbances on the current forest composition in terms of timing and spatial extent. Focusing on south-western Cameroon, we specifically addressed the three following questions: (i) does forest composition reflect past disturbances? (ii) if so, are these disturbances linked to historical human populations? (iii) and what were the timing and spatial extent of these past human-induced disturbances?

METHODS

Study site

The study site (2°10'–2°39'N 10°11'–10°53'E) is located in south-western Cameroon, east of the Campo-Ma'an National Park, in two forest management units (FMU) managed by the logging company Wijma (fig. 1). These FMU cover a total of 110,000 ha. The climate is equatorial, with two rainy seasons (March to June and September to November) and two intermediate dry seasons. The mean annual temperature varies between 24 and 26°C. The annual rainfall ranges between 1500 and 2000 mm (Olivry 1986). The geological substrate consists of old volcanic intrusions and Precambrian metamorphic rocks (Franqueville 1973). The topography is dominated by hills reaching a maximum altitude of 600 m. Dominant soils are classified as Ferralsols and Acrisols (van Gemerden et al. 2003). The vegetation belongs to the mixed forest including lowland wet evergreen littoral and semi-deciduous types (Letouzey 1985). Population density is less than ten inhabitants per km^2 (Afripop 2013). The Bantu ethnic groups Ntumu and Mvae are the main inhabitants of the region. Villages are located along roads (Carrière 1999).

Experimental design

To explore the impact of historical human disturbances on current forest composition, we performed a combined vegetation and archeobotanical sampling along one mega-transect composed of three transects (T1 to T3) of 3 km each (9 km in total). The two most distant transects (T1 and T3) were spaced 26 km apart. These three transect lines ran southwest through the two FMU (fig. 1). To draw the topographic profile of each 3 km transect, the slope was measured every 20 m with a clinometer. Other elements, such as streams and swamps, were recorded. A total of 12, 11, and 12 plots (P1 to P11/P12) of 0.2 ha were established along transects T1, T2, and T3, respectively.

All trees with a diameter at breast height (dbh) ≥ 20 cm in each plot were recorded. The dbh was also measured. The most common and readily identifiable species were directly named in the field and voucher specimens were collected for unidentified species for subsequent identification at the Gembloux Agro-Bio Tech (ULg) (J-L. Doucet, pers. com.). Information on species regeneration guild was compiled from Hawthorne (1995) and complemented by field observations (J.-L. Doucet, pers. obs.). Hawthorne (1995) defined four regeneration guilds (Pioneer, Cryptic Pioneer, Non-Pioneer Light-Demanders and Shade-Bearers) for forest tree species according to the exposure at seedling and older plant (sapling and tree) stages. Pioneer species are those whose seedlings require full light to develop (n = 34 species, 23%); non-pioneer light-demanding species can tolerate some shade in the seedling stage but require canopy openings to attain their adult size (n = 38, 26%); shade-bearers species can persist in the shade (n = 68, 47%). We were able to assign 96% of the taxa to one of these three categories.

In the centre of each plot, a pit of 0.5 × 0.5 m wide and 0.6 m deep was excavated to investigate the presence of human artefacts, charcoal, and charred seeds. Human artefacts were extracted to quantify the extent of human occupation. In each pit, 6 l of soil were collected in 10 cm layers (providing a total of 36 l per pit) and water-sieved through a 2 mm mesh sieve. After sieving, the refusals were dried and thoroughly sorted. Charcoal was separated from charred seeds, and oil-palm endocarps were isolated. All materials were counted and weighed on a precision scale to the nearest 0.1 mg. To detect noticeable human settlements, six pits with abundant human artefacts were enlarged to 1.0 × 1.5 m large and 2.0 m deep. These six large pits were established in plots n° 6 and 11 of transect 1; plots n° 4 and 7 of transect 2; and plots n° 3 and 7 of transect 3. The soil in these pits was extracted in layers of 20 cm and searched for the presence of artefacts.

Radiocarbon dating

To quantify the timing of human occupation, radiocarbon dating was performed for 10 organic pieces, including five oil-palm endocarps collected at different depths in plot n° 3 of transect 3, to establish a reference profile. One fragment of charcoal and four oil-palm endocarps, collected in plots located on hilltops to get reliable data from disturbed human sites (Oslisly & White 2003), were additionally dated. We assumed that the age of a given piece of pottery was equal to ages of nearby charcoal and oil-palm endocarps. This dating was carried out using accelerator mass spectrometry by the Poznań Radiocarbon Laboratory (Poz). Date calibration was carried out with OxCal V4.2.3. (Bronk Ramsey 2013) set with the atmospheric calibration curve IntCal13 (Reimer et al. 2013).

Statistical analysis

To test whether regeneration guild distribution was influenced by tree size, a chi-square test of independence was conducted. The trees were assigned to 10 cm wide diameter classes, and large trees (≥ 100 cm) were grouped. Classes

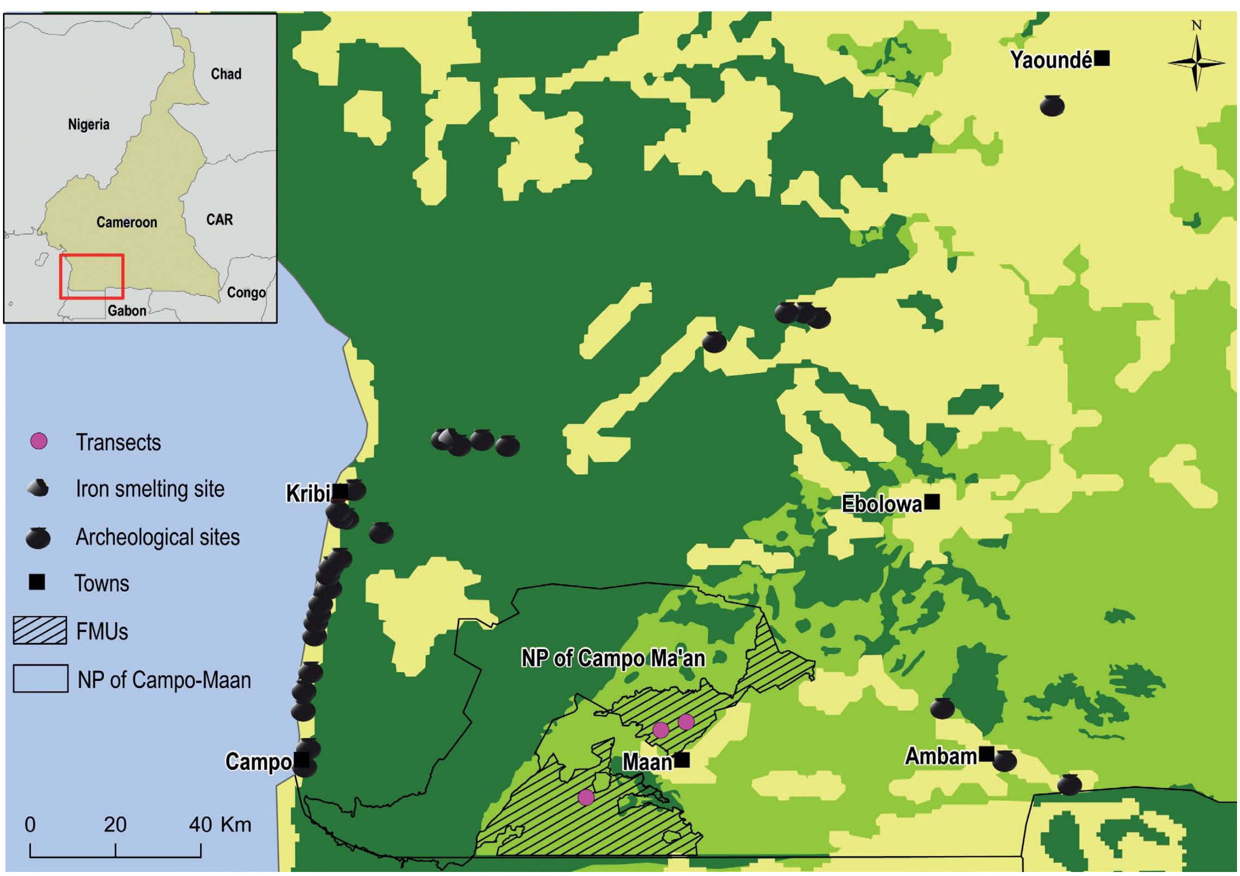

Figure 1 – Map of southern Cameroon with modern vegetation types and the mega-transect mentioned in text. The map is adapted of the Congo Basin vegetation map of Verhegghen et al. (2012) and the Cameroon phytogeographical map of Letouzey (1985). The dark green, light green and yellow colours shown in background correspond to the wet evergreen forests, the mixed evergreen and semi-deciduous forests and the rural area outside the forest, respectively.

where expected frequencies were less than 5% were merged with the neighbouring classes in order to satisfy the application conditions of the chi-square test. To determine whether the different transects and plots experienced similar human-induced disturbances, a linear mixed model with three factors (transects, plots within transects, and depths) was carried out respectively on abundance (grams per litre) of charcoal and oil-palm endocarps. Transect and plot were considered as random effects, while the soil depth was defined as a fixed effect. A logarithmic transformation was performed on the abundance of charcoal and oil-palm endocarps to meet the assumption of normality. Statistical analyses were performed using Minitab software (version 16, Minitab Inc., State College, Pennsylvania).

RESULTS

Forest structure and composition

We recorded a total of 1322 trees (dbh ≥ 20 cm) in the thirty-five 0.2-ha plots. These trees were classified into 146 species, 122 genera, and 39 families (electronic appendix 1). The average and maximum (95th percentile) dbh of trees were 38.7 and 82 cm, respectively. The stem density (trees (dbh ≥ 20 cm) ranged from 115 to 250 ha^{-1} (average 189 ha^{-1}), and basal area ranged from 18.2 to 50.7 $m^2\ ha^{-1}$ (average 29.2 $m^2\ ha^{-1}$).

Mean diameter distribution across the whole study area showed the classical reversed-J shape of old-growth tropical forests. The distribution of species regeneration guild was highly dependent on tree size (χ^2 = 158.13, df = 14, *P* < 0.001). Small trees (63% of total trees), with the diameter than or equal to 50 cm dbh, had more shade-tolerant species while large trees had more light-demanding species (pioneers and non-pioneer light-demanding) (fig. 2).

Abundance, distribution, and age of the potsherds

Potsherds were found in four pits scattered over the three transects on hilltops or at 250–500 m from streams (fig. 3).

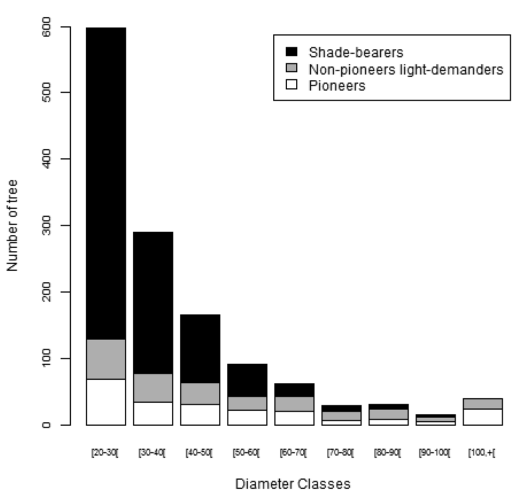

Figure 2 – Distribution of trees in the regeneration guild across the dbh classes.

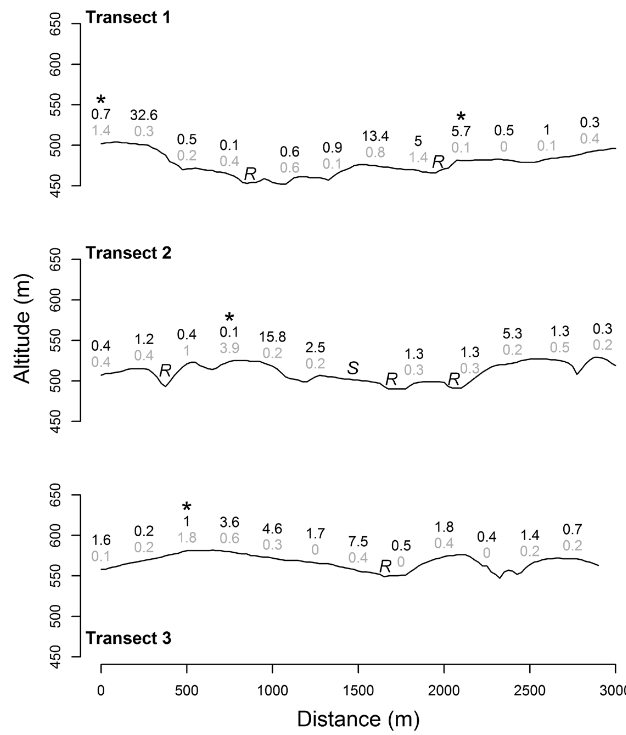

Figure 3 – Topographic profile with the distribution of evidence of human presence (potsherds, *) and activity (the abundance of charcoal and oil-palm endocarps in grams is indicated in black and grey, respectively) along the three line-transects. Rivers (R) and swamps (S) are indicated.

Potsherds were found in two pits on transect 1 at depths between 0 and 50 cm. On transect 2, potsherds were located at between 0 and 40 cm in depth. On transect 3, potsherds were found in one pit at between 0 and 80 cm. The potsherds showed no specific decoration and their small size (between 13 and 41 cm^2) (fig. 4) did not allow establishment of a ceramic typo-chronology.

Potsherds were often associated with charcoal and almost always with oil-palm endocarps (fig. 3), indicating that these plots were likely to have known human settlements. The dating of oil-palm endocarps close to potsherds showed two time-periods for human occupancy in the area (table 1). The most recent potsherds (extracted at between 0 and 20 cm deep) dated from two-three centuries ago, while the oldest (extracted at between 30 and 80 cm) dated to 1810 and 2160 BP.

Abundance, distribution, and age of the oil-palm endocarps

Oil-palm endocarps were extremely frequent throughout the study area, in 32 pits out 35, and at all depths up to 60 cm (fig. 3), but with varying abundance (0.01 to 1.5 g L^{-1}) (electronic appendix 2A). We detected a significant difference between plots ($F_{(32,160)}$ = 3.39, p < 0.001) but not between transects ($F_{(2,160)}$ = 0.71, p = 0.50). Abundance of oil-palm endocarps were also significantly different between depths ($F_{(5,160)}$ = 3.93, p = 0.03) (table 2). Oil-palm endocarp abun-

Table 1 – Raw dates BP with calibration.
Dated material (DM): C = Charcoal; E.g. = *Elaeis guineensis*; Pot. = Potsherds. The reference profile is indicated in bold.

	Sample	Age (BP)	Calibration (BP) 95.4%	Depth (cm)	DM	Archeology	Plots	Transect
Reference profile	**Poz-49323**	**260 ± 30**	**-3/431**	**0-20**	**C**	**Pot.**	**3**	**3**
	Poz-49324	**1810 ± 30**	**1824/1628**	**20-40**	***E.g***	**Pot.**	**3**	**3**
	Poz-49327	**2160 ± 30**	**2356/2308**	**60-80**	***E.g***	**Pot.**	**3**	**3**
	Poz-49328	**2005 ± 30**	**2039/1881**	**80-100**	***E.g***	**-**	**3**	**3**
	Poz-49329	**2090 ± 35**	**2151/1951**	**140-160**	***E.g***	**-**	**3**	**3**
Decreasing order of age	Poz-49334	150 ± 25	283/2	0- 20	*E.g*	Pot.	4	2
	Poz-49330	145 ± 30	284/0	20-30	C	Pot.	9	1
	Poz-49335	1540 ± 30	1520/1360	20-40	*E.g*	-	7	1
	Poz-49331	1705 ± 35	1699/1538	30-40	*E.g*	-	10	2
	Poz-49333	1790 ± 30	1819/1619	30-40	*E.g*	-	9	3

dance was highest between 20 and 30 cm depth (fig. 5). Radiocarbon ages indicated that these oil-palm endocarps were burnt between 1810 and 1540 BP (table 1).

Abundance, distribution, and age of the charcoals

Charcoal was found in all pits and at all depths up to 60 cm deep (fig. 3) but with varying abundance (0.01 to 15.9 g L^{-1}) (electronic appendix 2B). We found that charcoal abundance differed significantly between plots ($F_{(32,160)}$ = 4.73; $P < 0.001$) but not between transects ($F_{(2,160)} = 0.49$; $P = 0.62$) (table 2). Most of the charcoal (58%, 67 g to 116.3 g) was found between 0 and 20 cm depth (fig. 5), although charcoal profiles varied between plots (electronic appendix 2B). Ac-

Figure 4 – Potsherd found in the study area. The two fragments above were found between 0 and 40 cm depth in plot 4 on transect 2. The third fragment below was found between 10 and 20 cm depth in plot 9 on transect 9.

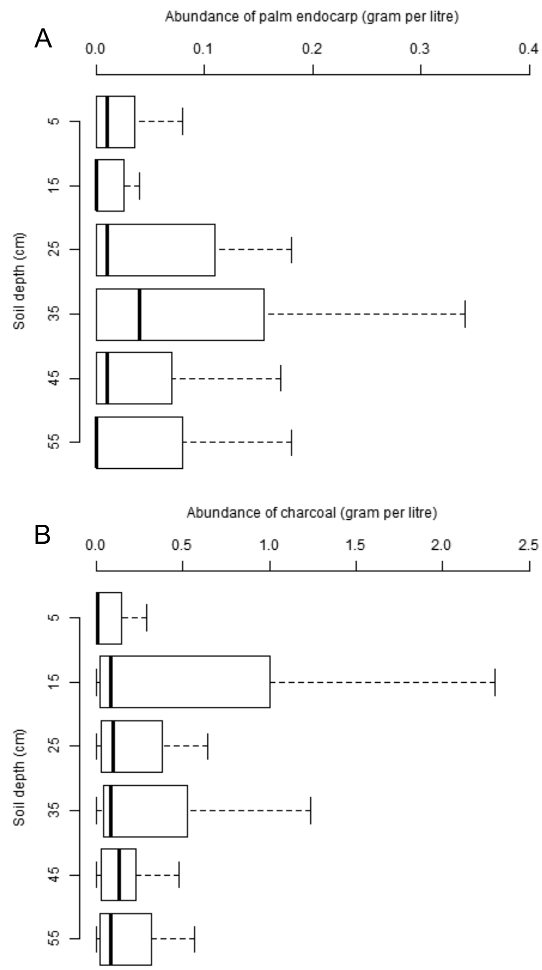

Figure 5 – A, average abundance of oil-palm endocarps (grams per litre) in each soil layer. The depths correspond to the midpoints of the layers; B, average abundance of charcoal (grams per litre) in each soil layer. The depths correspond to the midpoints of the layers. Error bars represent standard deviation from the average (grams per litre).

Table 2 – Summary of linear mixed model with three factors (transects, plots within transects, and depths) performed on the abundances (grams per litre) of oil-palm endocarps and charcoal.
Transect and plot were considered as random effects, while the soil depth was defined as a fixed effect.

Sources of variation	Effect	df	Oil-palm endocarps		Charcoal	
			F	*P*	*F*	*P*
Depth	Fixed	5	3.93	0.031	2.29	0.124
Transect	Random	2	0.71	0.501	0.49	0.619
Plot (Transect)	Random	32	3.39	< 0.001	4.73	< 0.001
Depth*Transect	Random	10	0.51	0.882	0.95	0.488

cording to radiocarbon ages (table 1), charcoal found in the top soil layers at between 0 and 20 cm of the soil profile were two or three centuries old.

DISCUSSION

The aim of this study was to determine timing and spatial extent of past human disturbances in the dense forests of south-western Cameroon in relation with current forest composition. We found oil-palm endocarps and charcoal in almost all pits, indicating wide-spread human occupancy and anthropogenic fire. We also found potsherds attesting for human settlements in four sites across the area. Radiocarbon dating of selected material showed that human occupation occurred in two periods: between 2200 and 1500 BP, and from three centuries ago until now. This bimodal pattern has already been reported in the littoral and south-eastern forest of Cameroon (Oslisly 2006, Oslisly et al. 2013a, Morin-Rivat et al. 2014) and elsewhere in Central Africa (Wotzka 2006, Oslisly et al. 2013a). The latter period of human occupancy may have favoured light-demanding tree species that now dominate the canopy.

Evidence of past human occupancy

Potsherds found on hilltops and near streams were always associated with a large amount of oil-palm endocarps. This pattern suggests that past human occupation was common in the study area, as reported for Lopé reserve in Gabon and the Banyang Mbo sanctuary in western Cameroon (Oslisly & White 2003). Radiocarbon dates suggest that these populations were probably the first Bantu farmers (Neumann et al. 2012a, Oslisly et al. 2013b). In southern Cameroon, several sites containing pottery were found between Yaoundé, Kribi and Campo, on the Atlantic coast, and near Ambam (Lavachery et al. 2005), close to the border between Cameroon–Gabon and Equatorial Guinea. Most of these sites were dated between 2600 and 2000 BP (Lavachery et al. 2005). The populations were known to practice iron metallurgy (Essomba 1998). We did not find any direct sign of metallurgy in this study but an iron furnace dated to 2200 BP has been located at Makouré, approximately 90 km northwest of the study area (Lavachery et al. 2005). The absence of dates between 1540 and 260 BP confirmed the population "crash" previously reported (Oslisly et al. 2013a, Morin-Rivat et al. 2014). There is as yet no clear explanation for this demographic change, although Oslisly et al. (2013b) mention diseases or famines. A second period of human occupancy three centuries ago is consistent with the re-population phase by Bantu populations (Mohammadou 1999).

Slash-and-burn agriculture

The abundance of charcoal across the study area at various soil depths suggests a mosaic of burnt areas at different times and at varying intensities. Natural fires can occur in tropical rain forests (Hart et al. 1996) but rarely spread over large areas. Large fires require a particular combination of conditions – a long dry season, low relative humidity, dry litter, and high frequency of lightning (Tardy et al. 1996) – that are unusual in the understory of dense forests (Cochrane 2009). The high frequency of recent fires observed throughout the study area is most likely due to slash-and-burn shifting cultivation. In the littoral forests of Cameroon and Gabon, and south-western Nigerian forests Letouzey (1985), White & Oates (1999), and Oslisly & White (2007) found charcoal and artefacts in many places in these forests suggesting historical human clearing for agricultural use of a few centuries ago.

The presence of oil-palm endocarps throughout the study area, among which the most recent fragments, dated at between two and three centuries old, could be explained by intensive and widespread human activities, as suggested by Gillet & Doucet (2013). According to Maley (2002), Central Africa has been subject to forest expansion with a decline in oil-palm (*Elaeis guineensis*) tree populations since the 13th century. The presence of this species until recently (145 BP) indicate that there were likely enough openings in the forest (Brncic 2003). Indeed, *Elaeis guineensis* is a pioneer species that grows in various types of disturbed forests and regenerates abundantly post-cropping (Hawthorne 1995). Its seed dormancy is broken by fire (Swaine & Hall 1986).

Effects of past human disturbances on current forest composition

We showed that the upper canopy of the study area is dominated by light-demanding tree species as suggested by Letouzey (1985). A similar forest composition was reported elsewhere in southern Nigeria (White & Oates 1999), in Gabon (Brunck et al. 1990), and in northern Congo (Gillet & Doucet 2013), and the abundance of large light-demanding species probably results from historical human disturbances. Focusing on *Lophira alata*, one of the major light-demanding tree species of the wet evergreen littoral forest in southern Cameroon (Letouzey 1985), management-inventory data for 110,000 ha revealed that the population has the highest number of individuals in the diameter class between 80 and 90 cm (Wijma 2007, 2011). As the species annual diameter increment is estimated to be 4.5 $mm.y^{-1}$ (Biwolé et al. 2012), most of these trees should be aged between 178 and 200 years. The coincidence between the recent human disturbance that occurred two or three centuries ago and the age of this emergent light-demanding tree species support the hypothesis of past anthropogenic impacts on current forest composition. Indeed, the present lack of regeneration of the *L. alata* in mature forests (Letouzey 1985) suggests that its recruitment may have been favoured in larger disturbed zones than those created by natural disturbances (van Gemerden et al. 2003). In the second half of the 18th century and in the early 19th century, various ethnic groups from the Adamawa Plateau in Cameroon have invaded all lands in the south of their starting area, forcing savanna's Bantu populations of northern Sanaga to seek refuge in the southern forest (Mohammadou 1999, 2004) until they occupied the whole southern Cameroon, Equatorial Guinea and northern Gabon (Alexandre 1965). In the 19th century, after controlling this broad phenomenon, European colonisation would have led to human migrations from forest zones to along roadsides, leaving large areas derelict (Diaw 1997). Today, non-selective and frequent disturbances, such as forest clearing for slash-and burn agriculture, followed by a long period of recovery, are no longer observed in dense forests (van Gemerden et al. 2003).

Possible role of past climate change

The current abundance of long-lived light-demanding species in the upper canopy may also reflect recent climate-induced disturbance. Pollen data from northern Gabon showed a drought period during the Little Ice Age, between the 15th and 17th centuries, and a return to a more humid period during the 18th century (Ngomanda et al. 2007). Olivry (1986) and Maley & Vernet (2013) reported a similar trend in northern Cameroon and in the Lake Chad, and specifically identified two main drought events in the early 18th century. The previously estimated age of the long-lived light-demanding species (*L. alata*) and the enduring presence of *E. guineensis*, two to three centuries ago, coincide with this recent climate change (18th century) that may have induced also disturbances and favoured the regeneration of light-demanding species. Indeed, Ngomanda et al. (2007) showed in Gabon that climate variations recorded during the Little Ice Age affected the structure of mature forests allowing the formation and persistence of the canopy gaps. The return to a wet period in the late 18th century, marked by an evergreen rainforest expansion in the African forest, which would have continued until now (Maley 2002), could explain the lack of current regeneration of the large long-lived light-demanding species in the study area (Letouzey 1985).

SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of (1) list of tree species found in the study area and their guilds defined following Hawthorne (1995); and (2) abundance of oil-palm endocarps (A) and of charcoals (B) at the various soil depths in each plot (grams per litre).

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