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Of trees and men: new insights into man-environment relationships in the moist forests of central Africa during the late Holocene

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Rougier Gérer la forêt, faire vivre le bois

Morin-Rivat Julie (2017). *Of trees and men: new insights into man-environment relationships in the moist forests of central Africa during the late Holocene.* PhD thesis. Université de Liège – Gembloux Agro–Bio Tech, 206 p., 5 tabl., 25 fig., 15 appendices.

Short summary

In central Africa, vegetation history has been documented by paleoenvironmental studies (especially palynology), which mainly concerned the way climate has shaped the forest landscapes. Human impacts in this region have hardly been studied so far, especially at local scale. The main objective of this PhD is to propose an approach based on archaeology and the use of charred botanical remains found in soils, either wood charcoal or seeds, in order to document the Holocene anthropogenic impacts on the forest structure and composition. When coupled with the diachronic analysis of human activities, these land-use biomarkers can allow a better understanding of the relationship between man and his environment in central Africa during this period. Thereby, the first part of this PhD introduces the conceptual framework and the materials and methods used during the research. Then, the second part constitutes the core of the work, and presents the chronology of human activities in the northern Congo Basin, the use of biomarkers to discrimate between these activities, either domestic or agricultural, and the effect of the recent anthropogenic activities in the dynamic of several light-demanding tree populations. Finally, the third part draws the main recommendations of the work, and formulates potential for additional research.

Extended summary

In central Africa, tropical forests house a unique biodiversity, and afford indispensable ecosystem services, including food supply and carbon storage. They currently undergo, however, increasing anthropogenic pressure. In the context of global change, and in order to propose potential scenarios of evolution, there is an urgent need for knowledge regarding forests evolution over time, involving new data about their current state, and their past.

Paleoecological studies traditionnaly document vegetation history, especially the role of climate in shaping the forest landscapes. They remain few in central Africa, however, notably due to difficulties regarding fieldwork accessibility and a huge diversity in terms of plant species. More specifically, the relationship between human and his environment remains a field of investigation relatively new in this region.

The work presented in this PhD thesis was undertaken in a pluridisciplinary approach, at the crossroads between archaeology and ecology. The search for evidence of human activities in the northern Congo Basin, a region little explored by previous archaeological surveys, and the use of charred botanical remains in order to classify these activities, constitute two of the main contributions of this thesis. The last contribution consists in the establishment of a cause-effect relationship between the human history of the 19th century and the current depletion of light-demanding tree populations.

Chapter 1 presents the key concepts relative to tropical ecology, to African tropical forests, and the specificities of light-demanding tree species. Then, it retraces the chronology of climate change, and of human history in central Africa. Finally, it exposes the objectives and the outline of this PhD.

Chapter 2 deals with the materials and methods used for the research, the resources, paleological and archeological proxies and data, the methods used, and the study area.

Chapter 3 presents the spatiotemporal framework of human presence in the northern Congo Basin. It discusses the current knowledge gaps in terms of human activities. It stresses a hiatus in human occupation between ~1300 and 600 yrs BP in the study area.

Chapter 4 proposes a methologogy based on the acquisition and the statistical analysis of charred botanical remains found in soils. It showed a spatial opposition between domestic and agricultural spaces. The combination of charred oil palm endocarps and potsherds would indicate villages, whereas wood charcoals are more frequent in fields.

Chapter 5 gathers and analyzes big datasets focused on the Sangha River Interval (SRI), and relative to paleoecology, archaeology, history, and dendrology during the last 1,000 yrs. In particular, it highlights the potential effect since the European colonization of land-use changes on the regeneration of four light-demanding tree populations.

Chapter 6 concludes the PhD by summarizing the results of the previous chapters. It underlines the importance of the chronology, the identification of past human activities within the dense moist forest, and the impacts of the recent human history on the current forests landscape in central Africa. This last chapter identifies several remaining knowledge gaps, and proposes potentials for additional research.

Keywords: archaeology – soil charcoal – radiocarbon dating – history – Congo Basin – tropical forest

Morin-Rivat Julie (2017). *Des arbres et des hommes: nouvelle perspectives sur la relation homme-environnement dans les forêts humides d'Afrique centrale à l'Holocène récent.* Thèse de doctorat. Université de Liège – Gembloux Agro–Bio Tech, 206 p., 5 tabl., 25 eteHlo fig., 15 annexes.

Résumé court

En Afrique centrale, l'histoire de la végétation est documentée grâce aux études paléoenvironnementales (palynologie principalement), lesquelles concernent surtout le rôle du climat dans le façonnage des paysages forestiers. Les impacts humains dans cette région ont été peu étudiés jusqu'à présent, en particulier à l'échelle locale. L'objectif principal de ce doctorat est de proposer une approche achéologique basée notamment sur l'analyse des restes botaniques carbonisés trouvés dans les sols, charbons de bois et graines, pour documenter les impacts anthropiques de l'Holocène récent sur la structure et la composition forestières. Couplés à l'analyse diachronique des activités humaines, ces biomarqueurs d'usage des terres peuvent permettre de mieux comprendre la relation entre l'homme et son environnement en Afrique centrale pendant cette période. Ainsi, la première partie de ce doctorat introduit le cadre conceptuel et les matériels et méthodes utilisés pour la recherche. Ensuite, la seconde partie constitue le cœur de ce travail et présente la chronologie des activités humaines dans le nord du bassin du Congo, l'utilisation des biomarqueurs pour identifier ces activités, qu'elles soient domestiques ou agricoles, et enfin l'effet des activités anthropiques récentes dans la dynamique de plusieurs populations d'arbres héliophiles. Enfin, la troisième partie tire les principales conclusions de ce travail, et formule les recommandations pour des recherches complémentaires.

Résumé étendu

En Afrique centrale, les forêts tropicales hébergent une biodiversité unique et procurent des services écosystémiques indispensables. Toutefois, elles subissent actuellement une pression anthropique croissante. Dans le contexte des changements globaux et dans le but de proposer des scénarios d'évolution, il est nécessaire de connaître le passé des forêts et les influences anthropiques qu'elles ont subies, afin de mieux prédire leur avenir.

Traditionnellement, les études paléoécologiques documentent l'histoire de la végétation, en particulier le rôle du climat dans le façonnage des paysages forestiers. Elles restent pourtant peu nombreuses en Afrique centrale, notamment à cause des difficultés d'accès au terrain et de la grande diversité en matière d'espèces végétales. Plus spécifiquement, la relation entre l'homme et son environnement demeure un champ d'investigation relativement récent dans cette région.

L'approche adoptée par cette thèse de doctorat se veut pluridisciplinaire, à la croisée entre l'archéologie et l'écologie. La recherche d'indices d'activités humaines dans le nord du bassin du Congo, une région peu explorée par les précédentes recherches archéologiques, et l'utilisation des restes botaniques carbonisés pour déterminer ces activités, constituent deux de ses principales contributions. Sa dernière contribution significative consiste en l'établissement d'une relation de cause à effet entre l'histoire humaine du $19^{ème}$ siècle et le ralentissement de la régénération de certaines populations d'arbres héliophiles.

Le Chapitre 1 présente les concepts clés relatifs à l'écologie des forêts tropicales et les spécificités des espèces d'arbres héliophiles. Puis, il retrace la chronologie des changements climatiques et de l'histoire humaine en Afrique centrale. Enfin, il expose les objectifs et le plan de la thèse.

Le Chapitre 2 a trait aux matériels et méthodes utilisés pour la recherche. Il présente les ressources, les indicateurs ainsi que les données paléoécologiques et archéologiques. Il décrit aussi les méthodes utilisées, ainsi que la zone d'étude.

Le Chapitre 3 présente le cadre spatial et temporel de la présence humaine dans le nord du bassin du Congo. Il discute des lacunes relatives à la connaissance des activités humaines. Il souligne l'absence d'occupations humaines entre ~1300 et 600 BP dans la zone d'étude.

Le Chapitre 4 propose une méthodologie basée sur l'acquisition et l'analyse statistique des restes botaniques carbonisés trouvés dans les sols. Il montre une opposition spatiale entre des espaces domestiques et agricoles. La combinaison d'endocarpes de palmier à huile carbonisés et de tessons céramiques indiquerait la présence de villages, tandis que la présence de charbons de bois supposerait davantage l'existence de champs.

Le Chapitre 5 rassemble et analyse d'importants jeux de données centrés sur l'Intervalle de la Sangha. Les données sont relatives à la paléoécologie, l'archéologie, l'histoire et la dendrologie durant le dernier millénaire. En particulier, il souligne l'effet des changements d'usage des terres sur la régénération de quatre populations d'arbres héliophiles (*Erythrophleum suaveolens*, *Pericopsis elata*, *Terminalia superba* et *Triplochiton scleroxylon*). Il met particulièrement en exergue le rôle de la colonisation européenne.

Le Chapitre 6 conclut la thèse en synthétisant les résultats des chapitres précédents. Il souligne l'importance de la chronologie, de l'identification des activités humaines passées au sein des forêts denses humides et les impacts de l'histoire humaine récente sur les paysages forestiers d'Afrique centrale. Ce dernier chapitre identifie plusieurs lacunes en termes de connaissance et propose des pistes de recherche.

Mots-clés : archéologie – charbons de sol – datation radiocarbone – histoire –bassin du Congo – forêt tropicale

List of abbreviations

^{14}C: radiocarbon
δ^{13}C: a proxy for the C3 (carbon from trees)/C4 (carbon from grass) ratio
A: identified Phase A
AD: Anno Domini (= calendar date after 0)
AMS: Accelerator Mass Spectrometry (for radiocarbon dates)
B: identified Phase B
BC: Before Christ (= calendar date before 0)
BIC: Bayesian Information Criterion
BP: Before Present (i.e. before 1950)
C: Cameroon, charcoal or carbon (specified in the text)
CAR: Central African Republic
CE: charred endocarp
C. s.: *Canarium schweinfurthii*
dbh: diameter at breast height (for measuring trees) that corresponds to 1.30 m in height
DF: degree of freedom
DM: dated material
DRC: Democratic Republic of Congo
E. g.: *Elaeis guineensis*
F: *F*-statistic value
FMU: Forest Management Unit
G. d.: *Gilbertiodendron dewevrei*
ha: hectar
IC: Ivory Coast
Iron.: iron slags (artifacts)
ka: thousand years, according to the international standard ISO 31-1 for quantities and units related to space and time
Lith.: lithics (artifacts)
Ma: million years, according to the international standard ISO 31-1 for quantities and units related to space and time
MLM: Mixed Linear Model
N. sp.: *Nauclea* sp.
ODE: ordinary differential equations
OPE: oil palm endocarp *Elaeis guineensis*
OSL: optically stimulated luminescence (for dating)
p: probability value
Pot.: pottery (artifacts)
RC: Republic of the Congo
SQL: Structured Query Language
SRI: Sangha River Interval
sp.: species
SSTs: Sea Surface temperatures
^{238}U/^{230}Th: ratio between radioactive uranium and thorium
yrs: years

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Postmodern in history asserts, first, that all historical consciousness is an ideological product of the present and only reflects power relations in the present: "The past does not exist." Second, it maintains that even had it existed, the past cannot be known, because its direct traces (written texts or archaeology) are interpreted and hence "invented" by readers in the present ("deconstruction"). Third, it insists that objectivity is not only impossible to attain but that it is wrong to strive for it because the main point of interest in historiography is the subjective interpretation of a given author. Fourth, there is no genuine divide between fact and fiction. Finally, to strive for a consensus is hypocrisy because that is tentamount of imposing the relative view of one person or of an oligarchy on all others.

Jan Vansina (1929–2017) – *Living with Africa* – 1994
In memoriam

Foreword

This PhD project is a child of the CoForChange project (EraNet-Biodiversa, EU, ANR/NERC, France and UK, head: Dr. Sylvie Gourlet-Fleury) *“Predicting the effects of global change on forest biodiversity in the Congo Basin”*. It also benefited for unpublished data, fieldwork funding and lab analyses from the FRFC project (No. 2.4577.10, F.R.S./FNRS, Belgium) *“Dynamics of light-demanding tree species and grasses in the humid forests of Central Africa in relationship with past anthropogenic and climate disturbances”*, the TROPDIV-Project (PPR 10.000, ULg-GxABT, Belgium, the King Leopold III Funds for Nature Exploration and Conservation (Belgium). It also benefited from the PACODEL (ULg-GxABT, Belgium) and the Laboratoire de Foresterie des Régions tropicales et subtropicales (TERRA FAC, ULg-GxABT, Prof. Jean-Louis Doucet) for additional support in communicating the results. The PhD candidate was personaly funded by the Belgium *Training Fund for Research in Industry and Agriculture* (FRIA – F.R.S. /FNRS, Belgium).

Prof. Jean-Louis Doucet (ULg-GxABT, Belgium) and Dr. H. Beeckman (RMCA, Belgium) assured the scientific supervision of the PhD candidate. The axe Gestion des Ressources forestières (BIOSE dpt., ULg-GxABT), the Laboratoire de Foresterie des Régions tropicales et subtropicales (TERRA FAC, ULg-GxABT), and the Wood Biology Service (RMCA, Tervuren) also provided scientific and logistical support to this work. The NGO Nature+ (Belgium) and the forest companies SFID-Mbang – Rougier Group (Douala, Cameroon) and Pallisco (Pasquet Group, Douala, Cameroon) provided logistical support during the fieldwork, as well as scientific data. In the framework of the collaboration agreement between the Laboratoire de Foresterie des Régions tropicales et subtropicales, the NGO Nature+, and the forests companies SFID-Mbang and Pallisco, the companies greatly helped in the achievement of the fieldwork activities, by providing a full access to their forest concessions, technical staff, facilities (vehicules, accomodations, tools), and data. The forest companies ALPICAM (Douala, Cameroon), Wijma (Douala, Cameroon), ALPI Pietro and Sons (Kika, Cameroon), Mokabi SA – Rougier Group (Impfondo, Rep. of the Congo), BPL-Lopola (Lopola, Rep. of the Congo), CIB – OLAM Group (Brazzaville, Rep. of the Congo), and IFO – Danzer Group (Ouesso, Rep. of the Congo), IFB (CAR), SOFOKAD (CAR), Thanry – TCA (VicWood, CAR), SCAF (Fadoul Group, CAR) also provided logistical support and scientific data, during the CoForChange project, in particular.

The scientific production consists in three research articles that are included in the present document. They form the three core chapters:

1) Morin-Rivat J, Fayolle A, Gillet JF, Bourland N, Gourlet-Fleury S, Oslisly R, Bremond L, Bentaleb I, Beeckman H, Doucet JL. 2014. New evidence of human activities during the Holocene in the Lowland Forests of the Northern Congo Basin. *Radiocarbon* 56: 209–220. doi:10.2458/56.16485.
http://orbi.ulg.ac.be/handle/2268/159081

2) Morin-Rivat J, Biwole A, Gorel AP, Vleminckx J, Gillet JF, Bourland N, Hardy OJ, Livingstone Smith A, Daïnou K, Dedry L, Beeckman H, Doucet JL. 2016. High spatial resolution of late-Holocene human activities in the moist forests of central Africa using soil charcoal and charred botanical remains. *The Holocene* 26: 1954–1967. doi:10.1177/0959683616646184.
http://orbi.ulg.ac.be/handle/2268/197852

3) Morin-Rivat J, Fayolle A, Favier C, Bremond L, Gourlet-Fleury S, Bayol N, Lejeune P, Beeckman H, Doucet JL. 2017. Present-day central African forest is a legacy of the 19th century human history. *eLife* 6: e20343. doi:10.7554/eLife.20343. http://orbi.ulg.ac.be/handle/2268/205439

Due to the great number of references, they are all reported at the end of the manuscript.

The full list of publications and communications of the PhD candidate can be consulted on the ULg academic platform:
http://orbi.ulg.ac.be/browse?type=authorulg&rpp=20&value=Morin-Rivat%2C+Julie+p128552
and http://orbi.ulg.ac.be/browse?type=authorulg&rpp=20&value=Morin%2C+Julie+p128552

First part Introduction

Chapter 1 General introduction

On the continent where the humans lived, only one banyan tree grew now. It had become first King of the forest, then the forest itself. It has conquered the deserts and the mountains and the swamps. It filled the continent with its interlaced scaffolding. Only before the wider rivers or at the margins of the sea, where the deadly seaweeds would assail it, did the tree not go.

And at the terminator, where all things stopped and night began, there too the tree did not go.

Brian W. Aldiss – *Hothouse* – 1962

This first chapter aims at introducing the key concepts and the context of the research presented in this PhD dissertation, along with its relevance, the objectives and the structure of the document.

Arbre branche 3 – Véronique LG Morin

1.1. Rationale

Tropical moist forests worldwide are irreplaceable hotspots of biodiversity (Gibson et al. 2011). They constitute important providers of ecosystem services at different scales (Morris 2010). For instance, they participate to an essential part of the global carbon stocks (Lewis et al. 2009), host a unique biodiversity (Parmentier et al. 2007) and afford shelter, supplies and resources for the millions of people who live there (Mayaux et al. 2013). These forests are nonetheless threatened by current global change (Pereira et al. 2012, de Wasseige et al. 2015). This includes the human-driven changes of the Anthropocene (Lewis and Maslin 2015, Boivin et al. 2016), a new geologic period defined by the current massive human impact on the planet (Schimel et al. 2013), but whose starting date, probably since the industrial era, is still debated (Ellis et al. 2013, Butzer 2015, Piperno et al. 2015). In his popular book *Collapse*, Diamond (2005) reviewed, indeed, numerous cases of catastrophic land-use intensification, even though this deserves some nuances (e.g. Trigger 2006, Wills et al. 2014, Iles 2015). Nonetheless, degraded forest landscapes (Laporte 2007, Morris 2010, Gond et al. 2013, Fayolle et al. 2014a, 2014b), young fallows dominated by short-lived pioneer species (Aubréville 1947), cascade effects of faunal depletion (Kurten 2013), and soil erosion (Chikanda 2009) would represent good examples of side-effects of this increasing human pressure.

Moist forests were formerly considered as pristine ecosystems that means primary forests without any change of anthropogenic origin in their structure and species composition over time (Willis et al. 2004). These environments, however, are far from being “virgin”, and multiple lines of evidence for past anthropogenic disturbances have been recently unearthed across the tropics (Barton et al. 2012 and references therein), including central Africa (Logan and d’Andrea 2012, Neumann et al. 2012a). Beyond these paleoenvironmental and archaeological proofs concealed in soils, when we look up to the trees themselves, vegetation patches of various ages also testify to a disturbed forest history (Aubréville 1947, Letouzey 1968, 1985, Willis et al. 2013). Negative environmental impacts could have derived from past agriculture and metallurgy (Diamond 1987), but it raised the issue of the previous and more discrete anthropogenic impacts that cannot be attributed to food-production or iron-smelting practices (Iles 2015), and perpetuate the misleading concept of diffusionism linked to the notion of “civilization” (Pyne 1997).

In this framework, the fate of African tropical forests is intrinsically tied to that of human populations (de Wasseige et al. 2015, Venter et al. 2016; ***Figure 1.1***). Future decisions and orientations in terms of environmental policies are, however, difficult to picture out in the absence of a broader view both in time and space (Malhi et al. 2013a). Which is the resilience capacity of moist forests after destructive events? What was the impact of past human disturbances compared to climatic fluctuations? Can we infer results of past situations to predict future changes? As our knowledge remains limited in any case, the exploration of the archives that forests conceal can give us the opportunity to broaden our perspective (Willis and Birks 2006, Kiahtipes 2016).

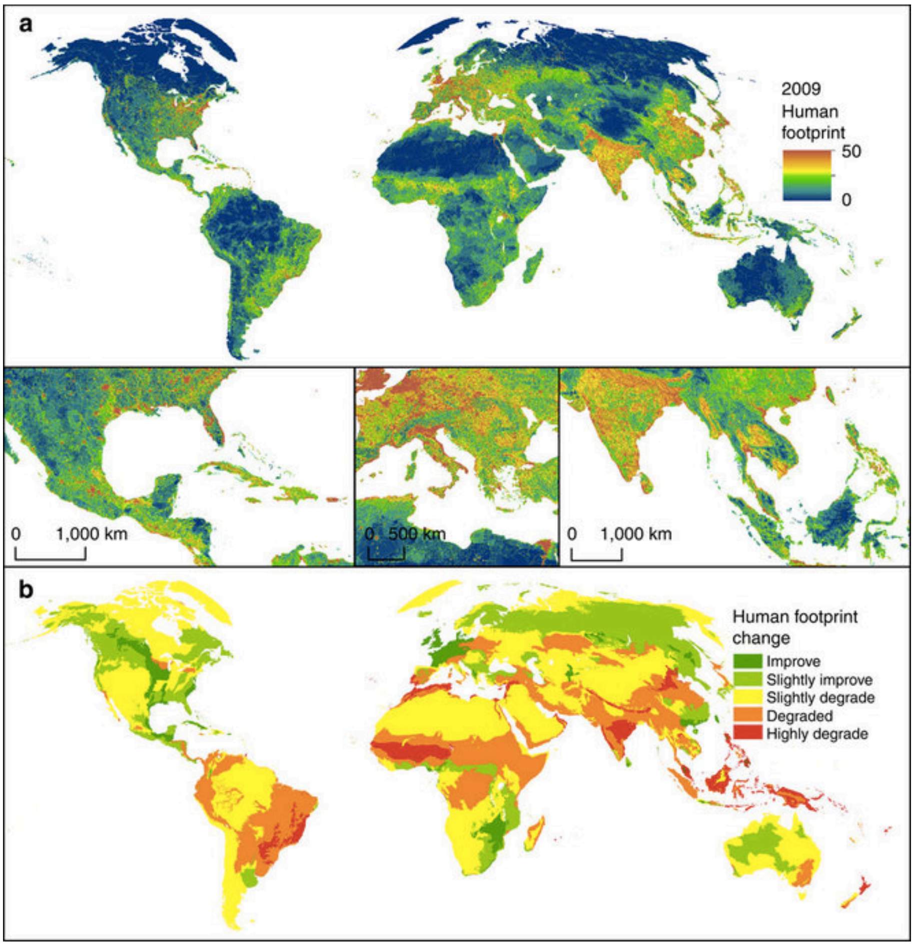


Figure 1.1. Current state and recent change in the global human footprint. (**a**) The global human footprint map for 2009 using a 0–50 cool to hot color scale, and (**b**) absolute change in average human footprint from 1993 to 2009 at the ecoregion scale. Data on human footprint change are summarized by ecoregions to allow for interpretation of broad patterns. Inset panels in **b** show focal regions that span the full breadth of the human footprint pressure scale. (Reproduced from *Nature Communications*, with the courtesy of Venter et al. 2016).

Three kinds of records can be used to reconstruct forest history. The most visible is the forest itself, by observing tree species composition (Aubréville 1947, Letouzey 1968, 1985, Fayolle et al. 2014a, 2014b), tree growth (Detienne et al. 1998, Worbes et al. 2003, De Ridder et al. 2013a, 2013b, 2014, Battipaglia et al. 2015, Fétéké et al. 2015, Groenendijk et al. 2015), and tree life-history (Poorter et al. 2006, Rutishauser et al. 2011). Secondly, beneath the tree line lie lacustrine and soil archives, in which paleobotanical remains (e.g. pollens, phytoliths, sedimentary charcoal) (Brncic et al. 2007, 2009, Aleman et al. 2013, Lézine et al. 2013, Tovar et al. 2014, Kiathipes 2016), charred macrobotanical remains including soil charcoal (Höhn and Neumann 2012, Hubau et al. 2012, 2013, 2015), and also archaeological artifacts (e.g. de Maret 1986, Lavachery 2001, Clist 2005, Oslisly 2013a, 2013b, de Saulieu et al. 2015), constitute primary witnesses of natural and anthropogenic disturbances within the forest. Finally, for the most recent times, the third category of records comprises the historical and ethnographical archives (Robineau 1967, Kaspi 1971, Pourtier, 1989, Burnham 1996, Copet-Rougier 1998, Giles-Vernick 2000, Coquery-Vidrovitch 1998, Manning and Akyeampong 2006, Freed 2010, Gendreau 2010, Stock 2013), in the form of maps, pictures, testimonies and administrative descriptions covering the modern period.

By presenting several elements of those three aspects, this PhD specifically tackles the question of the relationship between man and his environment in central Africa during the late-Holocene (2500 BP to the present). Its focal point is a combined archaeological and ecological analysis, including dated evidence of past human activities within the forest and dendrological data.

1.2. The multidimensional aspects of tropical forests

1.2.1. Explaining diversity in the tropics

Tropical moist forests encompass about 1,094 million ha, and thus represent 10% of the global forest cover (Mayaux et al. 2004, FAO 2012). They are considered as the most ancient *terra firma* ecosystems in the world (Couvreur and Backer 2013, Pereira 2016). They host a unique biodiversity, and constitute the most diverse terrestrial ecosystems (Gentry 1988, Richards 1996, Whitmore 1998, Condit et al. 2002, Wright 2002, Losos and Leigh 2004, Turner 2004, Parmentier et al. 2007). This biodiversity drops from the equator to the poles, a phenomenon commonly called “altitudinal gradient in diversity” (Gaston 2000, Linder 2001, Willis et al. 2003, Davies et al. 2004, Kreft and Jetz 2007, Pereira 2016, Miraldo et al. 2016; ***Figure 1.2***). This gradient has been explained by several theories (Gaston 2000, Willig et al. 2003), which are still largely challenged (Mittelbach et al. 2007, Rohde 2013). These theories are related to historical disturbances, environment stability, habitat heterogeneity, stochastic phenomena, productivity, and species interactions. As these theories are complementary, interdependent or too specific, they are commonly grouped into three main categories (Mittelbach et al. 2007, Mannion et al. 2014): 1) the historical factors theory, 2) the area hypothesis, and 3) the available environmental energy.

1) The historical factors theory is based on the assumption that past climatic events have had a variable impact according to the latitude. Tropical regions have been less disturbed, and have thus accumulated more species during a longer time span, especially during the Eocene (56 Ma–33.9 Ma, ***Figure 1.3***), where a tropical climate reigned on almost the whole surface of Earth during a long time period, suitable for evolution under tropical conditions. This theory is linked to hypotheses dealing with environmental stability or, conversely, with the frequency and intensity of past disturbances on species diversity at a regional scale.

2) The area hypothesis postulates that the greater diversity observed in the intertropical area might be linked (i) to its surface, greater than any other ecological region in the world, (ii) to the non-linear gradient of temperatures from the equator to the poles (variations are more marked beyond the latitudes 20°N and 20°S), and (iii) to the abundance in heterogeneous meso- and microenvironments favorable to local adaptations in this area, large and climatically homogeneous.

3) The available environmental energy hypothesis relies on the idea that the quantity of available energy per surface unit defines the species richness of this surface. Productivity is higher under tropical latitudes because of a greater concentration of solar energy. This would lead, therefore, to greater population size and greater plant diversity, supporting a high carrying capacity. Correlatively, another convergent hypothesis postulates that the better speciation in the tropics would rely on greater mutation rates in organisms with a greater metabolism.

A fourth hypothesis, the niche conservatism performs the synthesis between the ecological and evolutionary processes in order to explain this altitudinal gradient of diversity. According to Wiens and Donoghue (2004), and Kissing et al. (2012), it involves three principles: 1) groups presenting a high species richness in tropical regions have come from those regions, and have later dispersed in temperate regions; this involves less time for speciation in those newly colonized regions; 2) the tolerance to cold, and in particular, to negative temperatures, has determined the dispersion of those tropical groups in temperate regions; and 3) an important number of those groups have come from tropical regions, for they have occupied larger regions than today.

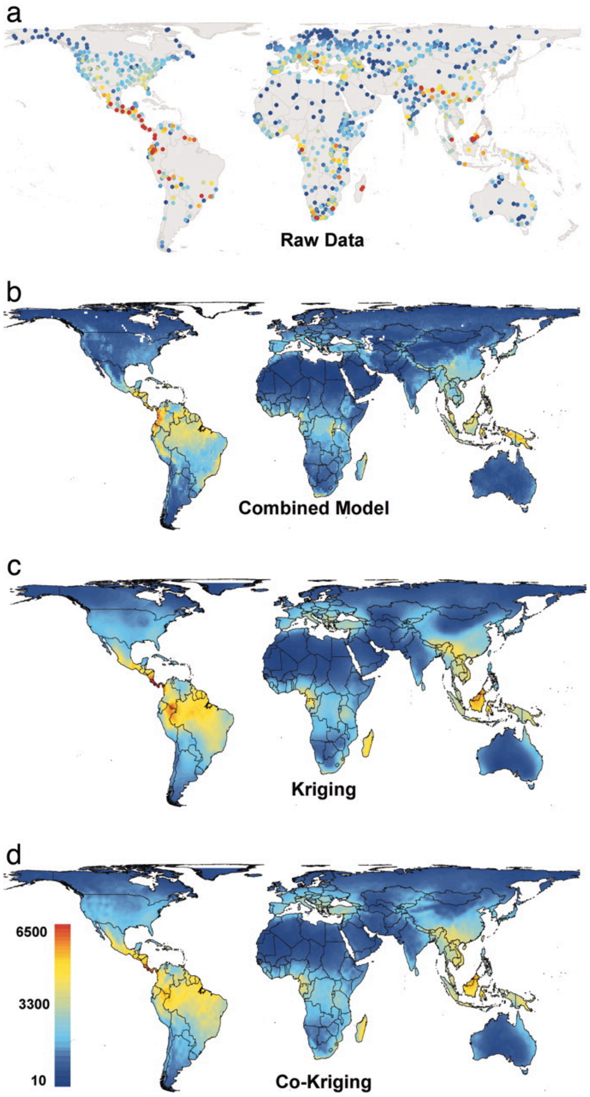
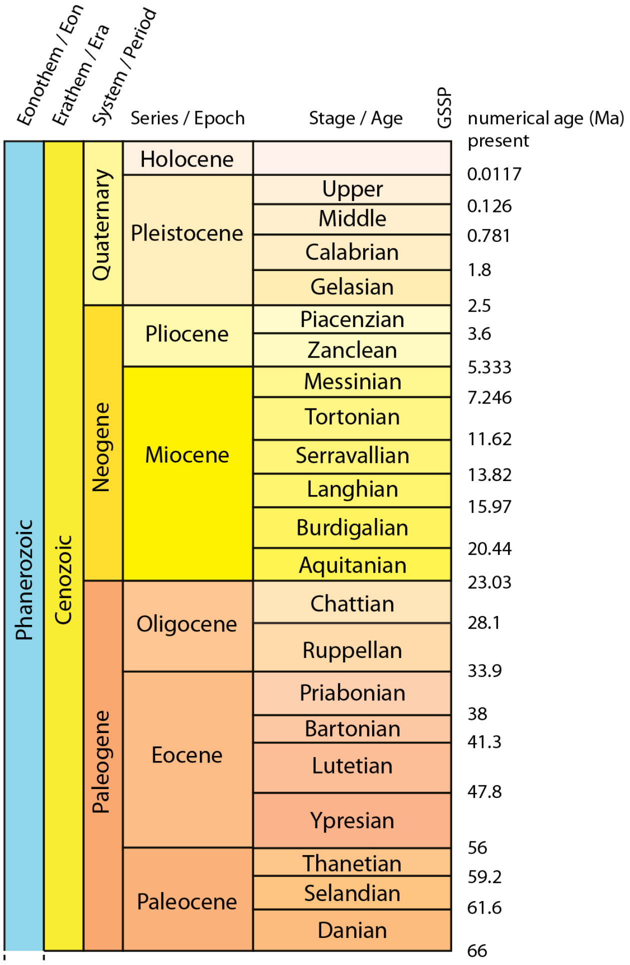


Fig. 1.2. Global patterns of vascular plant species richness.
a) The geographic distribution of the richness data of vascular plants for the 1,032 geographic regions analyzed (each dot presents the mass centroid of the geographic entity. b-d) The species-richness map show area-standardized predictions of three different global models across an equal grid (ca. 12,100 km^2, ca. 1° latitude x 1° longitude near the equator). b) combined multipredictor model, c) ordinary kriging of species richness, and d) ordinary co-kriging (Kreft and Jetz 2007, Copyright 2007 year National Academy of Sciences).



Eonothem / Eon	Erathem / Era	System / Period	Series / Epoch	Stage / Age	GSSP	numerical age (Ma)
						present
Phanerozoic	Cenozoic	Quaternary	Holocene			0.0117
			Pleistocene	Upper		0.126
				Middle		0.781
				Calabrian		1.8
				Gelasian		2.5
		Neogene	Pliocene	Piacenzian		3.6
				Zanclean		5.333
			Miocene	Messinian		7.246
				Tortonian		11.62
				Serravallian		13.82
				Langhian		15.97
				Burdigalian		20.44
				Aquitanian		23.03
		Paleogene	Oligocene	Chattian		28.1
				Ruppellan		33.9
			Eocene	Priabonian		38
				Bartonian		41.3
				Lutetian		47.8
				Ypresian		56
			Paleocene	Thanetian		59.2
				Selandian		61.6
				Danian		66

Figure 1.3. Excerpt of the current International Chronostratigraphic Chart 2014 showing the geological periods of the last 66 Ma.
Redrawn and adapted from Cohen et al. (2013, updated in 2014).

1.2.2. A matter of scale

The validity of the above-mentioned hypotheses strongly depends on the temporal (period and duration) and spatial (e.g. global, continental, regional) scales. Massive species extinction, contraction and biome fragmentation have arisen since the Jurassic (200 Ma BP), due to continent drift, tectonic activity and successive episodes of glaciation. Tectonic activity, along with climate variations from the Paleogene[1] to the Quaternary periods, would have also broadly influenced biomes distribution (Hardy et al. 2013). In particular, tropical biomes would have derived from refuges dating to those contraction phases (Crame 2001, Richardson et al. 2001). Refuges would have, therefore, constituted new sites for speciation and diversification, as well as cradles for the colonization of higher latitudes by tropical species (Mittlebach et al. 2007).

At global scale, species diversity differs from one tropical region to another, with South and Central America holding the greatest diversity (Dirzo and Raven 2003). In comparison, African tropical moist forests are relatively poor, a deficit in diversity that could be explained by more accentuated disturbances during the late-Pleistocene (Baker and Couvreur 2013).

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[1] We chose to use here the most recent terminology of Cohen et al. 2013 (updated in 2014) that replaces the Tertiary by the Paleogene and Neogene periods.

At continental scale, or even at regional scale, climate plays a determinant role in the species composition of tropical forests (Field et al. 2009, Blach-Overgaard et al. 2010, Toledo et al. 2011, Fayolle et al. 2014b, Mannion et al. 2014), and in particular rainfall (Philips et al. 1994, Condit et al. 2004, Ouédraogo et al. 2016).

At a more local scale, intrinsic and extrinsic competition and dispersion processes come into play. Light availability has been described as being the most limiting variable for the establishment and the growth of tropical trees (Baker et al. 2003). According to Chazdon (1988), less than 2% of daylight reaches the ground, because of forest vertical stratification. The presence and number of gaps in the canopy contribute, therefore, to increase light availability (Brokaw 1987, Denslow et al. 1990). Previous research has also highlighted the role of substrate, soil and topography to explain beta-diversity in tropical forests (i.e. the comparison of species diversity in number of endemic taxa between ecosystems, or along environmental gradients; Pyke et al. 2001, Poulsen et al. 2006, Gourlet-Fleury et al. 2011, Fayolle et al. 2012). These factors could deeply influence tree species distribution (Condit et al. 2002, Hardy and Sonké 2004, John et al. 2007). In particular, edaphic factors have often been invoked as chiefly conditioning species distribution (Hall and Swaine 1981, Poulsen et al. 2006, Fayolle et al. 2012, Ouédraogo et al. 2016). Providing a study involving a high number of species, the percentage of soil-dependent species can range between 15 to 30% according to the type of tropical forest (Clark et al. 1999, Sollins 1998). Nonetheless, most of those works only relied on landscape criteria, such as topography and slope, or on existing soil classifications (Clark et al. 1998, 1999).

Other studies, by contrast, have for long proven the importance of chemical elements in species distribution (Sabatier et al. 1997, Sollins et al. 1998, Potts et al. 2002, John et al. 2007, Tuomisto et al. 2008). Such studies, requiring additional work regarding sample collection and lab analysis, have recently developed in African tropical contexts (e.g. Hall et al. 2004, Peh et al. 2011, Dedry 2012, Gorel 2012, Bourland 2013, Gillet 2013, Bourland et al. 2015, Vleminckx et al. 2016).

1.3. Central African forests

1.3.1. Diversity and endemism

Compared to America and Asia, central Africa holds the poorest plant diversity of the three tropical basins (Parmentier et al. 2007, Couvreur and Baker 2013). Two hypotheses could explain this specificity: 1) an impoverishment of plant diversity in Africa over time after an important loss of humid forest due to climate change (Pan et al. 2006, Kissling et al. 2012), or 2) at the opposite, an increasing in diversity in America and Asia because of a combined effect of tectonic and climate change (Backer and Couvreur 2013). Both hypotheses would not be mutually exclusive (Backer and Couvreur 2013).

Linder (2001) used the quadrat method to assess plant diversity and endemism in sub-Saharan Africa, where 1) diversity was the number of inventoried species among a selection of 2,000 ligneous species by 2.5°-side quadrats, and 2) endemism was expressed using an index (i.e. the number of times a species was present per quadrat, with values attributed to species). The results, in agreement with previous research (e.g. White 1983), have underlined strong variations in diversity and endemism in the African forests, with higher rates from Liberia to Sierra Leone, and from the Guinean Gulf to the Albertin Rift (Linder 2001).

Regarding species diversity, endemism and distribution, White's work (1983) still acts as a reference, because it has synthesized and interpreted previous studies (e.g. Robyns 1948, Monod 1957, Lebrun 1961, Aubréville 1962, Léonard 1965, Troupin 1966, Caballé 1978), and because it has invited to new research in tropical Africa (e.g. Boulvert 1986, Ndjele 1988, Linder et al. 2012, Fayolle et al. 2014b). White identified eight centers of endemism in Africa, separated by nine transition zones (***Figure 1.4***). In the framework of this PhD, we will focus on the Guineo-Congolian regional center of endemism, a floristic region (i.e. phytocoria) localized between 6°N and 6°S. According to White (1983), it would account for 80% of the endemic plant species, and stretches up to West Africa with nonetheless a separation formed by the Dahomey Gap (i.e. the transition zone between the Guineo-Congolian and the Sudanian regions, large of ca. 200 to 300 km; White 1979, Salzmann and Hoelzmann 2005). In addition, White (1983) proposed to split this center in three sub-centers of endemism, according to the presence of the Congo and Ubangi rivers, and the wide marches of the northern Congo Basin (see ***1.3.2.*** on vegetation, and ***Chapter 2*** relative to the study area): 1) the upper Guinean (from Sierra Leone to Ghana), 2) the lower Guinean (from southern Nigeria to the southwestern Republic of the Congo), and 3) the Congolian (covering essentially the current Democratic Republic of Congo, DRC).

1.3.2. Vegetation types in the Congo Basin

The Agreement at Yangambi (DRC) on the nomenclature of African vegetation types (Aubréville 1957) has constituted a major advance regarding the harmonization of former classifications, which were numerous, imprecise, and sometimes contradictory (e.g. Schimper 1935, Robyns 1948). A criticism has emerged from White (1983), however, who spoke in favor of a new classification accounting for the actual diversity of the Congo Basin, instead of an orientation favoring the vegetation types observed in West Africa only. White (1983) thus proposed four main groups of vegetation that were: 1) the secondary formations due to human impact, 2) the edaphic formations (e.g. the mangroves, or the grassy vegetation on hydromorphic soils), 3) the formations due to altitudinal variations > 1,000 m), and 4) the formations related to the Guineo-Congolian dense forests on *terra firma* soils. Among the latter, he defined four variants: 1) the costal hygrophilic evergreen forests, 2) the mixed humid semi-evergreen forests, 3) the monodominant humid evergreen and semi-evergreen forests, and 4) the outlying dry semi-evergreen forests.

In the Guineo-Congolian center of endemism, mixed semi-evergreen forests constitute, by far, the most important type in terms of surface covered. They are composed of evergreen and deciduous tree species that thrive with mean annual rainfall comprised between 1600 and 2000 mm. Deciduousness depends on the severity of the dry season, a character shared by numerous tall light-demanding tree species (see ***1.3.3***; White 1983). A recent study of Fayolle et al. (2016) demonstrated that semi-deciduous forests were constituted of taller trees than evergreen forests, with denser stands and a greater biomass.

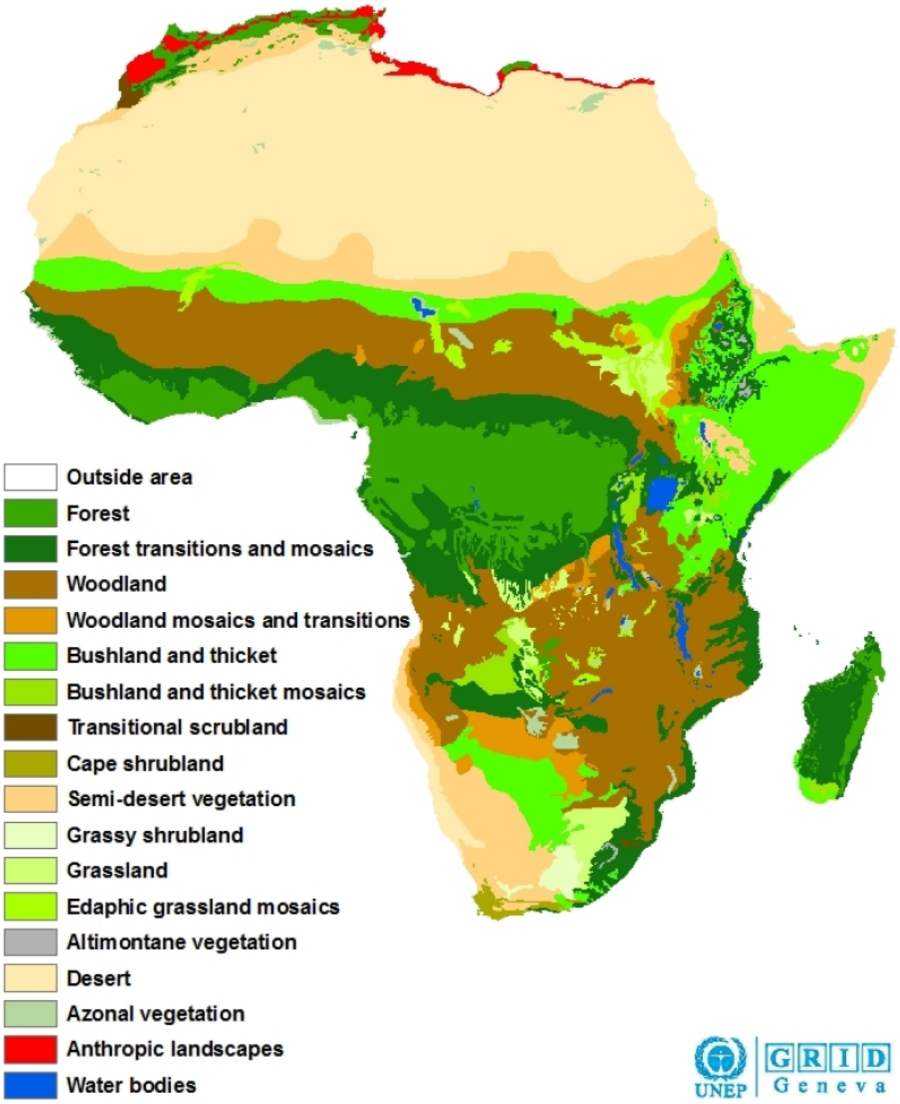


Figure 1.4. UNESCO/AETFAT/UNSO (White's) vegetation map of Africa.
The Guineo-Congolian regional center of endemism ("I" in White's classification) is indicated in medium green (labeled "Forest").
Source: http://geonetwork.grid.unep.ch/geonetwork/srv/en/metadata.show?uuid=cc2fbd96-ae4c-4593-910f-c103b1b51299

Moreover, an area of ca. 400-km wide, and located between 14° and 18°E, separates the Lower Guinean and Congolian sub-centers of endemism (White 1979). This zone west of the Ubangi River is commonly called the "Sangha River Interval" (hereafter SRI), and forms the meeting point and borders between southeastern Cameroon, the northern Republic of the Congo and the southern Central African Republic. It hosts, among others, marshes, flooded forests, and semi-evergreen vegetation (de Namur 1990). White (1979) described rainfall of the SRI as slightly lower than in the neighboring areas, and drew the conclusion that it could have been the case during the drier phases of the late-Pleistocene and the Holocene (see ***1.4. Climate***). Past climate changes could have lead to forest contraction and fragmentation, to the benefit of more open vegetation between the existing savannas of the Sudanese and Zambezian regions (Letouzey 1968, Maley 2001a, 2002). Differences in substrate and soil have also been invoked to explain the floristic peculiarities of the SRI: the presence of more sandy soils in the north, due to Carnot sandstones parent material (Boissezon et al. 1969, Gourlet-Fleury et al. 2011, Fayolle et al. 2012). Diversity and endemism seem to be poorer in this particular area (Fayolle et al. 2012). However, in-depth inventory and description of the flora only date to the very recent years (Gillet and Doucet 2012) because of difficulties relative to accessibility, and could have previously led to biased interpretations.

1.3.3. The case of light-demanding tree species

Moist mixed semi-evergreen forests are characterized by the presence of numerous tall light-demanding tree species, such as *Erythrophleum suaveolens* (Guill. & Perr.) Brenan (Guion 2012, Gillet 2012, Gorel et al. 2015), *Pericopsis elata* (Harms) Meeuwen (Bourland 2013, De Ridder et al. 2014, Bourland et al. 2015), *Terminalia superba* Engl. & Diels (De Ridder 2013, De Ridder et al. 2013a, 2013b), and *Triplochiton scleroxylon* K.Shum (Hédin 1930, Gorel 2012). Some of those species are not restricted to the mixed semi-evergreen forests, but they have an optimal growth in this type of environment (White 1983). In tropical Africa, light-demanding tree species are by far the most logged for timber (Doucet 2003, Ruiz Pérez et al. 2005), contributing to almost 85% of the annual wood production of the Congo Basin in the early 2000s (Ruiz Pérez et al. 2005, ATIBT 2012). Moreover, such emergent trees are often mentioned as useful trees. For instance, *Canarium schweinfurthii* Engl. and *Ricinodendron heudelotii* (Baill.) Pierre ex Heckel produce fruits that are consumed by people (Dounias and Hladik 1996, Mbida Mindzie et al. 2000, Fankap et al. 2001).

Their light-demanding character is more or less pronounced depending on their ecology (Doucet 2003). Following the work of Oldeman and van Dijk (1991), Doucet (2003) proposed a more precise classification based on development ranges, in which each species may know an optimal development. He defined three main categories for emergent trees: 1) the strict to moderate light-demanding tree species that are not able to regenerate without an important disturbance of the forest cover, 2) the semi-light-demanding tree species that need gaps in the canopy at one stage of their development, including the early phases, and 3) the shade-tolerant tree species that are able to root and grow in the forest shade (***Figure 1.5***). Recently, ecophysiological studies have refined ongoing classifications by precisely analyzing light-requirements species by species (see e.g. Biwolé 2015, Biwolé et al. 2015b for *Lophira alata*). Several emergent long-lived light-demanding tree species share common traits including deciduousness and anemochoria (Hawthorne 1995, Bénédet et al. 2013). This last trait can lead to a gregarious distribution of the stems, as exemplified by *Pericopsis elata* populations (Bourland 2013, Bourland et al. 2015) or *Triplochiton scleroxylon*.

Natural factors, such as soil characteristics and rainfall, have also been invoked to explain the particular geographic distribution of the light-demanding tree species (see e.g. Hall et al. 2004). Climate variations and soil fertility, for instance, could explain the spatial distribution of *Triplochiton scleroxylon* (Swaine 1996, Gorel 2012) and other light-demanding tree species (see Vleminckx et al. 2016 for southern Cameroon). Nonetheless, this is undoubtedly a trickier subject of discussion, implicating more than one cause.

Moreover, previous research in central Africa has stressed that several light-demanding tree populations were characterized by Gaussian distributions in their diameter, typical of a deficit in regeneration (Doucet 2003, Sepulchre et al. 2008). This could mean that few young stems root and grow, threatening both the viability of these tree populations and the sustainability of logging in case of timber species. Current timber exploitation is very selective, by logging tall trees only, but it also cut the best seed trees (Bourland 2013).

Paradoxically, the canopy gaps created by logging are usually not large enough for the establishment of young light-demanding timber trees (Doucet 2003), which constitutes a further obstacle to their natural regeneration. It seems, therefore, that in comparison with today, different conditions prevailed in the past, which were related to climatic and/or anthropogenic disturbances, and which favored these species (White 1983, Hart et al. 1989, Bourland 2013). It also appears that changes happened, at a date that remains to determine, which had deeply impacted tree regeneration.

Light-demanding trees mainly belong to secondary forests, which have been defined as surface of tree regrowth (Hédin 1930). The wide extend of this forest type adds support to the idea of past disturbances affecting tropical forests, and demystifies the assertion of landscapes entirely “virgin”, “intact”, or “primary”, notably from anthropogenic impact (Hart et al. 1996, Willis et al. 2004, Barton et al. 2012, and references therein, see also Wirth et al. 2009 who proposed a detailed review of the terminology used in the literature). In Cameroon, the broad presence of tree species from secondary forests has been attributed for long to slash-and-burn agriculture practiced by the local populations (Hédin 1930). Only a regular burning of the forest, in particular for agricultural purposes, could have modeled forest composition by increasing the amount of light-demanding species (Doucet 2003). Clearings have been described as being punctual and shifting, and usually sparing useful and tall trees, including light-demanding trees (Hédin 1930, Carrière 1999, 2002, Carrière et al. 2002). This observation meets the “intermediate disturbance hypothesis”, well-explained by Molino and Sabatier (2001), whose research in French Guiana, using different disturbance intensities, has showed that intermediate disturbance levels, including post-logging regrowth, resulted in high species richness and the long-term maintenance of pioneer and light-demanding species (see also Gourlet-Fleury et al. 2013).

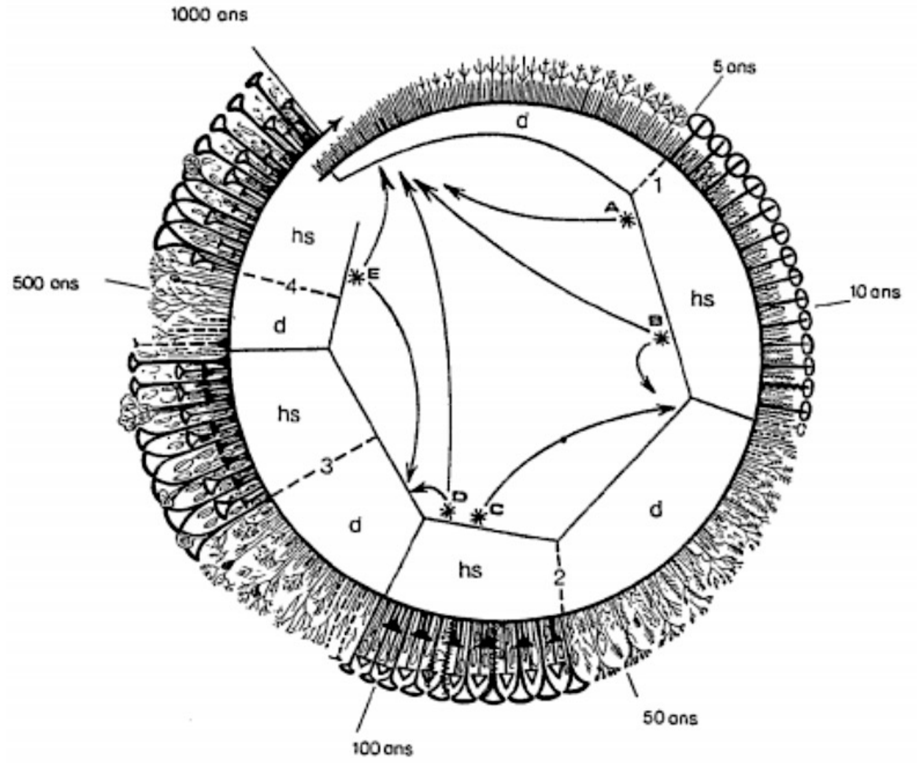


Figure 1.5. Sylvigenetic cycle showing the different stages of forest development over time, including the regeneration in open areas, the growth, the maturity and the decline of the forest trees (after Hallé et al. 1978).

1.4. Past and current climate change in central African moist forests

The constitution of current landscapes derives from a long history of climatic fluctuations, more particularly during the Quaternary (***Figure 1.3***), characterized by alternate cycles of glaciation and interglaciations in the northern hemisphere (Start and Prell 1984, Maley 1996, Ruddiman 2007), whose cold spells have also driven retraction and distribution shifts on the northern fauna and flora (Petit et al. 2002, Willis and Andel 2004). This alternation was caused by Milankovitch cycles that are variations of orbital parameters entailing shifts, of more or less long duration, in the amounts of solar radiations distributed on earth (Hays et al. 1976, Imbrie and Imbrie 1980, Dansgaard et al. 1993, Bond et al. 1997, 2001).

These climate anomalies have also had significant repercussions on lower altitudes, as the northern cooling resulted in an increasing aridity in the southern hemisphere (Maley and Brenac 1998, Maley 2001b, Marchant and Hooghiemstra 2004, Mayewski et al. 2004, Gasse et al. 2008, Wanner et al. 2011). During the cooler and drier phases, large areas of the African continent were covered by montane forests, which encircled forest patches resulting from particular geographic situations (e.g. higher temperature and moisture along rivers; White 1993, 2001, Maley 1996, 2004, Maley and Brenac 1998, Sosef 1996, Leal 2001, 2004, Senterre 2005, Weldeab et al. 2007, Tchouto et al. 2009). Conversely, during interglaciation phases, forest has recolonized large regions from these so-called refuges (Senterre 2005), shuffling the cards of speciation and species expansion (Sosef 1994, 1996, Hardy et al. 2013).

1.4.1. From the Paleocene to the Pliocene: the emergence of current species

In central Africa, open vegetation prevailed during the first half of the Eocene (***Figure 1.3***), followed by the expansion of the first Fabaceae-dominated woodlands during the Eocene (since the Lutetian, ~47.8 Ma; Jacobs 2004). The tall tree species that we can observe today in the dense moist forest would only date to the end of the Lower Miocene (~23.03–16 Ma; Salard-Chebolfaeff and Dejax 1991, Jacobs 2004), with important morphological innovations dating to the Upper Miocene (~10 Ma; Plana 2004). The climatic fluctuations over time and the continental drift from the Paleogene (~65–23.03 Ma) to the Quaternary (~2.6 Ma to today) eras have largely determined biomes distribution on Earth, as well as the major lineages of the Angiosperms (Dynesius and Jansson 2000, Plana 2004). Tropical forests in Africa covered, indeed, 22 million of km^2 during the Eocene (~56–33.9 Ma), 15 million of km^2 during the Miocene (~23.03–5.333 Ma), 10 million of km^2 during the Pliocene (~5.333–2.58 Ma), and 3.4 million of km^2 during the Holocene (after ~11 ka), which corresponds to current situation (Kissling et al. 2012).

The cooling and drying of the Paleogene and Neogene have led to a strong reduction of the tropical forest surfaces (Boltenhagen et al. 1985). Moist forest species have thus been identified as relicts dated to the Paleogene and Neogene transition (Plana 2004). The speciation in large and morphologically homogeneous groups (e.g. the Fabaceae) dated to this Miocene period (Plana 2004). The alternation between glacial and interglacial episodes is a characteristic of the Quaternary. Nine of the glacial have been estimated to be decisive in the process of forest fragmentation (Hamilton 1982, Hamilton and Taylor 1991, Sosef 1994). In particular, tropical forests have suffered from the glacial extension from the end of the Middle- (~0.781–0.126 Ma) to the Upper Pleistocene (~0.126–0.0117 Ma) (Maley 1996).

1.4.2. The Pleistocene: glaciation, general refuge theory and controversies

Modification of the vegetation during the Pleistocene have been demonstrated in several sites using proxies such as pollen, carbon and oxygen isotopes, and phytoliths (Richards 1986, Vincens et al. 1994, 1998, Reynaud-Farrera et al. 1996, Elenga et al. 1992, 1994, 1996, 2001, 2004, Maley and Brenac 1998, Thomas 2008, Bayon et al. 2012a, 2012b, Lézine and McKey 2013, Lézine et al. 2013). In this field, lake Barombi Mbo in Cameroon still acts as a reference (Maley and Brenac 1998, Maley 2001a; ***Figure 1.6***). Its pollen curve has showed, indeed, a period of relative stability of the forest between ~25.8 and 21 ka (end of the Lower Pleistocene), with a high rate of arboreal pollen, and specifically of evergreen species belonging to the Caesalpiniaceae sub-family (Fabaceae). Forest regression has occurred between ~20 and 11 ka, due to the cooler and drier conditions that prevailed during the Last Glacial Maximum (~19–14 ka; Dechamps et al. 1988, Maley 1996, Maley and Brenac 1998, Gasse 2000, Oslisly 2001). This period was characterized by higher rates of grass pollen (Poaceae and Cyperacea), which corresponded to open forest formations and meadows (Bonnefille 2011). Grassy vegetation was at its maximum around 15 ka. With the advent of the Holocene (since ~11 ka), forest vegetation expanded again, with peaks of pioneer species (e.g. *Musanga* sp. and *Macaranga* spp.) representing up to 30% of the total identified pollen.

During the Last Glacial Maximum, forest patches have persisted in areas called “refuges”, which were separated from each other by large savannas (Leal 2004, Hardy et al. 2013; ***Figure 1.7***). The refuge theory postulates that forest has retreated from certain regions, whereas others have been spared. This means: 1) the opening of dry pathways between certain islands and coasts due to marine regression, 2) the descent downslope of montane and submontane vegetation, 3) the shrinkage of the forest massif and the disappearance of tall trees at the favor of grassy vegetation, 4) the maintenance of the forest in river galleries and humid basins, and 5) the potential extinction of certain species (Plana 2004). In this framework, mountain areas have been targeted as refuges, including the Cameroon line (i.e. the volcanic islands of the Guinean Gulf to the lake Chad basin) and the Albertan Rift, at the exception of the wide refuge of the Congo Basin (Colyn et al. 1991, Maley et al. 1996, Maley and Brenac 1998). These forest refuges have remained little affected by the subsequent climatic fluctuations, and as they are considered species-rich biomes, they experience peculiar attention regarding their management (White 1983, Küper et al. 2004, Tchouto et al. 2009).

Nonetheless, the refuge theory has raised several issues. Their geographic localization has been first assessed using patterns of species richness and endemism (e.g. Van Rompaey 1993, 1996, Sosef 1994, 1996, Linder 2001, Senterre 2005, Tchouto et al. 2009), then using patterns of intraspecific genetic diversity (Daïnou et al. 2010, Dauby et al. 2010, Debout et al. 2010), the latter leading to controversial results (see Hardy et al. 2013). Indeed, the localization and extent of these forest refuges differ between publications (e.g. Maley 1996, 2001b, Sosef 1996, Léal 2001, Anhuf et al. 2006, Tchouto et al. 2009; ***Figure 1.7***) At the moment, it seems still difficult to know if the refuges have acted as source of new species (including the processes of an allopatric speciation between fragmented populations), or as a reservoir that would have accumulated species, with a low extinction rate during relative climatic stability (Plana 2004, Provan and Bennett 2008).

Thanks to their phylogeographic comparison, Hardy et al. (2013) drew three important conclusions regarding past refuge areas: 1) the specificities of a particular habitat could have induced a high rate of endemism, 2) there is still little information concerning the extent of forest fragmentation and the localization of these fragments, thus challenging the common belief of a changing distribution of the forest massif over time, and 3) the dimension and localization of the refuge areas could have changed, with regard to forest heterogeneity and species autecology and, therefore, species survival abilities (but see Webb and Peart 2000).

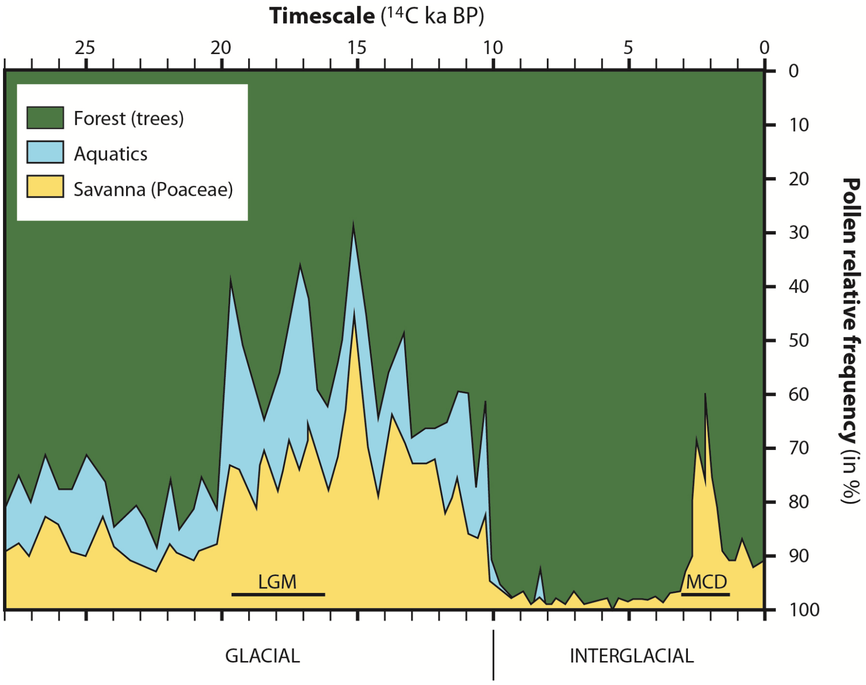


Figure 1.6. Vegetation dynamics during the last 28 ka BP at lake Barombi Mbo (Cameroon), using the relative frequencies between arboreal (trees), aquatic (Cyperaceae), and grass (Poaceae) pollen.

The relative frequencies (y axe, in %) were calculated according to the total pollen for the identified taxa, the spores excluded (redrawn after Maley and Brenac 1998, and Maley 2001a). A major climatic disturbance (MCD) could be seen around 2500 BP (see also 1.4.3 relative to the Holocene). LGM: Late Glacial Maximum.

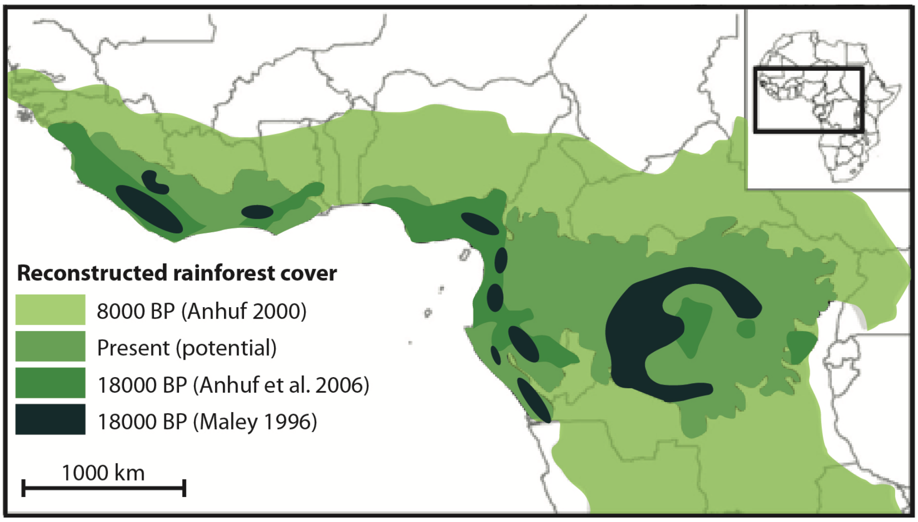


Figure 1.7. Changes in the hypothetic distribution of the Guineo-Congolian forest for the last 18 ka BP.

The extent and localization of refuge areas during the Last Glacial Maximum (LGM) differ between publications (redrawn after Hardy et al. 2013; citing Anhuf 2000, Anhuf et al. 2006, and Maley 1996).

1.4.3. The Holocene: climatic fluctuations and human migrations in the African forests

The Holocene (since ~11 ka) corresponds to the current Quaternary interglaciation period. Global warming that has arisen just before and during the Holocene (~14.8–5.5 ka), and called the “African Humid Period”, started with the last Heinrich event (i.e. a natural and massive discharge of icebergs leading to a release of great amounts of fresh water in the North Atlantic ocean, and a change in the thermohaline circulation; Bond et al. 1992, Broecker et al. 1992, deMenocal et al. 2000). This wetter period was itself interrupted by a short dry period call the “Younger Dryas” (~12.5–11.5 ka; Gasse 2000). The general warmer climate of the Holocene, compared to the previous Pleistocene period, suits vegetation expansion in Africa, which was at its maximum during the African Humid Period (~8–4 ka; DeMenocal et al. 2000, Hély et al. 2009, Vincens et al. 2010, Lézine et al. 2013, Willis et al. 2013). However, it also raises issues regarding current global change and its future evolutions (Willis and Birks 2006, Willis et al. 2007, 2010).

Subsequently, major climatic disturbances occurred between 4 and 2 ka, which provoked massive destruction of the central African forests (Maley 1992, 2001a, 2002, Maley and Brenac 1998, Maley 2004, Ngomanda et al. 2009a, 2009b, Lézine and McKey 2013, Lézine et al. 2013). The first event was centered around 2.8–2.5 ka in regard of a peak of Poaceae during this period, confirming the expansion of a grassy landscape to the expense of woodlands (***Figure 1.6***; Elenga et al. 1996, Maley and Brenac 1998). This also led to the creation of the Dahomey Gap in Togo and Benin (Salzmann and Hoelzmann 2005, Hély et al. 2009). This event would have caused important human migrations, because of the hyperarid conditions that prevailed in the Sahara, which forced people to become more mobile (Ngomanda et al. 2009b).

This was followed by a more destructive event between ~2.5–2 ka, which opened the core of the tropical forest (Maley and Brenac 1998, Maley 2004, Elenga et al. 2004, Ngomanda et al. 2009a, 2009b, Neumann et al. 2012a, 2012b). This event was characterized by a more pronounced seasonality, with catastrophic rainfall during the wet season and a drier and longer dry season (Elenga et al. 2004, Weldeab et al. 2007, Ngomanda et al. 2009b, Neumann et al. 2012a, 2012b). This would have created a savanna corridor from Cameroon to Angola, which allowed human communities to access areas they could not reach before (Maley 2001, 2004, Neumann et al. 2012a, 2012b, Lézine et al. 2013, Oslisly et al. 2013b; see ***1.5. Archaeology***). Using a linguistic analysis based on the vernacular names of the pioneer trees *Musanga cecropioides* R.Br., *Elaeis guineensis* Jacq., and *Canarium schweinfurthii*, Bostoen et al. (2013) showed, besides, that the way the forest retreated after 2.5 ka influenced the dispersion of the Bantu languages. It is worth mentioning here that new works have recently refined previous results by separating the 2.5-ka-event from another dramatic event centered around 4 ka BP (Lézine and McKey 2013, Lézine et al. 2013, Maley et al. in press, J. Maley pers. com.)

Since 2 ka until today, more stable conditions returned, as shown by arboreal pollen taking the precedence on grass pollen, leading to a new forest expansion in the Congo Basin (Elenga et al. 1996, Fairhead and Leach 1998, Maley and Brenac 1998, Vincens et al. 1998, Maley 1999, Elenga et al. 2004). The savanna surface still remained wide, and the subsequent decadal climatic fluctuations of the last 1,000 years could have affected the vegetation. In particular, the Medieval Climate Anomaly (~1.1 ka–0.7 ka) was characterized by a drier climate in the tropical regions (Verschuren et al. 2000, Verschuren and Charman 2008, Mayewski et al. 2004, Ngomanda et al. 2007). The same way, the Little Ice Age (~0.6–0.2 ka) induced a drier climate in western central Africa (Ngomanda et al. 2007, Russell and

Johnson 2007, Lane et al. 2011), though it was slightly wetter in east Africa due to differences between the western and eastern monsoon regimes (Verschuren et al. 2000, Russell and Johnson 2007).

Bayon et al. (2012a) recently reopened a hot debate concerning the impact of climate vs. human on the African tropical vegetation (see also Bayon et al. 2012b, Neumann et al. 2012b, Maley et al. 2012). Based on a geochemical analysis, the authors stated that anthropogenic activities have more impacted the forest cover during the Holocene than climate did (Bayon et al. 2012a). By reaffirming their expertise on this topic using numerous paleoenvironmental and archaeological examples, Maley et al. (2012) and Neumann et al. (2012b) demonstrated, conversely, that even if human activities have had a tangible effect on the African vegetation, the impact of climatic fluctuations has been greater and could not be challenged.

1.4.4. Global warming and its upcoming consequences

For more than thirty years, studies on greenhouse gas due to anthropogenic emissions have demonstrated Earth global warming (e.g. Petit 2001, Solomon et al. 2007). The increasing melting of the icecap, indeed, has lead to a rise of the sea level of about 0.25^{-1} cm per year between 2003 and 2009 (Gardner et al. 2013). Moreover, other climatic modifications have been also assessed, which were related to e.g. rainfall, atmospheric humidity, winds, radiations, vegetation composition, plant functioning (Lloyd and Farquhar 2008, Makarieva et al. 2009).

The experts of the Intergovernmental Panel on Climate Change (IPCC) proposed six scenarios of global warming including different level of societal evolutions and greenhouse gas emissions (Solomon et al. 2007, IPCC 2014), with a decisive choice between energy resources, either sustainable or fossil (Rocle 2009). Their results forecasted a global temperature increasing of between 1 and 2.9° C at the end of the 21th century, for the most optimistic scenario (B1), and of between 2.4° and 6.4° C, for the most pessimistic (AIF1) (Solomon et al. 2007, IPCC 2014; ***Figure 1.8***).

Contrasted results have emerged from the application of such scenarios. For instance, the African tropical forests would undergo stronger increasing in temperature and drying than in the other tropical basins (Lewis et al. 2004). By contrast, according to another study, Amazonia could be the most negatively affected by climate change (Zelazowski et al. 2011). The most optimistic scenario (i.e. an increase in temperature of 2°C) predicted an expansion of the forests at the end of the 21st century in the tropical basins, and particularly in Africa. By contrast, the most pessimistic scenario (i.e. an increase in temperature of 4°C) anticipated a contraction up to 40% of the dense moist forests due to the general drying of the continent (Solomon et al. 2007, Zelazowski et al. 2011; ***Figure 1.8***). The latter would lead to the hardly total opening of the SRI (Zelazowski et al. 2011).

Nevertheless, several authors called for caution regarding the use of such models (e.g. Hannah et al. 2011, Dynesius and Jansson 2000), as they are highly sensitive to approximation, and as it still seems difficult to apply past climatic fluctuations to predict future changes.

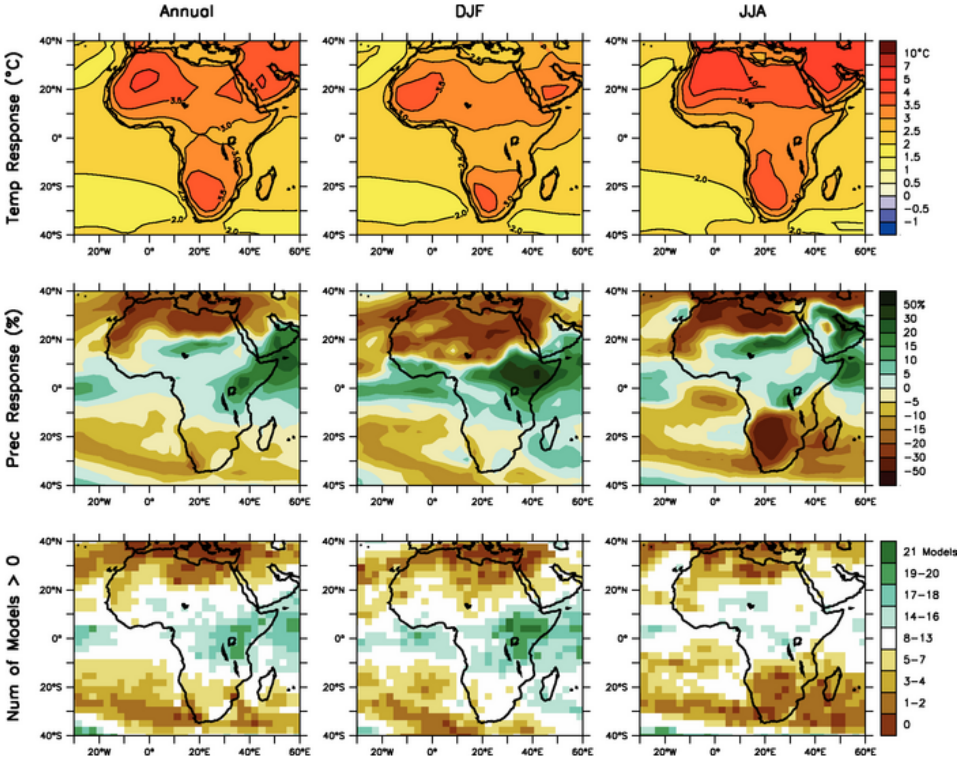


Figure 1.8. Temperature and precipitation changes over Africa from the MMD-A1B simulations. Top row: Annual mean, DJF (December, January, and February) and JJA (June, July, and August) temperature change between 1980 to 1999 and 2080 to 2099, averaged over 21 models. Middle row: same as top, but for fractional change in precipitation. Bottom row: number of models out of 21 that project increases in precipitation (Solomon et al. 2007).

1.5. Archaeological challenges in the Congo Basin

Tropical Africa has long suffered from a reputation of *terra incognita* (de Prédals 1950, Brion 1962). Indeed, maps on the geography and localization of human populations only date to the 19th century, and to its very end as far the Sangha River Interval is concerned compared to the Atlantic coast (Robineau 1967, Burnham 1996). Today, research on human presence in central Africa, and on its potential impact on the tropical forest, benefits from more and more results coming from different fields, among which anthropology, archaeology, linguistics, and genetics constitute primary data providers (e.g. Bahuchet and Guillaume 1979, Patin et al. 2009, Batini et al. 2011, Verdu and Destro-Bisol 2012, Bostoen et al. 2013, 2015, Grollemund et al. 2015, Kiahtipes 2016). In this part, we will present the main archaeological and historical periods defined for central Africa.

1.5.1. The Stone Age

The Stone Age in central Africa is separated into three periods: 1) the Early Stone Age (ESA), characterized by Oldowaï and Acheulean tools, and dated to 3.3 or 2.6. Ma (Klein 1999, Harmand et al. 2015), but with few age estimations of archaeological evidence in CAR (e.g. de Bayle des Hermens 1975, Gotilogue 2000), 2) the Middle Stone Age (MSA), dated to 200 ka BP to 40/50 ka BP in the central African forests (e.g. Cornelissen 2002, 2003, 2013, Barham and Mitchell 2008, Taylor 2011, 2014; R. Oslisly pers. com.), and 3) the Late Stone Age (LSA), characterized by microlithic and flake tool industries (Tshitolian tradition), since

40 ka BP, and that could constituted the first period of visible anthropogenic impacts on the landscapes (e.g. Shum Laka in Cameroon, Mosumu in Gabon, and the Ituri Forest in DRC; Mercader et al. 2000, Mercader and Brooks 2001, Lavachery 2001, Cornelissen 2002, 2003, 2013, Taylor 2014; see Oslisly et al. 2006 for a synthesis of the LSA industries. The Lupemban tradition either belongs to the MSA or the LSA depending on the regions (R. Oslisly pers. com.).

1.5.2. The Neolithic stage

In central Africa, the Neolithic period has been hardly documented (Oslisly et al. 2013b). In certain sites, it could separate the Stone Age from the Iron Age, with a transition dated to between 4 to 8 ka BP (Oslisly et al. 2013b). The definition of Neolithic relies on the evidence of domestication in the archaeological sites, stock (cattle, in particular) and crops (especially cereals) (Oliver and Fagan 1975). This innovative process has been first thought to originate from Egypt and the Near East (e.g. Murdock 1959), but its early presence in other hearths around the world (Willis et al. 2004), and in Africa in particular (Barton et al. 2012, Neumann et al. 2012a), is now attested and cannot be challenged.

The definition of Neolithic also includes the making and use of pottery (e.g. Shum Laka, date to 7 ka BP; Lavachery 2001), the first pyrotechnology before iron smelting. Several authors (e.g. de Pédrals 1950, Huysecom 1992, Gosselain 1995, 2000, 2002, Gallay et al. 1998, Livingstone Smith 2000a, 2000b, Mayor et al. 2011) described pottery as a technology exclusively made by women in western and central Africa, which well exemplifies the sexual division of labor in traditional societies (Dahlberg 1983, Testart 1985, Herbert 1993).

Vegeculture practiced in the vicinity of the forest villages is not excluded in the northern fringes of the Congo Basin, as well as the use of polished stone axes, hoes, adzes (Oliver and Fagan 1975), which could had long persisted and coexisted parallel to other lifestyles, including the use of iron metallurgy as well (Kay and Kaplan 2015). It seems, therefore, that the Stone Age to Iron Age transition includes more than one elements belonging to all cultural periods (Oslisly 2001, Diamond and Bellwood 2003, de Maret 2005, Kiahtipes 2016).

1.5.3. The Early Iron Age

This period would have started in relationship with major climatic disturbances centered around 4000 BP (Maley et al. in press, J. Maley pers. com.) and 2500 BP (see ***1.4. Climate***) that opened the forest cover. Populations of Bantu-speakers have come from the north and move into the forest (Diamond and Bellwood 2003, Phillipson 2005, Livingstone Smith 2007), possibly in search for new lands to cultivate (Vansina 1995, Clist 2005).

Vansina (1990) described two migration waves that populations of Bantu-speakers (Phillipson 2005) have followed between 4000 and 2000 BP: the first westwards, and the second eastwards, the latter restricted to the margins of the Congo Basin (***Figure 1.9***). Between 2900 and 2600 BP, the western Pygmy people has split into sub-groups, possibly because they have fled before the Bantu waves (Verdu et al. 2009). Vansina (1991) stressed that the expansion process would have been slow and progressive, and could follow kinship rules related to birthright and succession, leading to the split and moving of family groups to a few kilometers apart (Vansina 1995).

Between 2500 and 2000 BP, the Bantu people has progressively introduced iron smelting in the Congo Basin (Greenberg 1972, Schwartz 1992, Newman 1995, Phillipson 2005), a technology that allowed the creation of more efficient tools for clearing and cultivation, such as axes and hoes. The actual impact of the iron smelting on the forest, i.e. the logging for charcoal production to feed the furnaces, remains largely debated (Goucher 1981, Pinçon 1990, Bayon et al. 2012a, Neumann et al. 2012b, Lupo et al. 2015).

They have concomitantly participated to the expansion of shifting agriculture (Wilkie and Curran 1993, Stahl 2004), whose remnants could correspond to the charcoal layers found in soils that were mainly dated to between 2500 and 1500 BP (Gillet and Doucet 2013). For the first time, human populations have left their mark in their environment through their activities (van Gemerden et al. 2003, Brncic et al. 2007), amplifying to some extent the effects of major climatic changes (Maley and Brenac 1998, Maley 2000; see ***1.4 Climate***). Following a feedback loop, these forest clearings would also have widened the settlement of human populations within the forest (Schwartz 1992, Maley 2002, Neumann et al. 2012b, Bostoen et al. 2013, Gillet and Doucet 2013).

These Bantu populations have thus introduced slash-and-burn shifting agriculture further inland, in the favor of more open forest (Neumann et al. 2012a). The drier climate would also have allowed pearl millet cultivation (*Pennisetum glaucum* (L.) R. Br.), a crop traditionally grown in the Sudano-salhelian region (Neumann et al. 2012a, Ngomanda et al. 2009b), reinforcing the hypothesis of people coming from the “Grassfields”, a region located at current border between Nigeria and Cameroon (Collett 1982, Schwartz 1992, Maley 1992, Lavachery 2003, Quintana-Murci et al. 2008, Maley et al. 2012). It is worth noting that the more humid conditions that prevail today hinder such crop cultivation (Neumann et al. 2012a). A more marked seasonality would also have favored edible roots, tubers, corms, and other plants with underground storage organs, increasing, therefore, forest carrying capacity to the benefit of the newcomers (Piperno and Pearsall 1998). Additional resources, such as naturally growing fruits, non-timber forest products, game and fish, should be mentioned here and exemplified the food diversification of past populations (Neumann et al. 2012b).

1.5.4. An intriguing lack of human settlements

Oslisly (1995) first identified a gap between ~1300 and 600 BP following the Early Iron Age period, which has more particularly affected the tropical region. The compilation made by Wotzka (2006) of all available radiocarbon ages confirmed this hiatus (***Figure 1.10***). This has thus followed the Early Iron Age, and at the moment, it looks like a “Dark Age” that well illustrates the non-linear processes in central Africa’s history (Refrew and Bahn 2005).

This gap has been interpreted as a collapse of human occupation, whose pattern has been recently confirmed by Oslisly et al. (2013a, 2013b) regarding western central Africa. What has caused this hiatus remains to be determined, but two main hypotheses have been suggested that can be synthesized as follows: 1) a demographic drop due to the indirect effects of a more humid climatic episode, which could include lethal pandemic diseases (Oslisly 1998, 2001), among which bubonic plague (Oslisly 1998), malaria and trypanosomiasis (R. Oslisly pers. com.); 2) a degradation of the anthropogenic evidence due to taphonomic processes, including weathering, erosion, oxidation, and dissolution due to the acidic tropical soils (Surovell and Brantingham 2007). Both hypotheses are not exclusive, but archaeologists give less credit to the second one (R. Oslisly and A. Livingstone-Smith pers. com.)

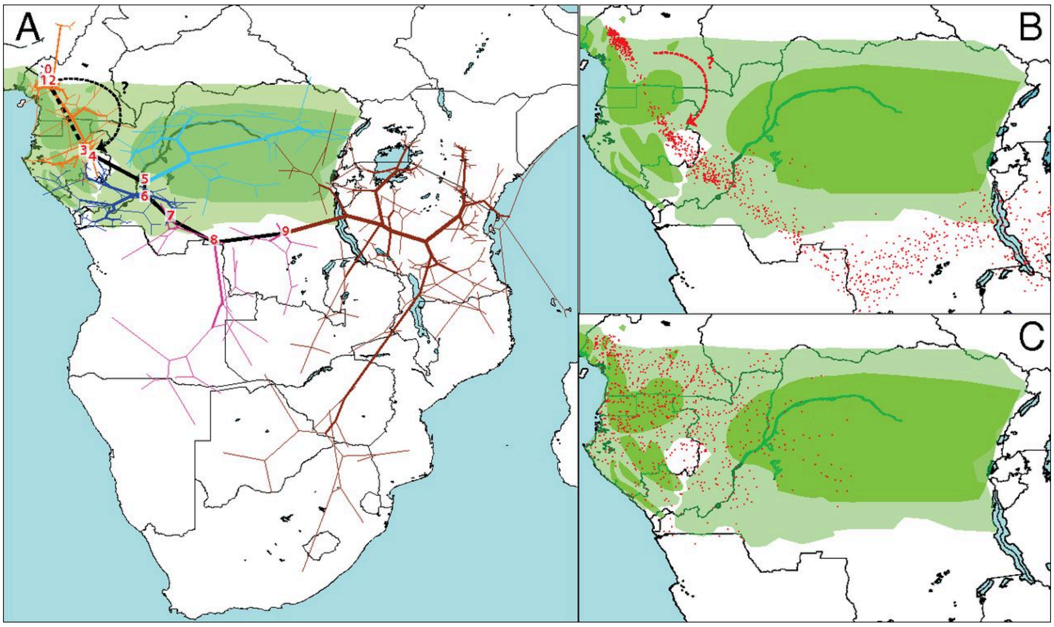


Figure 1.9. Ancestral migration route reconstruction.
(A) Ancestral migration route reconstructed on consensus tree by using geographical locations of contemporary languages and connecting ancestral locations by straight lines (true route will differ). Numbered positions correspond to nodes on the consensus tree. Curved dashed line indicates suggested migration route through savanna corridors (B). Lighter green shading corresponds to the delimitation of the rainforest at 5000 BP; the darker geen corresponds to the delimitation of the rainforest at 2500 BP. (B) Map showing the ancestral locations of the backbone node for the 100 trees in the Bayesian posterior sample; curved arrow is suggested route for the early migration based on a small number of reconstructed points that fall in rainforest. (C) Same as (B) but showing the ancestral locations of random migration routes for nodes 0–8 (After Grollemund et al. 2015).

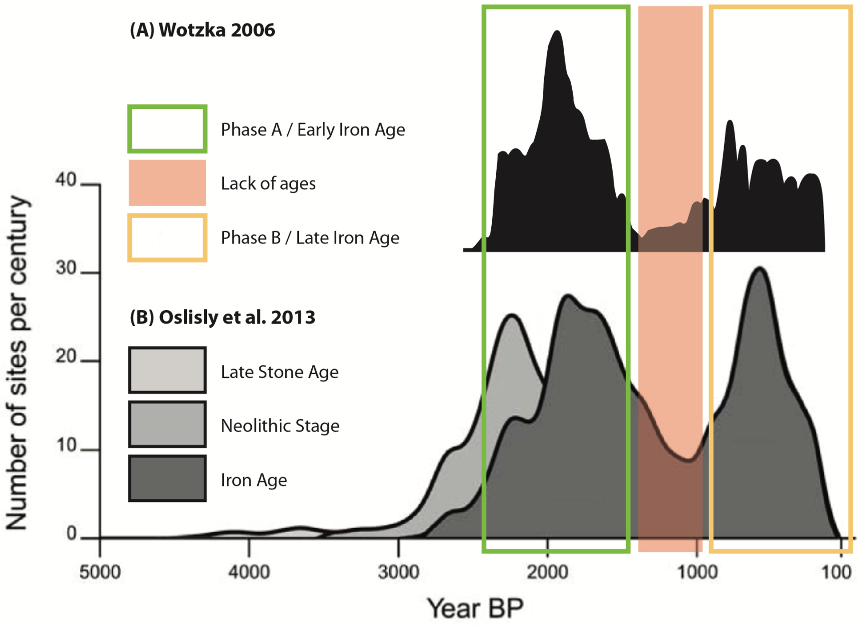


Figure 1.10. Comparison between the results of Wotzka (2006) and Oslisly et al. (2013b) based on radiocarbon ages in western central Africa.
(A) After Wotzka (2006); (B) Census of 585 ages for the last 5000 years BP, and corresponding cultural traditions (Oslisly et al. 2013b). Both curves underline an intermediate lack of ages between (~1300 and 600 BP; orange) corresponding to between Phase A (green, since 2500 BP) and Phase B (yellow) of the Iron Age.

1.5.5. The Late Iron Age

After this hiatus phase, people have progressively reinvested the dense moist forest, until the arrival of the European colonists. This last wave of settlement would have played an important role in shaping the forest landscape we know today, by impacting both forest structure and composition (Oslisly et al. 2013a, 2013b). Nonetheless, a precise chronology refining this phase of human expansion is still lacking, as research has more focused on the Early Iron Age period (Kiahtipes 2016).

Important amounts of charcoal have been found in the forest soils, especially after around 650 BP, up to the most recent times, supporting the hypothesis of a recent origin of light-demanding tree populations (Gruslin 2009, Guion 2011, Gorel 2012, Gillet 2013, Gillet and Doucet 2013, Bourland 2013, Bourland et al. 2015, Biwolé 2015, Biwolé et al. 2015a).

1.5.6. Since the colonial period

Indeed, since the 15th century (Köhler 2005, Gendreau 2010), the impact of the European presence could have buffer our perception of human cultures and activities in tropical Africa (Kiahtipes 2016). In particular, the history of the Europeans, through the Atlantic slave trade, then the establishment of concessionary companies using forced labor in the 19th century (Vennetier 1963, Burnham 1996), and finally the colonial administration, is intrinsically tied to the history of local forest people (Kiahtipes 2016).

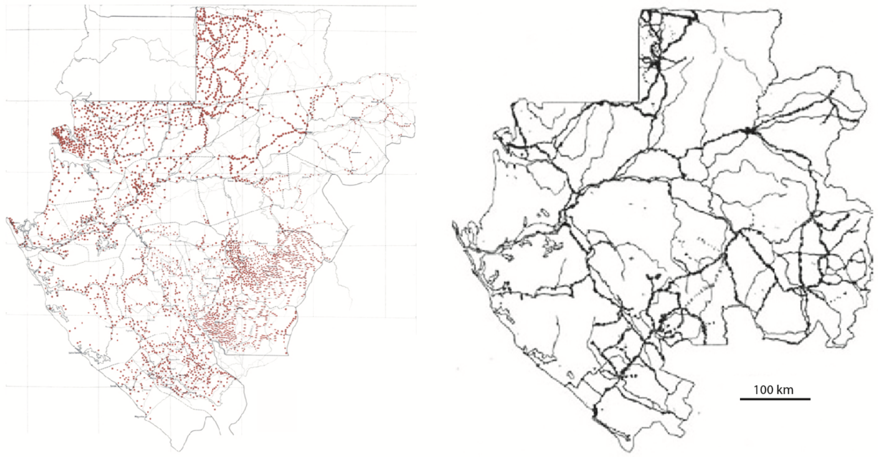
During the Triangular Trade, for instance, populations have been extracted from the forest (Köhler 2005), a phenomenon more intensive to the Atlantic coast but that had consequences further inland, as it induced the flight of entire groups southwards in the forest (Vennetier 1963, Burnham 1996). Forced labor and new diseases outbreaks have also decimated people until the end of slavery (Robineau 1967, Runge and Nguimalet 2005, Runge 2008, Runge et al. 2014).

The colonial rule has chiefly introduced the administration of the local populations (Vennetier 1963, Robineau 1967). In particular, this has resulted in the gathering of their settlements along the main communication axes, roads and rivers (Thiéry et al. 1945, Franqueville 1968, Laidet and Goulin 1974, Pourtier 1989, Clist 1995; ***Figure 1.11***), carrying on this way the undertaking of Arab populations several years before (Vansina 1990). The purpose was to better control and manage whole territories and local production (Geschiere 1982, Leplaideur 1985, Clist 1995, van den Berg and Biesbrouck 2000, Coquery-Vidrovitch 2001, Köhler 2005). The German regime even forbade people migrations, without taking into account families and lineages (van den Berg and Biesbrouck 2000). This lead to an increasing impact of land-use in the vicinity of the villages and along these roads (van den Berg and Biesbrouck 2000) that can still be observed today (Laporte et al. 2007, Gond et al. 2013, Aleman et al. 2013).

At the beginning of the 20th century, people were involved in major works projects (e.g. the railroad crossing the current Rep. of the Congo and Gabon) and in the colonial trade (Pourtier 1989, Vennetier 1963, Robineau 1967). They usually suffered from starvation (as exemplified by the colonial projects in the Great Lakes region at the end of the 19th century (Coquery-Vidrovitch 2001). *Funtumia elastica* (Preuss) Stapf has been a primary resource of natural rubber in southeastern Cameroon, implicating much labor force (Hédin 1930).

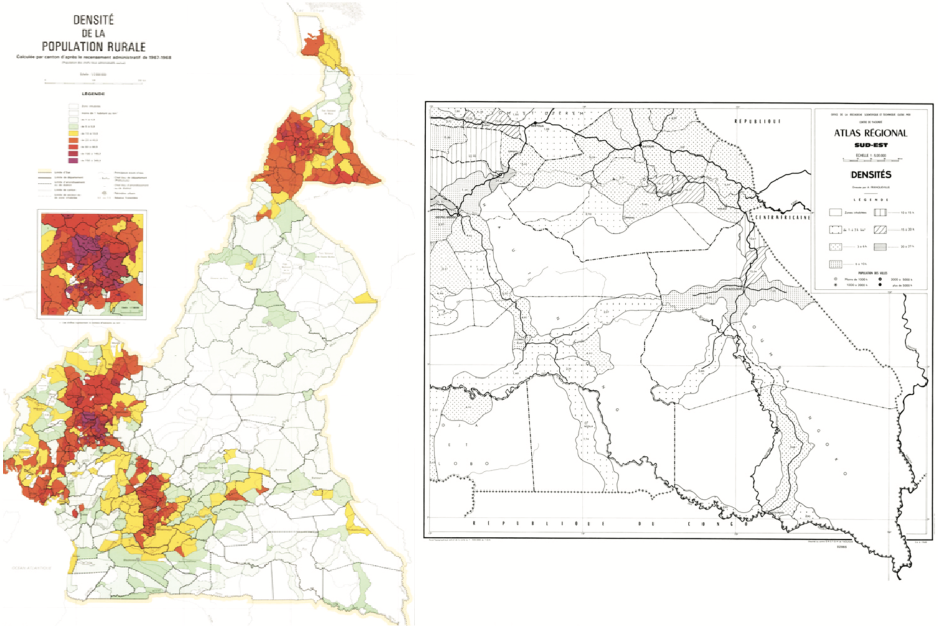
In the 1930s, Hédin (1930) reported dense human population in certain areas, notably close to cities such as Yaoundé (22 inhabitants/km^2), and locally degraded forests. Further inland, secondary forests were less present because of a lower population density (< five inhabitants/km^2 in the region of Ebolowa, and in the East close to Lomié and Yokadouma). The author described Boulou, Pahouin, Yaoundé, and Bakoko people as good land clearers and loggers (Hédin 1930).

Finally, rural exodus for the major works has been a great concern regarding the possibility to feed an increasing population without people for food production (Lotte 1953).



(A) Gabon in 1944

(B) Gabon in 1970



(C) Cameroon in 1967-1968

(D) Southeastern Cameroon in 1968

Figure 1.11. Population density and distribution in Gabon (A, B) and in Cameroon (C, D). (A) Population density and distribution in 1944 in Gabon (Énard 1944), and (B) in 1970 (Pourtier 1989). One point corresponds to 100 inhabitants; (C) Rural population density in 1967–1968 in Cameroon, from white (uninhabited) to purple (150–349.9 inhabitants/km^2) (Laidet and Goulin 1974) ; (D) Population density in southeastern Cameroon in 1968, white (uninhabited), dots (1–10 inhabitants/km^2), and stripes (10–27 inhabitants/km^2) (Franqueville 1968).

1.6. Current knowledge gaps

This review of the archaeological data has showed that the anthropogenic impact on the dense forest has only been discernable with the introduction of food production, and of shifting agriculture in particular. The climatic disturbances of the late-Holocene have chiefly opened the canopy, allowing the expansion of human populations within the forest, in landscapes suitable for crop agriculture (Neumann et al. 2012a, 2012b, Maley et al. 2012, Bostoen et al. 2013, Grollemund et al. 2015). By their cultural practices, people have only amplified the consequences of climate.

Several knowledge gaps have emerged, however, from this review, both in time and space:

1) The chronology faces too few radiocarbon ages and ages concentrated to the same sites and/or same regions. Conversely, whole regions have not been dated yet. Early archaeological phases such as the Neolithic that remains little documented. A hiatus phase of human occupation has been identified between 1300 and 600 BP, but its actual causes remain to be determined;

2) The geographic distribution of the archaeological sites shows concentrations, but at the reverse, little surveyed regions, and even entire archaeologically blank areas, all denoting an uneven treatment of the archaeological research in tropical Africa. This state of affairs could ensue from numerous difficulties, including too little human and financial resources, fieldwork accessibility, and a lack of methods adapted to the particularities of the tropical forests;

3) It remains difficulty to establish a cause-effect relationship between past human history, the presence of many old-growth light-demanding trees in the forests, and the current lack of young stems in their populations. Doucet (2003) first raised the hypothesis of a change regarding land-use since the colonization era (see also Kiahtipes 2016), and of its inherent emptying of the forest, to explain the senescing of light-demanding tree populations.

1.7. Objectives

In this PhD, we used a multidisciplinary approach, combining paleoecological, archaeological and ecological tools, in order to identify the factors of past transformations that affected vegetation in the northern Congo Basin. In this region, indeed, information remains fragmentary and scattered, especially regarding the human activities of the late-Holocene (2500 BP to the present), their consequences on the forest landscapes, and especially on light-demanding tree species. Did past human activities deeply impact the forest cover in regard to climatic events? Did all types of land-use affect tropical forests the same way? What was their ground surface area? What was the resilience capacity of forests and tree species after disturbance? Can an assessment of historical events help us understanding what happened to light-demanding tree species? Could results from past situations shed light on current and future silvicultural practices? All our interrogations can be summed up into these three research questions:

1) **What is the chronology of human presence in the northern Congo Basin**, and using what kind of evidence?

2) **What types of activities did people practice during the past**, what were their magnitude, severity, and potential impact on the forest cover?

3) **How old are current light-demanding long-lived tree populations**, and what could have been the causes of their current depletion?

The main objective of this PhD is to understand the impact of past human disturbances on the structure and composition of central African moist forests, using the particular case of light-demanding trees, during the late Holocene (after 2500 yrs BP).

1.8. Outline

The present PhD presents the results obtained using different research approaches (paleoecology, archaeology, history, dendrology, and forest ecology), and is articulated around four chapters, followed by a general conclusion (Chapter 6).

Chapter 2 introduces the materials and methods used, along with the study area in its multiple scales (i.e. local to regional).

Chapter 3 presents an assessment of new archaeological discoveries in the northern Congo Basin and their chronology (article published in *Radiocarbon*).

Chapter 4 deals with a systematic fieldwork method based on charred macrobotanical remains in two areas of southern Cameroon, so as to document at high resolution the spatial patterns of human activities (article published in *The Holocene*).

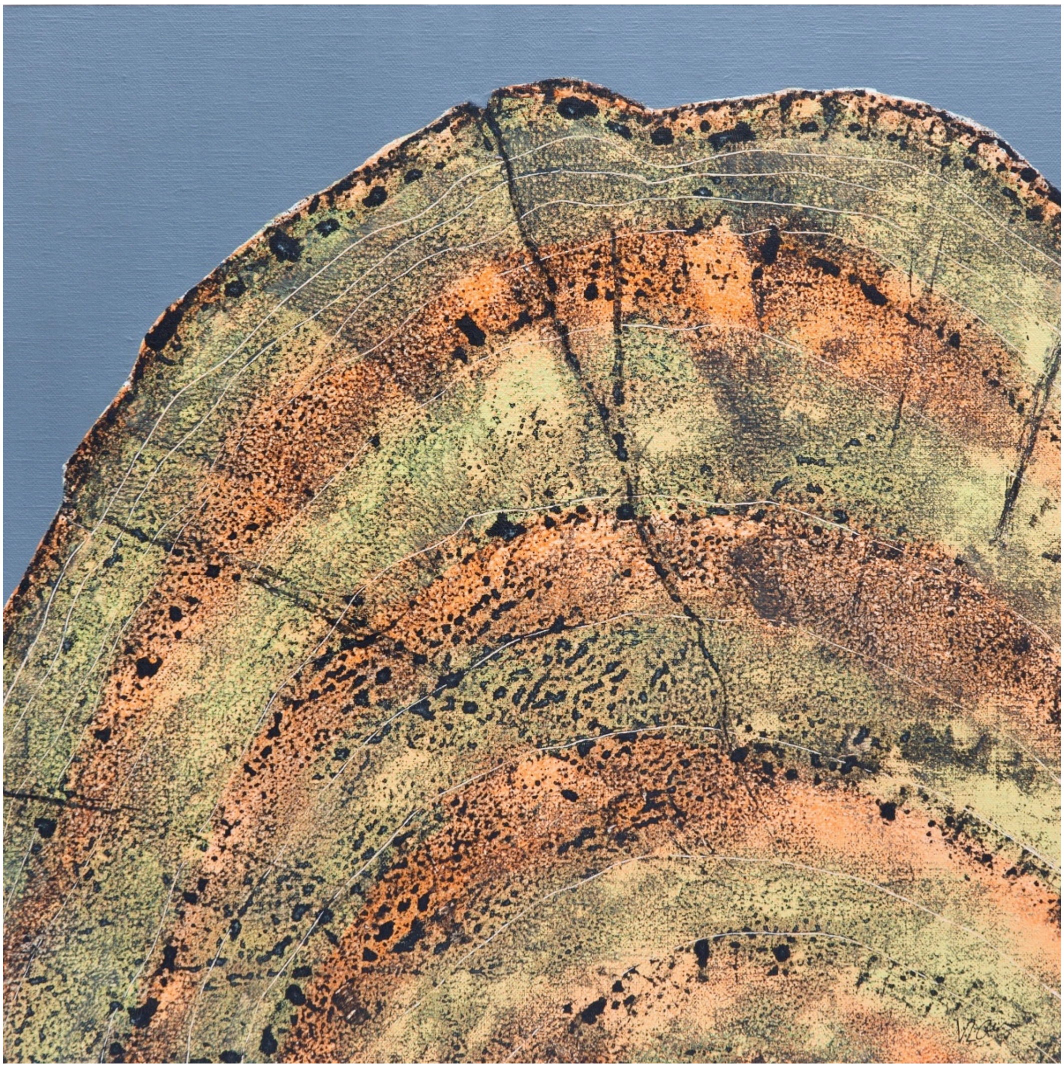
Chapter 5 addresses the historical impacts of human presence and activities on the forest environment, and light-demanding species in particular (article published in *eLife*)

Chapters 3, 4 and 5 constitute the core of the thesis, and correspond to scientific articles published in peer-reviewed journals with impact factor.

The concluding Chapter 6 summarizes the results, and invites to additional research.

Chapter 2 Materials and methods

After an introduction of the key concepts and the context of this PhD in **chapter 1**, **chapter 2** presents the different materials and methods used for the research, in particular the different datasets, their acquisition and further exploitation. This chapter ends with the description of the study sites in southern Cameroon and in the Sangha River Interval.



Cernes 3 – Véronique LG Morin

2.1. Introducing the PhD toolkit

In this PhD, we used a multidisciplinary approach by combining materials and methods from different research fields (Dincauze 2000), ranging from paleoecology to current ecology. It seemed important to us, therefore, to present them in a dedicated chapter.

Our main objectives with this review were: 1) to present the existing data and tools in order to identify the knowledge and methodological gaps, 2) to use up-to-date methods, and 3) to adapt and improve these methods to the specificities of our own objectives and fieldwork.

2.2. The sources

The documentation and data used in the framework of this research came from very diverse resources: 1) literature, including unpublished works (e.g. theses, and dissertations), 2) published and unpublished data from research projects (i.e. radiocarbon ages, big datasets), and 3) new data and materials from fieldwork campaigns conducted during the PhD.

2.2.1. Literature

Literature constitute the base of this PhD. Thereby, we used published and unpublished articles, books, reports, and dissertations in order to draw up an inventory of the existing works, data, issues, and knowledge gaps in terms of chronology and spatial distribution of previous research. Data extraction from publications represents, therefore, an important part of this PhD research. In **Chapter 5** in particular, we temporally correlated several proxies extracted from literature in order to discriminate between climate and anthropogenic impacts in the same area, i.e. the Sangha River Interval.

2.2.2. Existing data and methods

This research also benefited from several research projects (the CoForChange, and the FRFC project on light-demanding species, in particular) that provided big datasets regarding forest inventories (see **Chapter 5**). Tree growth monitoring was also obtained thanks to the continuous work for several years of technical teams in the forest companies (see **Chapter 5**).

Unpublished radiocarbon ages and artifacts were also of great support for the constitution of a chronology of the Sangha River Interval (Bourland 2013, Gillet 2013; **Chapter 3**).

We also relied on the methods developed in previous PhD and Master's dissertations, always in a collaborative perspective, and a wish for their continuous improvement. This means that we used previous sampling protocols (Bourland 2013, Bourland et al. 2015, Gillet 2013, Gillet and Doucet 2013, Vleminckx et al. 2014, 2016), then applied improved and harmonized protocols during fieldwork so as to get comparable data for further analyses (Dedry 2012, Gorel 2012, Biwolé 2015, Biwolé et al. 2015; **Chapter 4**).

2.2.3. Fieldwork

On-field investigation allowed us to acquire completely new materials and data in areas that were previously little investigated for archaeological and archaeobotanical research. In particular, we applied at two sites in southwestern (Site 1, i.e. Wijma) and southeastern Cameroon (Site 2, i.e. SFID-Mbang concessions) a sampling protocol for the acquisition of charred botanical remains, either charcoal pieces or charred seeds. The full methodology and results are presented in **Chapter 4**. The same method also supports the work of Biwolé et al. (2015), which demonstrates its application in the ecology field.

2.3. Data and proxies

After this short description of the resources, the following part will present the data and proxies used for the research. Most of proxies can be placed in the framework of the environmental archaeology as they touch: 1) materials from biological origin, and 2) the relationship between man and his environment (Renfrew and Bahn 2005). The origin of the data and proxies, either from literature, data-mining or fieldwork, is specified.

In **Chapter 5**, paleoenvironmental changes for the last 1000 yrs in the SRI were documented using a compilation of several proxies, coming from 34 published sites. They include SSTs, atmospheric dust signal, phytoliths, $\delta^{13}C$, pollen, charcoal influxes in lakes, grain size related to alluvial discharges, and chemical analyses (Laraque et al. 1998, DeMenocal et al. 2000, Runge and Fimbel 2001, Harris 2002, Runge and Nguimalet 2005, Brncic et al. 2008, 2009, Neumer et al. 2008, Runge 2008, Sangen et al. 2011, Sangen 2012, Aleman et al. 2013, Runge et al. 2014, Tovar et al. 2014, Lupo et al. 2015).

We determined the degree of frequency of each proxy with regard to all similar curves present in the same publication, which means a comparison of the *E. guineensis* pollen curve with all pollen curves in e.g. Brncic et al. (2009). The cutoffs were set using the full range of values, from the minimum to the maximum. In ***Figure 5.5***, color or gray scales at four levels were assigned depending on the proxy influx on the curve, with the lightest shade meaning the (rare) presence of the proxy, the light-medium shade, its presence, the medium shade, the frequent presence of the proxy, and the dark shade, its high frequency.

2.3.1. Sea surface temperatures

Sea surface temperatures (SSt) are calculated using the air bubbles trapped in the ice, or in the shell of foraminifera in marine or lacustrine cores (Dincauze 2000, Demoule et al. 2002). SSt are based on the ratio of oxygen stable isotopes $^{16}O/^{18}O$ (i.e. $\delta^{18}O$). The lower the value is set, the cooler the climate is (Dincauze 2000).

In **Chapter 5**, we used the SSt of marine core ODP 659 obtained for West Africa (DeMenocal et al. 2000), in order to have a broader picture of climate change in tropical Africa.

2.3.2. Dust signal

The atmospheric dust signal is based on the presence of allogeneic chemical elements captured in soil or lake sediments (Dincauze 2000). It is particularly used to document important climate changes (e.g. DeMenocal et al. 2000), or anthropogenic activities such as iron smelting (detection of peaks in iron and copper dust; Brncic et al. 2007, 2009). In **Chapter 5**, we used this proxy as a complementary indication of land-use.

2.3.3. Stable isotopes

Conventional isotope analyses are chiefly based on carbon (C), and nitrogen (N) isotopes (Dinauze 2000). In the framework of this PhD, we used published data on stable carbon isotopes ($\delta^{13}C$) (**Chapter 5**) to document past vegetation at local scale (i.e. micro-scale = < 1 km^2, Dincauze 2000). In particular, the C_3/C_4 ratio gives the proportion of forests or woodlands (trees, C_3, below 25‰) on savannas (grass, C_4, above 25‰; Dincauze 2000, White et al. 2000). This allowed us, therefore, to evaluate the degree of openness of the forest cover in the Sangha River Interval.

2.3.4. Grain size

Sedimentology in riverbanks through grain size classes is of great interest to document rivers flows (Dincauze 2000), especially when combined to $\delta^{13}C$ analyses and ^{14}C dating (e.g. Runge 2002, Runge and Nguimalet 2005). We used such published data in **Chapter 5** in order to reconstruct past terrestrial erosion due to anthropogenic pressure (i.e. agriculture).

2.3.5. Pollen

Pollen and spore study remains the most used to reconstruct past environments at a regional scale through the identification and count of pollen by species (Bourquin-Mignot et al. 1999, Dincauze 2000, Demoule et al. 2002). Pollen assemblages are found in anoxic environments (i.e. lake sediments, peats), and indicate climate change at the millennial to decadal scales (Dincauze 2000).

In **Chapter 5**, we used published pollen curves established in the Sangha River Interval (Brncic et al. 2007, 2009). We focused on light-demanding tree species for the last 1,000 years. The objective was to correlate the fluctuations of pollen curves with climate or anthropogenic disturbances.

2.3.6. Lake charcoal

Charred vegetal particles in lake are good indicators of past burning (Aleman et al. 2013). They can also be dated thanks to their inclusion in sediment laminates (Aleman et al. 2013).

In **Chapter 5**, we used published lake charcoal to apprehend past fire events for the last 1,000 years in the Sangha River Interval. The same way as for pollen curves, the objective was to establish potential links between climatic- or human-driven disturbances.

2.3.7. Charred botanical remains

Charred botanical remains represent the main proxies used for our research. Even if carbonization greatly preserves the organic matter, especially with regard to the tropical soil acidity, taphonomic processes still exist and cause a disintegration of a part of our study material (Dincauze 2000). This introduces a bias that one must keep in mind, but which can be reduced by using a systematic sampling.

In order to collect charred macrobotanical remains, we chose to use a systematic sampling (see **Chapter 4**), which was based on the excavation of equally spaced locations (Renfrew and Bahn 2008). Sampling was done linearly according to three main criteria:

1) the accessibility (paths, roads), 2) the proximity of watercourses for water-sieving the soil samples, 3) the presence of unlogged areas for botanical inventories.

At each site, the sampling ran through the three Forest Management Units (FMUs), granted to the forest companies SFID and Wijma, along independent transects, and took into account the variability in terms of vegetation. Swamps and watercourses were plotted along the transects, and the slope was measured every 20 m with a clinometer so as to indicate the topography (see ***Figure 4.2***).

The sampling itself consisted in small test-pits (50 × 50 cm) of 60 cm in depth excavated in the center of 40 × 50 m plots of botanical inventory. We yet avoided to sample in riverbanks, swamps, and steep slopes, because of erosion and colluvium processes (see Carcaillet 2001b). These plots were established every 250 m along each transect (***Figure 2.1***). Soil samples of 3 L were extracted by 10 cm-layers for further water-sieving (total = 18 L/pit), in order to avoid bias related to hand-picking the visible charcoal pieces only (Carcaillet and Thinon 1996).

Nonetheless, two limitations have emerged from such sampling: 1) the regular spacing of the test-pits *vs*. a stratified random sampling (based on probabilistic statistics to find or not archaeological evidence) increases the risk of missing or hitting archaeological evidence in a too regular pattern of distribution (Renfrew and Bahn 2008), and 2) the lineary application of this systematic sampling increases the risk of missing settlements or activities on both sides of the investigated transect. This sampling method was thus a first step in the development of archaeobotanical investigations in dense tropical forests, and should be improved in the future. However, this regular sampling allowed us to applied torroidal translations to test the correlations between variables with a minimum bias.

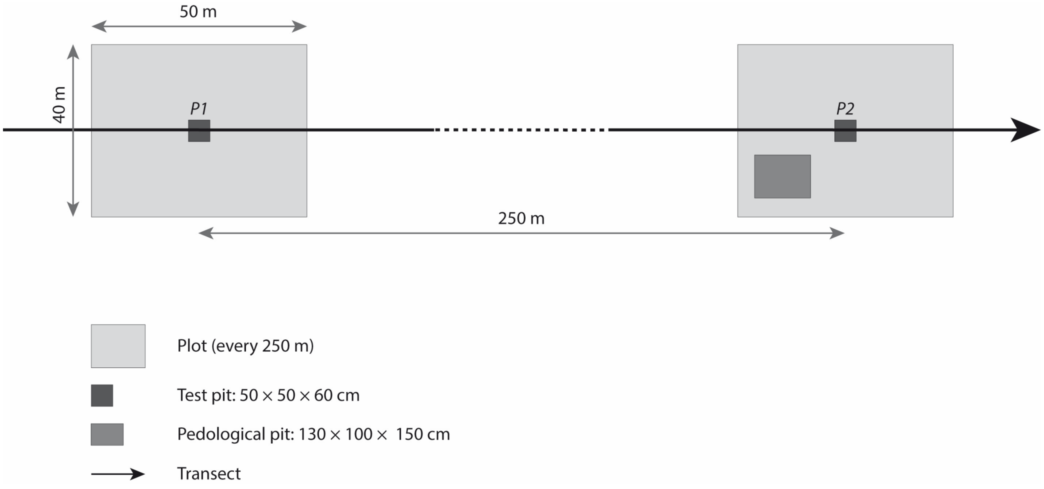


Figure 2.1. Sampling design used at Site 1 (Wijma) and 2 (SFID-Mbang).
Plots of botanical inventory were set every 250 m along the investigated transect. One test-pit was excavated at the center of each plot. Three pedological pits were also excavated in each transect.

The water-sieving was performed directly during fieldwork in the nearest watercourse through a 2-mm mesh sieve. We chose this mesh size as a good compromise between effort during fieldwork (excavation, sampling, transportation, and sieving), and the laboratory work (sorting, weighing, further possibility of taxonomical identification of charcoal ≥1 mm according to the definition of Scott 2010). The sieve refuses were naturally air-dried during fieldwork.

The sorting in laboratory was done manually, with the separation of the macroremains from the mineral fraction under a dissection microscope (×20). In this method, we found relevant to separate the remains into three categories: 1) wood charcoals, 2) charred oil palm endocarps (*Elaeis guineensis*), and 3) unidentified charred seeds (in the absence of an exhaustive reference collection for these biomes). Each sample was weighted by depth and by category on a precision scale (0.01 g in accuracy). This first attempt was successful, because the spatial analyses of these different categories of remains demonstrated divergences in their distribution.

2.3.8. Artifacts

Artifacts are human-made objects that indicate the presence of human settlements or activities in the investigated soils (Demoule et al. 2002). During this doctoral research, we did not conduct archaeological surveys or excavations, strictly speaking, but fortuitously found artifacts during the sampling of the botanical macroremains (**Chapter 4**). We also used previous research and discoveries in the same areas for comparison purposes, and with regard to radiocarbon ages (**Chapter 3**).

Potsherds were by far the most present, indicating the use of pottery, most probably in human settlements. Particularly at SFID-Mbang (southeastern Cameroon), these potsherds constitute completely new and unpublished artifacts related to cultures dated to the Early Iron Age. They were followed by lithics, found in very small quantities. In **Chapter 4**, fragment numbers were indicated by 10-cm layers, corresponding to the sampling protocol used for charred botanical remains (see ***Tables 4.3*** and ***4.4***).

2.3.9. Historical archives and ethnographic studies

Textual and visual archives constitute an interesting way to explore recent interactions between people and their environment. Among them one can cite maps, photographs, drawings, travels stories, testimonies, and synthetic works made by historians (Renfrew and Bahn 2005).

In **Chapter 5**, we proposed a selection of 12 references that illustrate key events covering the 15th century to the present in the SRI (Vennetier 1963, Robineau 1967, Kaspi 1971, Burnham 1996, Copet-Rougier 1998, Coquery-Vidrovitch 1998, Freed 2010, Giles-Vernick 2000, Manning and Akyeampong 2006, Laporte et al. 2007, Gendreau 2010, Stock 2013). These references more particularly focused on the changes that occurred during the colonial era, and thus their influence on people lifestyles in the forest.

In our opinion, further research on this topic should include a more thorough investigation of the published and dormant historical archives, in order to draw precise and local stories of past landscape modifiers (Dincauze 2000).

2.3.10. Forest inventories

Leaving the world of paleoecology and archaeology, ecological data were also of great interest to link past human impact and the current state of the forest. To do so, in **Chapter 5** we used published forest inventory datasets (Fayolle et al. 2014a) from 22 forest concessions in southeastern Cameroon (n = 6), southeastern Central African Republic (n = 6), and northern Republic of Congo (n = 10). These data derived from collaborations with forest companies, and were chiefly gathered in the framework of the CoForChange project.

The botanical inventories were conducted between 2000 and 2007, and corresponded to the systematic sampling of 1% of the concession area in 0.5 ha plots consecutively distributed along parallel and equidistant transects in forest concessions (Picard and Gourlet-Fleury 2008, Réjou-Méchain et al. 2008, Gourlet-Fleury et al. 2011, Fayolle et al. 2012, 2014a, Gond et al. 2013). This allowed us to use a big dataset of 1,765,483 trees with a dbh 30 cm, covering six million ha in the SRI (Fayolle et al. 2014a).

2.3.11. Tree growth and tree rings

An important element was to calculate the age of the light-demanding trees in the forest concessions, in order to identify the approximate date of their regeneration (see **Chapter 5**). Two means were used: 1) tree growth, and 2) tree ring data.

Tree growth was obtained by using repeated diameter measurements of 982 monitored trees on seven trails used for the permanent monitoring (n = 4 in Cameroon; n = 3 in the Republic of the Congo; Picard and Gourlet-Fleury 2008). We calculated the mean annual increment in diameter (MAI_d) by targeted light-demanding species (i.e. n = 367 *E. suaveolens*; n = 199 *P. elata*; n = 152 *T. superba*; and n = 264 *T. scleroxylon*). Nonetheless, these data are only estimations of tree growth and need more trees and more years of growth monitoring.

As this was only an estimation of tree growth, we also used published age data for these four species (Worbes et al. 2003, De Ridder et al. 2013a, 2013b, 2014). Nonetheless, these age data did not come from the same trees as those measured for estimating the mean tree growth, and sometimes come from remote areas (i.e. the Ivory Coast). Moreover, studied trees were cut at dbh or higher (because of buttresses) that rejuvenates the trees because of the primary growth, i.e. the stack of successive wood cones year after year (Wilson and White 1986). Finally, it remains difficult to identify tree rings in tropical trees (MRAC 2007, Groenendijk et al. 2015, Tarelkin et al. 2016).

In conclusion, the combination of tree growth and tree ring data allowed us to smooth the inherent biases of both methods. Interestingly, tree ring data through the cross-dating method are used to establish the calibration curves for absolute dating (Dincauze 2000, Évin et al. 2005). In the future, tree ring data from tropical trees could be integrated in regional calibration curves focused on the tropical zone.

2.4. Documenting time

The possibility of replacing past events in a chronological framework has long been a critical issue in archaeology. At the end of the 19th century, human technological innovation was balanced into two conceptions, diffusionism, held by Montelius and Worsae, and evolutionism, held by de Mortillet (Renfrew 1976, Renfrew and Bahn 2005). Diffusionism postulated that elements of culture – in a broad sense, notably including agriculture, art, and pyrotechnologies such as pottery and smelting – were invented only once in a certain point in the world. Those elements were transmitted by contact from this point to other areas (Renfrew 1976). “Civilization” came from the Near East (Childe) or Egypt, or even Germany. The latter was used in the 1920s-1930s by the Nazi’s propaganda (Renfrew 1976, Demoule et al. 2002). Evolutionism, by contrast, assumed that alike innovations could be made at different places at the same or different times under similar conditions, in a universal process (Renfrew 1976). This conception had, however, less success than diffusionism. The invention of radiocarbon dating by Libby in 1949 blew out both conceptions and brought a new way of thinking the chronology (Renfrew 1976).

2.4.1. Relative chronology

The relative chronology is defined by the spatial physical relationships between the archaeological units in a site (Renfrew 1976, Dincauze 2000, Demoule et al. 2002, Évin et al. 2005, Renfrew and Bahn 2005, Djindjan 2011). This implies the possibility to attest the anteriority or posteriority of a defined unit or layer in a stratigraphy with regard to the adjacent units.

Unfortunately, such stratification is rare or absent in the locations we investigated, just like *terra preta* soils in the Amazonian forests (i.e. anthrosols, Dincauze 2000), and questions our knowledge of tropical soil and archaeological site formation processes (Dincauze 2000, Renfrew and Bahn 2005). Indeed, we most often found artifacts and oil palm endocarps scattered along the reference soil profiles (**Chapter 4**), with no evidence for changes in color or grain size, yet indispensable to attest discrete modulations along the profiles (Dincauze 2000).

Nonetheless, we also found promising archaeological features such as dump pits, especially in the FMU 10.056 (SFID-Mbang), where charred remains and artifacts were stratified. We hope that future archaeological investigation and excavation will precise archaeological site formation in the African tropical forest.

2.4.2. Absolute dating

Absolute dating is related to the analyses in laboratory of samples in order to date one isotope (e. g. the ^{14}C, which is also called the radiocarbon; Demoule et al. 2002) or a ratio of two isotopes (e.g. ^{238}U/^{230}Th; Dincauze 2000, Demoule et al. 2002, Djindjan 2011). We will not describe all available dating methods, but we will focus on three: 1) the traditional radiocarbon dating, 2) the accelerator mass spectrometry (AMS) dating, and briefly 3) the optically stimulated luminescence (OSL) method.

Radiocarbon dating is still important for unstratified archaeological sites – such as those in tropical Africa (Oliver and Fagan 1975). There actually were two radiocarbon revolutions (Renfrew 1976): 1) the first concerns the use of radiocarbon for dating itself, while 2) the second is related to its calibration (Renfrew 1976). Calibration was first made by using known tree ages based on growth rings (Renfrew 1976, Demoule et al. 2002), but it has been improved since then by adding other proxies, such as laminated ocean core sequences to the calibration curves (e.g. Reimer et al. 2013).

The traditional radiocarbon dating is a quantification of the number of radioactive atmospheric carbon particles during a given time period. This method was the first developed by Libby in 1949 (Renfrew 1976, Dincauze 2000, Demoule et al. 2002), date set as the reference date for calibrations in BP (i.e. Before Present = 1950). The radiocarbon dating relies on four principles: 1) the half-life of the radiocarbon (i.e. 5,568±30 yrs BP, Libby et al. 1949), which means the constant decay of a half of its initial radioactive content following an inverse exponential curve, 2) the absence of contamination of the dated sample by more recent material, 3) the uniform distribution of the radiocarbon worldwide in order to use the method in any context, and 4) the variation in the atmospheric concentration of radiocarbon with time that allowed building up calibration curves (Renfrew 1976, Dincauze 2000).

The traditional method needs, however, a great quantity of charred matter (15 to 50 g for charcoal, source: Beta analytic) from biological origin (at the exception of bone or shell, because of a reservoir effect due to the high presence of calcium that ages the date; e.g. Zazzo et al. 2012). Among the biases, one can cite the problem of dating bulk samples, comprising several charred pieces not of the same age, and thus providing a greater uncertainty and larger time-ranges. It is worth mentioning that the radiocarbon method does not date the age of the fire, but the age of the carbon accumulation during the living of the organism (Évin et al. 2005). Therefore, we did not date our samples using this method, but only use already published dates (see **Chapter 5**).

The AMS method, by contrast, has added an important improvement to the radiocarbon dating by reducing the quantity of matter needed. It was very important in the framework of our research, as the charred macroremains we collected were often very small (> 1 mm in diameter; 2 to 100 mg for charcoal, source: Beta analytic). We preferred using the AMS method on 2- to 6-mm charred pieces (43 dates in **Chapter 3**, 50 dates in **Chapter 4**), and therefore avoided dating bulk samples. Moreover, we focused on short-lived material, such as charred endocarps, for an increased precision. The AMS method provides narrowed time-ranges and less age uncertainty (Dincauze 2000), and also allows the dating of tree rings (e.g. De Ridder et al. 2014)

For both radiocarbon methods, the results indicate a probability of distribution of the age at one or several time-periods, depending on the percentage of probability chosen, most often lying outside the 95% confidence envelope (corresponding to a standard deviation of two σ; Évin et al. 2005). In order to understand these results, data are fitted on calibration curves (e.g. Reimer et al. 2013). Calibration curves are developed on the basis of numerous curves and proxies, including ice cores (Renfrew 1976). It is very important to choose the appropriate curve according to the localization of the samples to date. In the framework of this research, we used the most recent curve set for the northern hemisphere, the IntCal13 atmospheric calibration curve (Reimer et al. 2013), though our study sites were located very close to the equator.

There are, however, four limitations to the radiocarbon method: 1) the need of organic matter to date, 2) the time-range limited to ~40,000 BP (Dincauze 2000, Djindjan 2011), 3) a plateau effect on the calibration curve (Reimer et al. 2013) for sites dated to 600 BP and younger (Oliver and Fagan 1975) that could be either 800 cal. BP or 400 cal. BP old (K. Neumann and D. Fuller, pers. com.) and thus need more archaeological evidence to narrow down the possible age (Oliver and Fagan 1975), and 4) a greater uncertainty since the Industrial Revolution (~AD 1850) with the release of greater quantities of radioactive carbon in the atmosphere, a phenomenon increased in the second half of the 20th century due to the nuclear bombs (World War II) and nuclear tests (since the 1960s). This latter issue is now partially smoothed thanks to the development of post-bomb curves of calibration.

Finally, the OSL method is a part of the thermoluminescence dating method (Dincauze 2000, Djindjan 2011). The thermoluminescence method was developed by Daniel (1953) and Aikten (1968). The principle relies on the measurement of the energy released by the radioactive isotopes stoked in the impurities of the crystalline minerals (Djindjan 2011). The heating of these impurities above 500°C resets the clock, and thus allows finding the date of this heating. The method can date quartzites up to 200,000 yrs and flints up to 400,000 yrs, to the present, with a precision of 10%. This particularly is thus applied to the minerals included in the backed clay, and notably to pottery using the OSL method (Djindjan 2011). In this PhD, we only used two OSL dates performed on two potsherds and taken from literature (Brncic 2003; see **Chapter 5**). Such dates remain, nonetheless, difficult to use in summed probability calibrations, as a complement of the radiocarbon ages.

2.4.3. Cumulative dating

The cumulative dating principle is to perform a summed probability distribution of a collection of radiocarbon ages that were analyzed together, and that give a mean age (Évin et al. 2005). We used this method in **Chapter 3** to compare our results with those of Wotzka (2006) and Oslisly et al. (2013a, 2013b). All analyses were performed using the OxCal v4.2.3 program (Bronk Ramsey 1995, 2001, 2013), which is both powerful and flexible. Requests were coded according to the structured query language (SQL). This type of analysis provided us a first estimation of temporal distribution of the disturbance events in the SRI. Results were expressed in probability densities for the whole summed age distribution. However, this method needed improvements, especially a smoothing of the most recent events (last four to two centuries), explaining the further use of the Bayesian principle in **Chapters 4** and **5**.

2.4.4. The Bayesian method

In the 18th century, the mathematician Bayes developed a particular branch of the probabilistic statistics (Évin et al. 2005, Bayliss 2007, Bayliss et al. 2007). The archaeological application of the Bayesian statistics allows to better answer the questions raised by the archaeologists: 1) by combining ages deriving from different methods (in our case, radiocarbon and OSL dates), and 2) by improving each date individually with regard to the archaeological context and the other dates included in the same analysis. The modeling can thus smooth the errors and exclude the low parts of the probability distributions from the edge of the graph.

In this PhD, our objective was to better estimate the temporal distribution of events in the study areas at different spatial scales (i.e. micro- to macro-scales = < 1 km^2 to 1^2–10^2 km^2, from area to locale, respectively, Dincauze 2000). Before performing the analyses properly speaking, we tested each date in order to detect possible outliers (Bronk Ramsey 2009). In **Chapter 4**, we performed a summed probability distribution of the radiocarbon dates calibrated in BP, combined with a Bayesian model (Bronk Ramsey 2009) on two sets of 25 AMS dates (one by site, i.e. Site 1 and Site 2, in southwestern and southeastern Cameroon, respectively).

In **Chapter 5**, we used the same method but focused on dates covering the last 1,000 yrs in a single region, the SRI. In this dataset of 63 radiocarbon dates, 38 came from the literature (Fay 1997, Lanfranchi et al. 1998, Brncic 2003, Moga 2008, Meyer et al. 2009, Oslisly et al. 2013b, Lupo et al. 2015), the other dates from our previous publications (i.e. **Chapters 3** and **4**). The use of the Bayesian method here was crucial given the great uncertainty of the calibration since the Industrial Era, which corresponded to the targeted period regarding the beginning of the depletion of the light-demanding tree populations in the area.

Nonetheless, two limitations of our own analyses could be presented here: 1) the limited presence “prior” (i.e. existing data) and “posterior” (i.e. limiting interpretations) archaeological knowledge because of a lack of precise archaeological framework, especially in the SRI; indeed, we are among the first to picture such a framework (with e.g. Oslisly et al. 2013a, 2013b, Lupo et al. 2015, Kiahtipes 2016), and this point must be improved in the future (see Ozainne et al. 2009 for a good application of these principles), and 2) the presence of many recent dates belonging to the last four centuries, which face the abovementioned plateau effect and the recent release of more radiocarbon in the atmosphere.

2.4.5. Crossing time and space

These very promising spatial analyses have been already used by Ozainne et al. (2014) to model the spatial expansion of early agriculture with time in West Africa. We adapted the reflections contained in this paper to our own problematics and data. Using the Bayesian distributions of the radiocarbon ages, we drew maps of the temporal patterns of the study sites by 200-years time-slices (see **Chapter 4**; Bronk Ramsey and Lee 2013). In our opinion, this constituted a first step in evaluating the hold of human settlements and activities on the landscape over time in the SRI (see e.g. Renfrew and Bahn 2005, and Chouquer 2008 for a reflection on the notion of landscape in archaeology).

2.5. Statistical analyses

As we saw above, the analyses of radiocarbon and non-radiocarbon ages are often based on statistics. The other statistical analyses used in this PhD will be briefly presented here, as they are detailed in **Chapters 4 and 5**, and most often refer to well-known analyses, or to recently published applications. All analyses were performed using the R software (https://www.r-project.org/).

We performed several tests in **Chapter 4**: Pearson correlation coefficients between the different categories of charred botanical remains to characterize human activities (**Chapter 4**), a Willcoxon test to determine the associations between those remains and the presence of pottery, and Mantel tests to validate the spatial structure of those remains. Mixed Linear Model (MLM) were to test whether the different transects (n = 6, three transects at each site) and test-pits experienced similar anthropogenic disturbance regimes.

The spatial representation of the archaeological evidence is very important in order to project e.g. land-use, population density, and the influence on landscape at diverse spatial scales, using prior knowledge such as ethnographic testimonies (Binford 2001). Nonetheless, it seemed difficult, in the framework of our own research, to define what covers the notion of territory, whose limits move both in time and space (Demoule et al. 2002, Chouquer 2008). We assumed that human settlement constitutes its core, surrounded by two concentric circles, the food-producing, then the supply territory (Leroi-Gourhan 1964 and 1965; see Kay and Kaplan 2015 for the application of such a conception). In **Chapter 4**, smaller scale spatial structures were characterized for each variable by calculating their spatial autocorrelation using Moran's *I* statistic (Moran, 1948). Torus-translations were finally performed using 4999 translations to avoid type I error inflation (Harms et al. 2001; Torocor 1.0 http://ebe.ulb.ac.be/ebe/Software.html, Vleminckx et al. 2014) in order to test the spatial dependence of the three categories of botanical remains (i.e. charcoal, oil palm endocarps, and unidentified seeds) with regard to the presence of pottery in a given plot. We put forward a limitation to this method due to the limited number of data points (J. Hébert, pers. com.), even if the analysis remains correct.

In **Chapter 5**, we aimed at detecting the main variation in the diameter distribution among 176 genera. We first assigned trees in 13 10-cm-wide diameter classes, from 30 cm at dbh to ≥ 150 cm at dbh, then performed a correspondence analysis (CA) of the genus diameter matrix followed by a clustering based on Euclidian distances and an average agglomeration method. We focused on four genera exhibiting unimodal distributions of their diameters (which derived from the structure corresponding to active tree populations i.e. negative exponential curve): *Erythrophleum*, *Pericopsis*, *Terminalia*, and *Triplochiton*, and fitted a parametric diameter distribution curve (Weibull; Rondeux 1999) on each diameter distribution in order to better estimate the mode and corresponding age of the diameter distribution. Growth modeling was used in order to account for the ontogenic variation in growth generally identified for tropical tree species (Hérault et al. 2011). Ordinary differential equations (ODE) were solved numerically to obtain the relationship between tree diameter and time (age).

2.6. Study area

This last part will present the locations where we extracted the data and proxies, and where we applied the above-described methods. It important to mention here that we used the term “site” to define a place of data and material collection, and not an “archaeological site” (following the definition proposed by Demoule et al. 2002, i.e. the presence of buried material evidence of human origin). In the latter case, it was most often specified.

For this PhD research, we worked at different spatial scales (Dincauze 2000). The localization of the study areas and sites are presented in ***Figure 2.2.***

More specifically, we worked in the Sangha River Interval (SRI), which is a 400-km-wide area in southeastern Cameroon, southern Central African Republic (CAR), and northern Republic of Congo (**Chapters 3** and **5**). The extremes that encompass the area are 0°–5° N and 13°–19° E (Gond et al. 2013). The climate is equatorial with alternating wet (March-May, September-November) and dry seasons (December-February, June-July; Gillet and Doucet 2012). Mean annual rainfall ranges between 1616 and 1760 mm (Lomié in Cameroon and Impfondo in the Republic of the Congo; www.climatedata.eu). Monthly average temperatures fluctuate around 25°C. The vegetation of the area corresponds to moist semi-deciduous forests of the Guineo-Congolian domain (White 1983, Gond et al. 2013, Fayolle et al. 2014b).

In **Chapter 4**, we compared two study sites, i.e. Site 1 (Wijma forest concessions, southwestern Cameroon) and Site 2 (SFID-Mbang forest concessions, southeastern Cameroon), two contrasted study sites in terms of climate, vegetation, soil and geological substrate. Both forest companies are under FSC certifications (Gorel 2012). All forest concessions belong to the permanent forest domain and legislation prohibits agriculture in the concessions. Current villages and associated shifting cultivation are only located along the roads (Carrière 1999, and personal observation). Current population density is less than 10 inhabitant/km^2 in Site 1 and less than 1 inhabitant/km^2 in Site 2 (Afripop 2013). The climate in both sites is equatorial, with two wet seasons interrupted by two dry seasons. The data collection was carried out between February and April 2012. In Site 1, we benefited from the work of A. Biwolé during his PhD (Biwolé 2015), and followed the same sampling as that used in Site 2.

Site 1 (2°10′–2°39′N, 10°11′–10°53′E) is located in southwestern Cameroon, east of the Campo Ma’an National Park, in two FMU (logging company Wijma). Monthly average temperatures fluctuate around 25°C and mean annual rainfall ranges between 1669 (Bitam station, Gabon) and 2740 mm (Kribi station; http://www.climatedata.eu). The topography is hilly with a maximum altitude of 600 m. The geological substrate entails old volcanic intrusions and Precambrian metamorphic rocks (Franqueville 1973), and is overlain by Ferralsols (red-dominant) and Acrisols (yellow-dominant) (van Gemerden et al. 2003). The vegetation belongs to the mixed forest including lowland wet evergreen littoral and semi-deciduous types (Letouzey 1985). The canopy is dominated by long-lived light-demanding species like *Lophira alata* (Ochnaceae) (Vleminckx et al. 2014).

Site 2 (3°45′–4°03′N, 14°17′–14°31′E) is located in southeastern Cameroon, north-east of the Dja Reserve, in three FMU (logging company SFID-Mbang, Groupe Rougier).

Monthly average temperatures fluctuate around 25.5° and mean annual rainfall ranges between 1518 mm (Mouloundou station) and 1616 mm per year (Lomié station; www.climatedata.eu). The topography is broadly flat, with altitude between 600 and 700 m. The geological substrate consists of weathered Precambrian schisto- quartzitic rocks (Vennetier 1963), overlain by Ferralsols (Martin and Ségalen 1966). The vegetation mainly belongs to the semi-deciduous forest types (Letouzey 1968, 1985), and presents also permanent or semi-permanent marshes (Collin-Bellier 2007, Cerisier 2009). Gleys, pseudogleys and hydromorphic soils are present in the vicinity of the marshes. Canopy is dominated by long-lived light-demanding species from the Cannabaceae (*Celtis* spp.), Malvaceae (*Triplochiton scleroxylon*) and Combretaceae (*Terminalia superba*) families (Fayolle et al. 2014a).

2.7. Conclusion

The aim of this chapter was to present all the elements mobilized in this PhD, as well as the study area. The different materials came from various sources, including published and unpublished literature, and samples directly taken from the field. The methods specifically used in the different chapters falls under either pure data-mining or statistical analyses. The study area is multiscale with regard to the different scopes of the research.

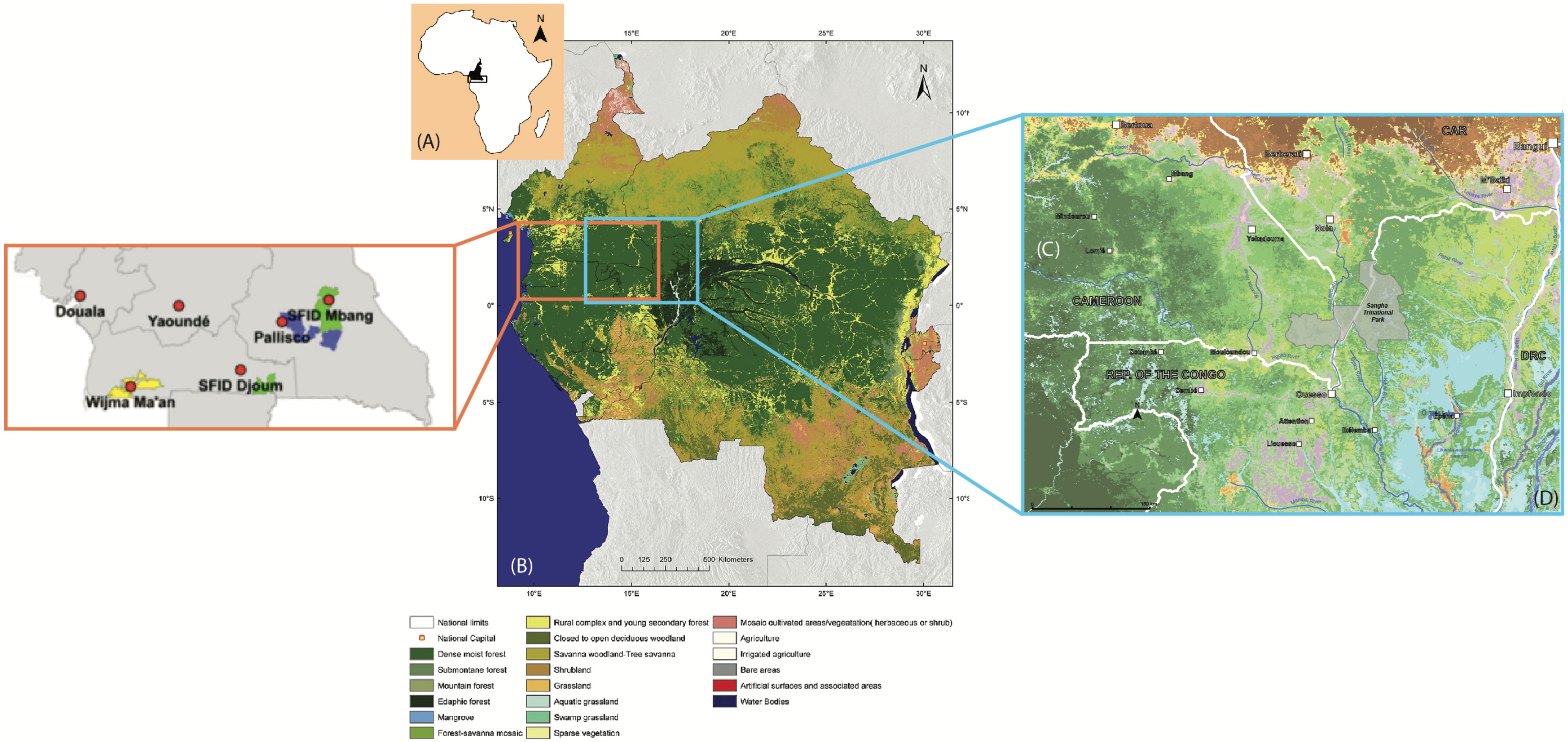


Figure 2.2. Location of the study areas in southern Cameroon and the Sangha River Interval.
(A) Africa with localization of Cameroon; (B) The tropical forests of the Congo Basin (adapted from Verhegghen et al. 2012); (C) Southern Cameroon and localization of the study sites presented in **Chapter 4**; (D) The Sangha River Interval, studied in **Chapters 3** and **5**.

Second part Characterization of past human impacts on central African tropical forests

Chapter 3 New evidence of human activities during the Holocene in the lowland forests of the northern Congo Basin

The presentation of the archaeological and ecological context in **Chapter 1** stressed the need for new research in tropical Africa, in order to make the link between past human activities and the current state of the forests. To do so, we presented in **Chapter 2** the materials and methods we used in the following chapters. **Chapter 3** thus provides new archaeological information from the northern Congo Basin. To date human presence in the forest constitutes, indeed, a first step to bridge one of our knowledge gaps.

Adapted from: Morin-Rivat J, Fayolle A, Gillet JF, Bourland N, Gourlet-Fleury S, Oslisly R, Bremond L, Bentaleb I, Beeckman H, Doucet JL. 2014. New evidence of human activities during the Holocene in the lowland forests of the Northern Congo Basin. *Radiocarbon* 56(1): 209–220. Doi:10.2458/56.16485

Les Arbres 10 – Véronique LG Morin

Abstract

In the last decade, the myth of the pristine tropical forest has been seriously challenged. In central Africa, there is a growing body of evidence for past human settlements along the Atlantic forests, but very little information is available about human activities further inland. Therefore, this study aimed at determining the temporal and spatial patterns of human activities in an archaeologically unexplored area of 110,000 km² located in the northern Congo Basin and currently covered by dense forest. Fieldwork involving archaeology as well as archaeobotany was undertaken in 36 sites located in southeastern Cameroon and in the northern Republic of Congo. Evidence of past human activities through either artifacts or charred botanical remains was observed in all excavated test pits across the study area. The set of 43 radiocarbon dates extending from 15,000 BP to the present time showed a bimodal distribution in the Late Holocene, which was interpreted as two phases of human expansion with an intermediate phase of depopulation. The 2300–1300 BP phase is correlated with the migrations of supposed farming populations from northwestern Cameroon. Between 1300 and 670 BP, less material could be dated. This is in agreement with the population collapse already reported for central Africa. Following this, the 670–20 BP phase corresponds to a new period of human expansion known as the Late Iron Age. These results bring new and extensive evidence of human activities in the northern Congo Basin and support the established chronology for human history in central Africa.

Key words: central Africa, radiocarbon, archaeology, artifacts, oil palm, tropical forest

3.1. Introduction

In the last decade, the myth of the pristine tropical forest has been seriously challenged (van Gemerden et al. 2003). As these areas are currently covered by dense forest, they were formerly regarded as intact (Willis et al. 2004). Multiple lines of evidence of ancient human activities have been recorded, however, across the tropics and these have likely influenced tropical forest structure and composition (Barton et al. 2012). Indeed, recent research has attested to early agriculture and land management dated to several thousand years ago in currently sparsely populated or depopulated areas (Barker et al. 2007, Summerhayes et al. 2010, Arroyo-Kalin 2012, Barton 2012, Barton et al. 2012, Haberle et al. 2012, Hunt and Premathilake 2012, Kennedy 2012, Kingwell-Banham and Fuller 2012, McNeil 2012, Rostain 2012, Sémah and Sémah 2012, Stahl and Pearsall 2012, Torrence 2012). In central Africa, artifacts (e.g. stone tools, potsherds, and iron slags) and charred botanical remains (e.g. charcoals and endocarps) constitute valuable witnesses of human history in the forests (van Gemerden et al. 2003, Wotzka 2006, Brncic et al. 2007, Höhn and Neumann 2012, Logan and D'Andrea 2012, Neumann et al. 2012a, Gillet and Doucet 2013, Oslisly et al. 2013a).

In tropical Africa, the current forest composition, specifically the dominance of long-lived light-demanding species in the canopy, have been mostly interpreted as the result of recent human activities (Aubréville 1947, Letouzey 1968, White and Oates 1999, Brncic et al. 2007, Greve et al. 2011). Recently, Bayon et al. (2012a) even asserted that human land-use intensification was the determining factor of the major vegetation change that occurred about 3000 yr ago, when rainforests were abruptly replaced by a forest-savanna mosaic in the course of a few centuries. However, such large-scale human-driven vegetation changes have largely been questioned. Paleoecologists and archaeologists indeed agree on the fact that this ‘rainforest crisis’ was related to a large climate change that led to a drier and more seasonal rainfall regime rather than due to human disturbance (Neumann et al. 2012b).

Patterns of human activities in central Africa have rarely been documented to date (Clist 1990, Wotzka 2006). Only a few Late Stone Age sites have been discovered for the Early and Middle Holocene (12,000–2500 BP) in all of central Africa (Cornelissen 2002). By contrast, archaeological studies have shown an increase in the number of sites with evidence of human occupation from the dry event of 2500 BP (Wotzka 2006, Oslisly et al. 2013b). From this time, the landscape opening allowed the expansion of human populations from the Cameroon-Nigeria border southwards to Gabon, Cameroon, the Republic of the Congo, and the Democratic Republic of Congo (Schwartz 1992, Lanfranchi et al. 1998, Clist 2006). These populations are considered ‘Bantu-speakers’, who produced pottery (Neolithic, around 3500–2000 BP), and somewhat later forged iron (Early and Late Iron Age, around 2800–1800 BP and 1000–200 BP, respectively) (Manima-Moubouha 1987, Oslisly and Peyrot 1992, Lanfranchi et al. 1998, Wirrmann and Elouga 1998, Assoko Ndong 2002, Holden 2002, Diamond and Bellwood 2003; Phillipson 2003; Lavachery et al. 2005; Clist 2006; Eggert et al. 2006, Oslisly 2006, Meister 2008, 2010, Meister and Eggert 2008). The Bantu question is often contradictory, however, and their economy has rarely been documented (Neumann 2005). The practice of slash-and-burn agriculture has only been attested at a few sites (Neumann et al. 2012a). Cattle raising was also impossible in dense forest due to the tsetse disease (Gifford-Gonzalez 2000). Nevertheless, iron tools seem to have allowed the populations to penetrate deeply into the forest across the whole Congo Basin (Schwartz 1992, Oslisly and Peyrot 1992, Eggert 1993). Under these conditions, populations are expected to have settled inland, but the largest sets of occupations appear to be restricted to zones where water is available: the Atlantic Ocean and the freshwater sources located further East *i.e.* the Congo River and the African Great Lakes. As few large sites have been excavated, however, our understanding of the extent of the Iron Age settlements remains limited (Lanfranchi et al. 1998).

Regarding the spatial distribution of archaeological excavations in central Africa (Clist 2006, Wotzka 2006), there is a growing body of evidence for past human presence in the Atlantic forests of Gabon and in SW Cameroon, but very little information is available further inland. This seems to be an artifact of documentation, probably due to a lack of archaeological surveys in dense forest compared to more accessible environments. We postulated that the ‘rainforest crisis’ of 2500 BP, by creating a more open landscape, may have fostered the settlement of populations even in areas that are covered by dense forest today. This study thus aims at finding new evidence of human activities in the lowland forest of the northern Congo Basin, in archaeologically unexplored areas. The following questions are specifically addressed. Were human settlements encountered in the study area? If so, since when were human populations present, and how were their activities distributed over time?

3.2. Material and methods

3.2.1. Study area

The study covers southeastern Cameroon (Eastern Region) and the northern part of the Republic of the Congo (Sangha and Likwala Departments) (***Figure 3.1***). The investigated areas represented 30,000 km² in Cameroon and 80,000 km² in the Republic of the Congo, between 3°65´N and 0°50´N (northern and southern, 350 km apart) and 13°50´E and

16°70´E (western and eastern, 550 km apart). A total of 36 study sites were sampled across the study area. The 11 sites in Cameroon are located between the Boumba and Dja/Ngoko rivers. The 25 sites in the Republic of the Congo are located between the Lobaye River, Mambili River and the Likwala-aux-Herbes swamps/Ubangui River. The climate is humid tropical with a 3-month dry season (December-February). Mean annual rainfall ranges between 1430 mm (Batouri, Cameroon), 1685 mm (Ouesso, Congo), and 1735 mm (Lomié, Cameroon). Monthly average temperatures fluctuate around 25° (Global Water Partnership 2009). The vegetation consists of semi-deciduous moist forest of the Guineo-Congolian domain, which is dominated by large emergent light-demanding trees (White 1983, Gillet and Doucet 2012). The prospected forests lay on weathered bedrock from the Precambrian schistoquartzitic complex in Cameroon (Vennetier 1963) and on Mesozoic sandstones and Quaternary alluvial deposits in the Republic of the Congo (Schwartz and Lanfranchi 1993). The relief is broadly flat across the study sites, but with decreasing altitude from the west to the east, between 600–700 and 350–460 meters, in Cameroon and the Republic of the Congo, respectively.

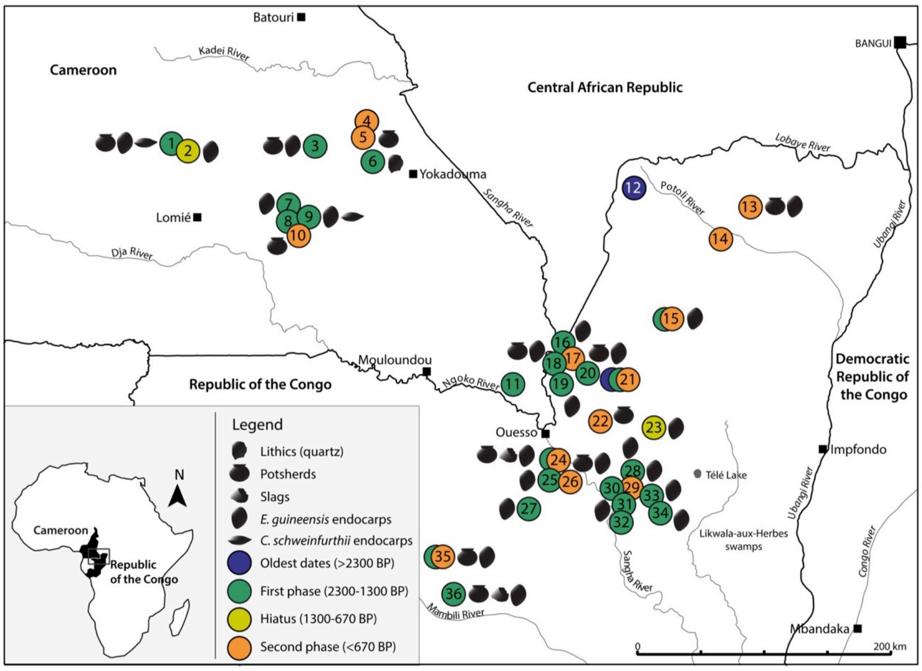


Figure 3.1. Location of the sites, the four phases as well as the archaeological and archaeobotanical findings are reported.

3.2.2. Sampling protocol and radiocarbon dating

Fieldwork was carried out in 6 fieldwork campaigns between 2008 and 2011. Study sites were selected along transects laid out along a vegetation gradient from *Gilbertiodendron dewevrei* monodominant forests to open canopy Marantaceae forests, over stands dominated by deciduous light-demanding tree species. A 1.3 × 1 × 2 m test pit was opened in each of the 36 study sites. The presence of artifacts (i.e. human made objects) and charred botanical remains (either charcoal or charred endocarps) was examined across the whole soil profile in 10-cm layers. Charred material was dated (a) that was associated with human settlement (e.g. next to potsherds) and/or (b) that allowed taxonomic identification (endocarps, charcoals); (c) that ensured accurate dating, wherever possible short-lived material (e.g. charred endocarps); and (d) that was derived from the uppermost 'charcoal layer' (latest fire event). All dates were obtained from fragments between 2 and 4 mm in diameter for charcoals, up to 8 mm in diameter for endocarps. In total, 43 accelerator mass spectrometry (AMS) dates were obtained by the Poznań Radiocarbon Laboratory (Poz) and the Leibniz-Laboratory for Radiometric Dating and Isotope Research of the University of Kiel (KIA). Calibration was performed using the OxCal v4.2.3 program (Bronk Ramsey 1995, 2001, 2013) with the IntCal13 atmospheric calibration curve (Reimer et al. 2013) (***Table 3.1***). Also, using the OxCal program, a summed probability distribution of the dates calibrated in BC/AD was performed so as to compare with Wotzka's group dispersion calibrations for central Africa (Wotzka 2006).

3.3. Results

3.3.1. Radiocarbon dates

A set of 43 radiocarbon dates was analyzed extending from 15,000 BP to the present time (***Table 3.1***). The dates were not evenly distributed across the time period, with most dates belonging to the Late Holocene. When focusing on this most recent period (< 2500 BP), a bimodal distribution was observed, documenting two phases of human expansion, with a contraction phase in between (***Figures 3.1*** and ***3.2***, ***Table 3.1***). The first phase of human expansion spans between 2300–1300 BP (350 BC–AD 650; 25 dates, 58%), while the second phase spans between 670–20 BP (AD 1280 to present; 14 dates, 33%; ***Figure 3.2***). Only four dates deviate from this bimodal distribution (9%). The two oldest dates (12,620 ± 55 and 4610 ± 35 BP, KIA-38067 and Poz-41789, respectively, ***Table 3.1***), correspond to charcoal samples, not identified yet, that may have been produced by natural fires in the absence of any other evidence of human activities. Two others dates (1200 ± 30 and 1050 ± 25 BP, Poz-41780 and KIA-45496, respectively) correspond to oil palm endocarps that may indicate sites of interest for the remaining human populations during the contraction phase.

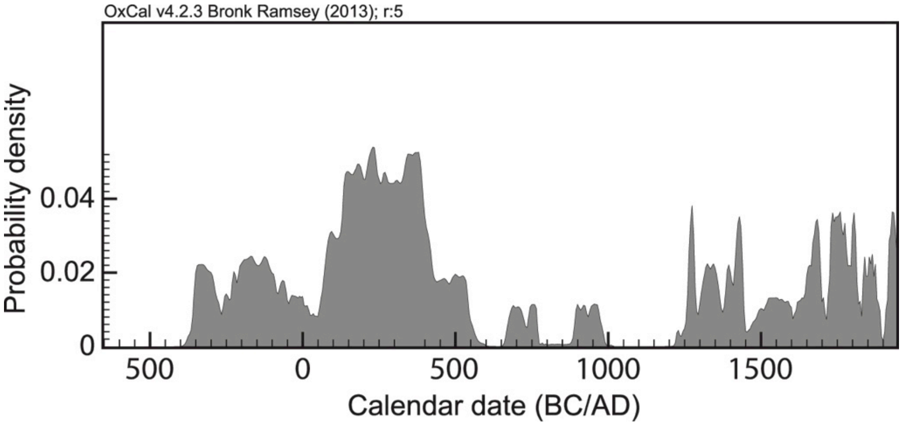


Figure 3.2. Summed probability distribution of the dates calibrated in BC/AD, *n* = 41 dates (the two oldest dates are excluded: KIA-38067 and Poz-41789).

Note that dates are concentrated in two time periods, centered on 2300–1300 BP (350 BC–AD 650) and after 670 BP (after AD 1280).

Table 3.1. Raw dates in years BP with calibrations.

Dates are ranked from the oldest to the most recent and classified into four groups: oldest dates (>2300 BP), first phase of human expansion (between 2300 and 1300 BP), intermediate hiatus phase (between 1300 and 670 BP), and second phase of human expansion (<670 BP). Country: C = Cameroon; RC = Republic of the Congo. 'Map nr' refers to the number indicated in ***Figures 3.1***. Dated material (DM): C = charcoal; CE = charred endocarp. Identified taxa: *E. g.* = *Elaeis guineensis*; *C. s.* = *Canarium schweinfurthii*; *G. d.* = *Gilbertiodendron dewevrei*; *N.* sp. = *Nauclea* sp. Artifacts: Lith. = Lithics; Pot. = Pottery; Iron. = Iron slags.

									Calibration		Artifacts			Charred botanical material		
Country	Site	Map nr	Depth (cm)	DM	Id. taxa	Lab nr	BP	±	68.2%	95.4%	Lith.	Pot.	Iron	C	*E. g.*	*C. s.*
Oldest dates (>2300 BP)																
RC	Mokobo	21	120	C	.	KIA-38067	12620	55	15115/14678	15218/14274	.	.	.	x	.	.
RC	Potoli River	12	145	C	.	Poz-41789	4610	35	5446/5301	5466/5086	.	.	.	x	.	.
First phase of human expansion (2300-1300 BP)																
C	Ndama	3	70	C	.	Poz-38701	2260	30	2330/2183	2345/2157	.	x	.	x	.	.
RC	Ikelemba 1	30	40	C	.	KIA-34143	2170	30	2301/2124	2311/2065	.	.	.	x	.	.
C	Messok 1	8	10	C	.	KIA-38938	2150	45	2301/2060	2309/2003	.	.	.	x	.	.
RC	Landjoué	35	60	CE	*E. g.*	Poz-41782	2130	30	2152/2056	2299/2001	.	x	.	x	x	.
RC	Ilamba 2	34	50	CE	*E. g.*	KIA-34144	2095	30	2115/2008	2145/1994	.	.	.	x	x	.
RC	Pikounda 1	25	50	CE	*E. g.*	Poz-41771	2090	30	2113/2004	2145/1991	.	.	.	x	x	.
C	Messok 2	9	50	CE	*C. s.*	KIA-45499	1980	25	1969/1890	1990/1880	.	.	.	x	x	x
C	Mbol	6	35	C	.	Poz-41773	1870	30	1868/1740	1877/1724	x	.	.	x	.	.
RC	Ikelemba 3	32	30	C	.	KIA-34147	1830	35	1816/1728	1867/1638	.	.	.	x	.	.
RC	Kabo	19	30	CE	.	KIA-37687	1800	30	1811/1699	1821/1626	.	.	.	x	x	.
C	Makalaya	7	50	CE	*E. g.*	KIA-38933	1795	40	1812/1635	1857/1607	.	.	.	x	x	.
RC	Ngombé	24	35	CE	*E. g.*	Poz-38702	1765	30	1718/1619	1811/1571	.	x	.	x	x	.
RC	Loundoungou	15	60	C	.	Poz-41788	1760	40	1721/1610	1812/1565	.	.	.	x	.	.
RC	Bomassa 2	18	35	CE	*E. g.*	KIA-39606	1715	25	1691/1568	1697/1555	.	x	.	x	x	.
RC	Ndoki River	20	45	CE	*E. g.*	KIA-39607	1715	25	1691/1568	1697/1555	.	x	.	x	x	.
C	Ndama	3	50	CE	*E. g.*	Poz-41790	1640	30	1598/1445	1614/1416	.	.	.	x	x	.
C	Mindourou 1	1	45	CE	*E. g.*	KIA-45497	1630	25	1561/1423	1601/1416	.	x	.	x	x	x
RC	Baï Bomassa	16	0	CE	*E. g.*	KIA-38066	1625	25	1556/1422	1567/1415	.	.	.	x	x	.
RC	Ikelemba 2	31	50	CE	*E. g.*	KIA-37684	1590	25	1524/1418	1534/1411	.	.	.	x	x	.
RC	Mambili River	36	65	C	.	Poz-38700	1590	30	1524/1417	1540/1407	.	x	x	x	x	.
RC	Liouesso	27	40	CE	*E. g.*	Poz-41770	1580	30	1518/1417	1535/1403	.	.	.	x	x	.
RC	Pokola 1	28	55	CE	*E. g.*	KIA-34141	1565	30	1516/1411	1528/1389	.	.	.	x	x	.
RC	Mokobo	21	75	C	.	KIA-38070	1535	25	1510/1381	1518/1356	.	.	.	x	.	.
RC	Ilamba 1	33	40	CE	*E. g.*	KIA-37686	1515	30	1415/1349	1518/1334	.	.	.	x	x	.
C	Boulou River	11	40	C	*G. d.*	Poz-41778	1510	30	1412/1351	1515/1327	.	.	.	x	.	.
Intermediate hiatus phase (1300-670 BP)																
RC	Komo River	23	40	CE	*E. g.*	Poz-41780	1200	30	1171/1077	1239/1013	.	.	.	x	x	.
C	Mindourou 2	2	35	CE	*E. g.*	KIA-45496	1050	25	968/932	1052/925	.	.	.	x	x	.
Second phase of human expansion (<670 BP)																
RC	Ngombé	24	35	C	.	Poz-38703	675	30	671/567	679/560	.	x	x	x	.	.
RC	Pokola 2	29	35	CE	*E. g.*	KIA-34142	620	25	652/558	658/551	.	.	.	x	x	.
C	Bali River 2	5	30	C	.	Poz-41775	590	30	637/547	652/537	.	x	.	x	.	.
RC	Pikounda 2	26	20	CE	*E. g.*	Poz-41772	520	30	546/516	626/507	.	x	.	x	x	.
RC	Djaka River	22	40	C	.	Poz-38696	335	35	460/317	482/308	.	x	.	x	.	.
RC	Ebaleki River	13	20	C	.	Poz-38697	315	30	430/309	467/302	.	x	.	x	x	.
RC	Landjoué	35	35	CE	*E. g.*	Poz-41781	290	30	429/299	458/288	.	x	.	x	x	.
RC	Mokobo	21	30	CE	*N.* sp.	KIA-37685	215	25	300/-2	305/-4	.	.	.	x	.	.

C	Messok 3	10	10	C	.	KIA-38934	205	30	296/-2	305/-4	.	x	.	x	.	.
RC	Bomassa 1	17	20	C	.	KIA-37683	200	25	290/-2	299/-4	.	.	.	x	.	.
C	Messok 3	10	210	C	.	KIA-38942	195	30	288/-2	303/-4	.	.	.	x	.	.
RC	Lopola	14	30	C	.	Poz-41784	140	25	270/12	281/6	.	.	.	x	.	.
C	Bali River 1	4	10	C	.	Poz-41774	110	25	257/33	268/16	.	.	.	x	.	.
RC	Loundoungou	15	20	CE	*E. g.*	Poz-41787	90	30	254/33	266/22	.	.	.	x	x	.
Total occurrences											1	14	2	43	24	2

3.3.2. Archaeological and archaeobotanical findings

Evidence of human activities either artifacts or charred botanical remains (e.g. edible fruits) were found across the whole study area (***Figure 3.1***). Artifacts were found in 13 test pits (36% of the sites) with dates spanning between 2260 ± 30 BP (Poz-38701) and 205 ± 30 BP (KIA-38934) (***Table 3.1***). Among them, lithics (quartz flakes) were found in only small quantities in one test pit at the Mbol site while potsherds were frequently observed across the study area (12 test pits, 33%, ***Table 3.1***). The potsherds (dated through charcoals) correspond to the two expansion phases described above: from 2260 ± 30 BP (Poz-38701) to 1590 ± 30 BP (Poz-38700) and from 675 ± 30 BP (Poz-38703) to 205 ± 30 BP (KIA-38934). Some of them, from both phases, showed a *roulette* decoration. In two sites in the Republic of the Congo, Mambili River and Ngombé, iron slags dating from 1590 ± 30 BP (Poz-38700) and 675 ± 30 BP (Poz-38703), respectively, were associated with potsherds.

Charred botanical remains were extracted from all test pits at different depths. Charcoals were the most numerous and could be found in all sites (***Table 3.1***). Several charcoal layers could occur in the same test pit, suggesting that the current dense forests had undergone repeated fire events during the Holocene. A total of 23 test pits provided charred endocarps, mostly oil palm endocarps (*E. guineensi*s Jacq., 64%), with dates covering the whole chronology from 2130 ± 30 BP (Poz-41782) to 90 ± 30 BP (Poz-41787). Endocarps of *Canarium schweinfurthii* Engl. were found in two test pits in Cameroon (Mindourou 1 and Messok 2), in association with potsherds in the latter pit. These endocarps were dated from the first phase of human expansion (***Figure 3.1***), at 1980 ± 25 BP (KIA-45499) and 1630 ± 25 BP (KIA-45497), respectively.

3.4. Discussion

3.4.1. Temporal and spatial patterns of human activities

The aim of this study was to identify the temporal and spatial patterns of human activities in archaeologically unexplored areas of the northern Congo Basin that are currently covered by dense forest. To document this aspect, archaeological and archeobotanical evidence was found across the whole study area. Two phases of human expansion were noted during the Late Holocene (2300–1300 BP and after 670 BP), with a contraction phase in between in which there is almost no evidence of human settlement (1300–670 BP). The dates from both phases were evenly distributed and thus demonstrated a similar spatial pattern in the history of human activities, though the most distant sites were located several hundred kilometers apart.

The archaeological evidence showed human presence in the forest block from 2300 BP, confirming the hypothesis of a first occupation of magnitude in the northern Congo Basin with visible traces of human settlements (Wotzka 2006, Brncic et al. 2007). This first population peak between 2300–1300 BP followed the major forest fragmentation after the

2500 BP climatic dry event (Maley 2002, Ngomanda et al. 2005), whereas the second population peak (670–20 BP) may be related to moderate climatic fluctuations in central Africa (Maley 2003) corresponding to the Little Ice Age in Europe (Brncic et al. 2007, Russell and Johnson 2007). The results presented here confirm and extend Wotzka's (2006) observations describing the same temporal pattern for central Africa. This two-peak curve structure seems indeed to be specific to the part of central and west-central Africa currently covered by dense forests. The differences seen in the amplitude of the two peaks may thus be explained by differences in the tempo of the wave of human expansion from east to west equatorial Africa after about 2500 BP and of the decline of human settlement from west to east that occurred during the last millennium (Wotzka 2006).

However, an uncertainty persists in interpreting the scarcity of dates between 1300 and 670 BP. Following the successful colonization of the Congo Basin by 'Bantu-speakers' from 2500 BP, several authors evoked a hiatus between 1400 and 800 BP (Oslisly 1998, 2001, Assoko Ndong 2002, Wotzka 2006). This hiatus has been interpreted as a population collapse that was caused by a wet climatic event (Schwartz 1992, Oslisly 2001, Assoko Ndong 2002). Oslisly (2001) postulated that a widespread epidemic disease could be at the origin of this hiatus. Such a hypothesis is still debated (Clist, reported by Wotzka 2006), although historical sources related major outbreaks of trypanosomiasis at the end of the 19th century (Sautter 1966, Oslisly et al. 2013a). Wotzka (2006) added that a lack of any human evidence may reflect differential destructive taphonomic processes, i.e. in this study a potential destruction of the archaeological remains during the Late Holocene due to the combination of a wetter period and of the acidity of equatorial soils (Eggert 1993, Schwartz and Lanfranchi 1993, Mbida et al. 2000). Given that the exact reasons of this large-scale event remain unclear, as well as its geographical extent, further results are needed to confirm any of these hypotheses.

3.4.2. Cultural evidence for human presence within the forest

Among the artifacts, potsherds were extremely frequent, with the oldest dating to 2260 ± 30 BP. Some from the 2300–1300 BP phase, as well as the 670–20BP phase, showed a so-called *roulette* decoration, a decorative technique that was invented ~4000 yr ago in West Africa. In this technique, a cylindrical object (carved or knotted) is rolled on the unbaked clay pots (Livingstone Smith 2007). This *roulette* technique has been attested in northwestern Cameroon around 2500–2000 BP during the Early Iron Age and persisted throughout the Late Iron Age (Livingstone Smith 2007). Despite its spread in a wide area from Senegal to the African Great Lakes, its dissemination into the central African forest block was very limited. Livingstone Smith (2007) reported a probable cultural boundary between farming and non-farming populations, which could be placed at the river Lom, northwest of Batouri (southeastern Cameroon). Our findings push this limit southwards and indicate that ~2200 BP the forest dwellers either knew the *roulette* decoration technique or had contact with populations that used it. The study area may be a contact zone between different cultures, which again raises the question of the connections between foragers and food producers (Bahuchet 1996, Clist 2006, de Luna 2012). Although the *roulette* decoration has been identified on potsherds, no precise typotechnological analysis based on shape and decoration has been carried out thus far.

The iron slags associated with potsherds in two sites in northern Republic of Congo demonstrate the presence of iron-smelting activities in sedentary settlements. The oldest site (Mambili River) dated to 1590 ± 30 BP (Poz-38700) represents the latest activity recorded for the Early Iron Age in the present study, whereas the other (Ngombé) occurs at the beginning of the Late Iron Age period (675 ± 30 BP, Poz-38703). Early Iron Age iron-smelting features dated to 2020–1800 BP have been excavated at Likwala-aux-Herbes River site in Congo (Eggert 1993), which is located near our discoveries. New archaeological surveys may allow outlining the framework of the Iron Age occupations.

Flakes of quartz were only discovered in one site (Mbol) dated to 1870 ± 30 BP (Poz-41773). In the Cameroonian forest, the Neolithic is attested to by such an expedient lithic industry associated with stone axes and hoes from 3000 BP. Lithics disappeared with the introduction of iron tools around 2800–2600 BP from the Central African Republic (Clist 2006). Our late date may indicate a recent use of stone flake industries in the forest by populations of foragers or an opportunistic use by food-producers. Nonetheless, as the quartz tools suggest neglected industries, efforts shall be made to understand their implications in forest people's lifestyles.

3.4.3. Economic behaviors

In addition to artifacts, plant remnants were used to demonstrate human activity. Charred botanical remains were discovered in all sites, especially charcoal. Several charcoal layers could be located in a same test pit, confirming the existence of repeated past fire events in the study area. Visible charcoal layers, in the absence of confirmed archaeological sites, may indicate the presence of ancient fields created by slash-and-burn agriculture (van Gemerden et al. 2003) or natural fires in periods of seasonal droughts (Hubau et al. 2013) though the latter seldom occur in the region (Maley 2002).

Our results mainly highlighted the recurrence of charred endocarps indicative of the economic behaviors of past populations (Neumann et al. 2012a). The most abundant were the endocarps of the oil palm *E. guineensis*, which appeared to be younger than 2200 BP in many of the study sites. Oil palm endocarps are frequently observed in archaeological sites in west and central Africa (Lavachery 2001, Lavachery et al. 2005, Logan and D'Andrea 2012). In palynological records, the increasing abundance of palm trees during the Late Holocene has led to controversial interpretations about its anthropogenic (Sowunmi 1999) versus natural origin, fostered by forest fragmentation after 2500 BP (Maley and Chepstow-Lusty 2001). Linguistic and archaeobotanical studies have well documented the antiquity of the use of products from oil palm and wild trees before agriculture (Bostoen 2005, D'Andrea et al. 2006, Blench 2007, Kahlheber and Neumann 2007). Current knowledge, however, is not decisive in favor of an ancient tree management with the preservation of useful trees and oil palms during the forest clearing, as proposed by several authors (Lavachery 2001, Mercader et al. 2006, D'Andrea et al. 2006, Oslisly and White 2007).

In this study, endocarps of *C. schweinfurthii* dated between 1980 ± 25 BP and 1630 ± 25 BP (KIA-45499 and KIA-45497) were found in two test pits in Cameroon. This result is consistent with previous findings in Early Iron Age sites (Oslisly et al. 2000, Neumann et al. 2012a). Indeed, the fatty components of *C. schweinfurthii* make this species attractive for populations that can use it for several purposes including cooking (Abayeh et al. 1999). An ancient use of *C. schweinfurthii* was attested to about 11,000 BP in DRC (Mercader et al. 2003) and to 8000 BP in northwestern Cameroon (Lavachery 2001). *C. schweinfurthii* endocarps have been found later, too, in Neolithic sites in Gabon. Hence, it could be hypothesized that more sedentary human populations at the premises of arboriculture have used this wild species from late Prehistory (Clist 2006). Nonetheless, as only few endocarps were found in the study area, no firm conclusions can be made as to whether this species was used extensively. Various charred seeds were also found in the test pits and further identification work is needed to study the economy of past forest populations.

3.5. Conclusion

This study gathered new and extensive evidence of past human activities during the Holocene in the northern Congo Basin, in archaeologically unexplored areas that are today covered by dense forest. Two phases of human expansion are highlighted, from 2300 to 1300 BP and from 670 to 20 BP, with an intermediate contraction phase. This chronology fits into the established archaeological framework and suggests a general trend in the history of human settlements across central Africa. The observed fluctuations in human populations raise the question of the extent of their impact on the environment through time. In particular, the second phase of human expansion may have triggered the recruitment of the long-lived light-demanding tree species some centuries ago, which currently dominate the canopy in the area.

Chapter 4 High spatial resolution of late-Holocene human activities in the moist forests of central Africa using soil charcoal and charred botanical remains

Chapter 3 showed that evidence of human presence could be found fortuitously when digging in the forest soil. The radiocarbon ages highlighted two phases of human activities, comforting the established archaeological chronology in central Africa. **In this chapter**, we go further on the exploitation of biomarkers of land-use, and present a systematic methology based on soil charcoal and charred botanical remains. These biomarkers allowed us documenting new dated archaeological evidence at two distant sampling sites, as well as determining two main types of human activities, i.e. domestic in villages, and agricultural out of archaeological sites.

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L'infinité de l'horizon – Véronique LG Morin

Abstract

Palaeoecological and archaeological studies have demonstrated that human populations have long inhabited the moist forests of central Africa. However, spatial and temporal patterns of human activities have hardly been investigated with satisfactory accuracy. In this study, we propose to characterize past human activities at local scale by using a systematic quantitative and qualitative methodology based on soil charcoal and charred botanical remains. A total of 88 equidistant test-pits were excavated along six transects in two contrasting forest types in southern Cameroon. Charred botanical remains were collected by water-sieving and sorted by type (wood charcoals, oil palm endocarps and unidentified seeds). A total of 50 Accelerator Mass Spectrometry ^{14}C dates were also obtained. Results showed that charred macroremains were found at multiple places in the forest, suggesting scattered human activities, which were distributed into two main periods (Phase A: 2300–1300 BP; Phase B: 580 BP to the present). Charred botanical remains indicated two types of land-use: (1) domestic, with oil palm endocarps most often associated with potsherds (villages) and (2) agricultural, with charcoal as probable remnant of slash-and-burn cultivation (fields). Oil palm endocarp abundance decreased with distance from the identified human settlements. Our methodology allowed documenting, at high resolution, the spatial and temporal patterns of human activities in central African moist forests and could be applied to other tropical contexts.

Keywords: archaeology, charred endocarps, human settlements, late-Holocene, oil palm, soil charcoal, tropical Africa

4.1. Introduction

Palaeoecological and archaeological evidence of ancient and scattered human activities have demonstrated that human populations have long inhabited the tropical forests worldwide (Willis et al. 2004, Barton et al. 2012). These biomes therefore cannot be regarded as pristine anymore, as they were occupied for several millennia by groups of hunter-gatherers, followed by farmers who settled in areas that are covered by dense forest today. In tropical Africa, it has been assumed that these human activities have had a substantial impact on vegetation structure and composition (Oslisly et al. 2013a). Specifically, early slash-and-burn shifting cultivation has been assumed to have formed scattered openings in the canopy that have allowed long-lived light-demanding trees to establish two to three centuries ago, and today, these trees represent an important component of canopy trees (Gond et al. 2013, Engone Obiang et al. 2014, Vleminckx et al. 2014, Biwolé et al. 2015). Nonetheless, this assumption raises three issues. The first relates to the distinction between anthropogenic and natural signals in the record, as natural fires have occurred irrespective of human presence, specifically during dry climatic events in the late-Holocene (i.e. after 2500 BP) (Hubau et al. 2015). The second issue concerns the observation scale, whether regional or local, of the anthropogenic disturbances and their impacts. The third deals with the quantitative and qualitative characterization of these human disturbances, especially in underexplored areas, because of difficulties related to fieldwork accessibility.

Numerous studies have documented an increasing human presence since the late-Holocene in tropical Africa (after 2500–2300 BP; De Maret 1986, Denbow 1990, Eggert 1992, Wotzka 2006, Oslisly et al. 2013b), probably mediated by a strong dry climatic event that has been recorded between 3000 and 2000 BP throughout central Africa (Elenga et al.

1996, Reynaud-Farrera et al. 1996, Maley and Brenac 1998, Vincens et al. 1999, 2010, Ngomanda et al. 2009b, Lézine and McKey 2013). Late-Holocene aridity resulted in a strong forest regression with patchy landscapes that may have contributed to the southwards expansion of Bantu-speaking populations, coming from the northwestern fringes of the Cameroonian forests (Schwartz 1992, Lanfranchi et al. 1998, Clist 2006, but see Eggert 1992 for a review of the archaeo-linguistic aspects). Nonetheless, human history has hardly been documented precisely, particularly in the dense forests of southern Cameroon. Until now, only a few archaeological sites have been excavated (e.g. Essomba 1998, Lavachery et al. 2005, Eggert et al. 2006, Meister 2008, 2010, Neumann et al. 2012a). The systematic surveys undertaken during rescue excavations since the 2000s have constituted an exception in the almost empty archaeological landscape (e.g. the Campo Ma'an National Park and the Lolodorf–Kribi–Campo road-axe in SW Cameroon, the Lom Pangar dam and the Bertoua–Garoua–Boulaï road-axe in SE Cameroon (Mbida Mindzie et al. 2001, Oslisly 2010). In contrast, archaeological findings in southern Cameroon have often depicted a rough image of scattered and localized human activities (Morin-Rivat et al. 2014). Indeed, they mainly consist of infrequent and incidental findings in the form of artefacts (e.g. stone tools, potsherds and iron slags) and charred botanical remains (e.g. charcoals and endocarps). Among the discoveries, wood charcoal is by far the most ubiquitous.

No agreed terminology or methods exist in charcoal studies, but rather a constellation of uses of charcoal to test various hypotheses in different biogeographical contexts (Scott and Damblon 2010). In particular, pedoanthracology (i.e. the weighing, dating and identification of charcoals buried in soils; Carcaillet and Müller 2005) has been developed then most often used in alpine and subalpine contexts (Thinon 1978, Carcaillet and Thinon 1996). Previous studies have dealt with treeline shifts and vegetation changes caused by Pleistocene natural paleofires, exacerbated by further late-Holocene anthropogenic burnings for agro-pastoral purposes (e.g. Carnelli et al. 2004, Di Pasquale et al. 2008, Carcaillet et al. 2009, Talon 2010, Touflan et al. 2010). Charcoal has also been used to detect the spatial patterns of fire regimes as well as fire-return intervals in boreal and temperate forests (e.g. Ohlson and Tryterud 2000, Gavin et al. 2003, Sanborn et al. 2006, Robin et al. 2011, De Lafontaine and Payette 2012, Novák et al. 2012). In the Neotropics, charcoal analyses have demonstrated that climate was either the dominant driver of paleofires at some sites or that both climate and human activity were the main drivers during the mid-Holocene, whereas fires have been mainly attributed to man during the late-Holocene (Tardy et al. 2000, Titiz and Sanford Jr 2007, McMichael et al. 2012). The Amazonian *Terra Preta* fertile soils constitute an emblematic example of dark earths from anthropogenic origin (Kämpf et al. 2003, Glaser 2007, Glaser et al. 2000, 2001). These soils have been described as a mixture of slash-and-burn residues, waste and residential refuse, accumulated during extended occupation of archaeological sites. These remains have mainly been dated to the late-Holocene (Glaser et al. 2000, Pessenda et al. 2004, Hammond et al. 2006, Bush and Silman 2007). In central Africa, charcoal analyses have mostly been limited to sedimentary micro charcoal from lakes or shallow depressions to detect ancient fire regimes at a regional scale (Brncic et al. 2007, 2009, Aleman et al. 2013, Tovar et al. 2014). Up until recent, studies on macro charcoal from soil have been scarce (Hart et al. 1996); however, they have been used lately in underexplored areas to link Quaternary fire events to past climate changes in the Democratic Republic of Congo (Hubau et al. 2012, 2013, 2015) and to test the relationship between anthropogenic disturbances and current vegetation in southern Cameroon (Vleminckx et al. 2014, Biwolé et al. 2015, Bourland et al. 2015). However, these recent studies have raised difficulties in the interpretation of the anthropogenic signal of disturbance. Issues namely arise related to either the sampling plan (Bourland et al. 2015) or to the quantitative methods, based on auger sampling (small sampled volumes) and charcoal hand-picking (Vleminckx et al. 2014). In addition, former soil charcoal samplings in the framework of archaeological research have highly been selective and have mainly considered points of interest in the landscape, such as ridges, watercourses or useful trees for local populations (Oslisly and White 2003), but they have rarely been systematic. In any cases, a systematic and quantitative sampling, such as we propose in the present study, is crucial, especially for high-resolution analyses (Dutoit et al. 2009, Théry-Parisot et al. 2010).

In this study, we aimed at defining the spatial and temporal patterns of past human activities at local scale, by using a systematic quantitative and qualitative methodology based on dated indicators of human presence (i.e. artefacts) and land-use biomarkers (i.e. charcoal and other charred remains). In particular, we tested the presence, over time and at local scale, of different types of human activities, which has, to our knowledge, never been demonstrated with such accuracy in tropical Africa. We particularly tackled the following research questions: (1) Can a precise methodology, based on charred macrobotanical remains from soil pits, be used to detect human land-use (as opposed to natural change)? (2) Can this allow for a good interpretation of human activity and settlement in tropical Africa covered by dense forest? (3) What are the temporal patterns of this human activity? (4) What is its spatial extent over land?

4.2. Materials and methods

4.2.1. Study sites

The study was carried out between February and April 2012 in southern Cameroon (***Figure 4.1***), in two contrasting study sites in terms of vegetation, soil and geological substrate (hereafter called Site 1 and Site 2). The climate in both sites is equatorial, with two wet seasons interrupted by two dry seasons. The sites are located in forest management units (FMU) that are under FSC certificates for sustainable forest management. All forest concessions belong to the permanent forest domain and legislation prohibits agriculture in the concessions. Current villages and associated shifting cultivation are only located along the roads (Carrière 1999, and personal observation). Current population density is less than 10 inhabitant/km^2 in Site 1 and less than1 inhabitant/km^2 in Site 2 (Afripop 2013).

Site 1 (2°10′–2°39′N, 10°11′–10°53′E) is located in southwestern Cameroon, east of the Campo Ma'an National Park, in two FMU (logging company Wijma). Monthly average temperatures fluctuate around 25°C and mean annual rainfall ranges between 1669 (Bitam station, Gabon) and 2740 mm (Kribi station; http://www.climatedata.eu). The topography is hilly with a maximum altitude of 600 m. The geological substrate entails old volcanic intrusions and Precambrian metamorphic rocks (Franqueville 1973), and is overlain by Ferralsols (red-dominant) and Acrisols (yellow-dominant) (van Gemerden et al. 2003). The vegetation belongs to the mixed forest including lowland wet evergreen littoral and semi-deciduous types (Letouzey 1985). The canopy is dominated by long-lived light-demanding species like *Lophira alata* (Ochnaceae) (Vleminckx et al. 2014).

Site 2 (3°45′–4°03′N, 14°17′–14°31′E) is located in southeastern Cameroon, north-east of the Dja Reserve, in three FMU (logging company SFID-Mbang, Groupe Rougier). Monthly average temperatures fluctuate around 25.2° C and mean annual rainfall ranges between 1518 mm (Mouloundou station) and 1616 mm per year (Lomié station; www.climatedata.eu). The topography is broadly flat, with altitude between 600 and 700 m.

The geological substrate consists of weathered Precambrian schisto-quartzitic rocks (Vennetier 1963), overlain by Ferralsols (Martin and Ségalen 1966). The vegetation mainly belongs to the semi-deciduous forest types (Letouzey 1985). Canopy is dominated by long-lived light-demanding species from the Cannabaceae (*Celtis* spp.) and Malvaceae (*Triplochiton scleroxylon*) families (Fayolle et al. 2014a).

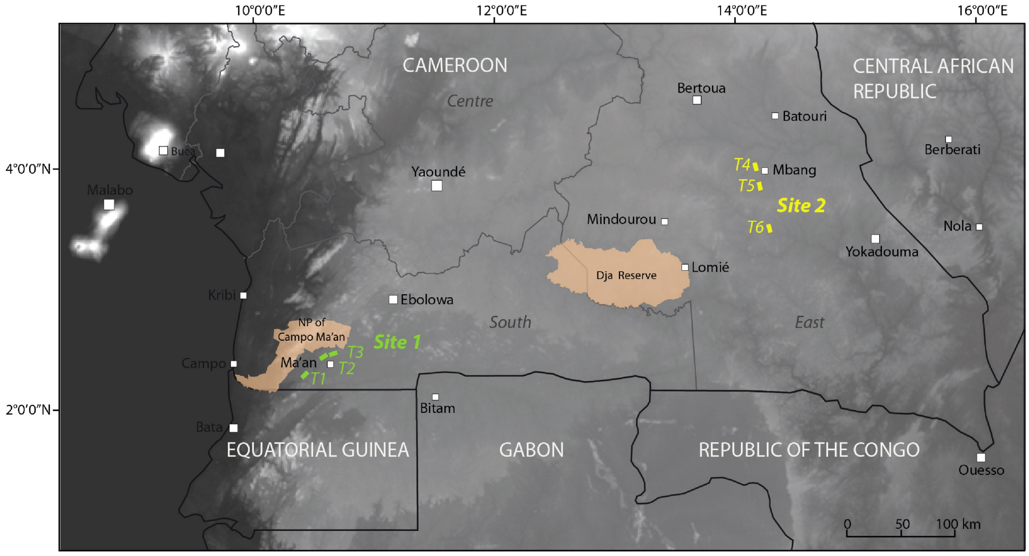

Figure 4.1. Location of the two study sites in southern Cameroon: Site 1 (in green) in the South Region near the Campo Ma'an National Park, Site 2 (in yellow) in the East Region near the Dja Reserve (park and reserve in light orange).

4.2.2. Sampling design

To document past human activities in the two study sites, we performed a systematic sampling along three transects in each study site that ran across all the FMU at each site (T1, T2 and T3 in Site 1; T4, T5 and T6 in Site 2) (***Figure 4.1***). We specifically chose unlogged areas in the forest concessions. In Site 1, transects were each 3 km long (9 km in total), the two most distant transects (T1 and T3) were 26 km apart. In Site 2, they reached 4.8 km (14.4 km in total). The two most distant (T4 and T6) were 63 km apart. Transects were shorter at Site 1 because of difficulties during fieldwork. At both sites, watercourses and swamps were located along transects. Along each transect, the slope was measured every 20 m with a clinometer to draw the topographic profiles. Sampling in riverbanks and swamps, including on steep slopes, was avoided because of inherent erosion and colluvium processes (in agreement with Carcaillet 2001b). At each transect, a test-pit of 0.5 m×0.5 m wide and 0.6 m deep was excavated every 250 m after removing the organic layer. We thus obtained a total of 12, 11 and 12 test-pits (P1 to P11/12) in T1, T2 and T3 of Site 1 and 19, 18 and 16 test-pits (P1 to P16/18/19) in T4, T5 and T6 of Site 2 which provided a total of 88 sampling test-pits for both sites (35 for Site 1 and 53 for Site 2). The skeletal content as well as the structure and colour of the soil were described (Carcaillet 2001b), but no stratigraphic change was detected. Artefacts were extracted and inventoried by 10-cm layers. Reference pedological pits of 1 m × 1.3 m wide and 1.5 m deep were also excavated within each site (6 in Site 1 and 9 in Site 2) between 10- and 20-m distance from the test-pits. The reference soil profiles were oriented in a northwards direction. They were used for comparison purposes with the test-pits of the age–depth relationship.

4.2.3. Macrobotanical remains collection

To avoid human bias by hand-picking the visible charcoals and macroremains only (Carcaillet and Thinon 1996), fixed volumes of 3 L of bulk soil were sampled by 10-cm layers, providing a total of 18 L of soil per test-pit. The soil samples were transported to the nearest watercourse and water-sieved directly on site through a 2-mm mesh sieve. The intermediate 2-mm mesh size constituted a good compromise between efforts during fieldwork, the sorting in laboratory and the possibility of further taxonomical identification on the macro charcoal fragments (i.e. ≥1 mm according to the definition of Scott 2010). Sieve refuses were subsequently air-dried.

In the laboratory, the charred botanical remains were manually separated from the mineral refusal under a dissection microscope (×20). To test whether the different categories of remains represent the same signals of human activity, we sorted them into three categories: (1) wood charcoals, (2) charred oil palm endocarps (*Elaeis guineensis*) and (3) unidentified charred seeds (in the absence of an exhaustive reference collection for these biomes). All materials were separately dried and subsequently weighted by depth and by category on a precision scale (0.01 g in accuracy).

4.2.4. Statistical analysis

For each study site, we tested Pearson correlation coefficients (using classical parametric test) between the quantities (g/L) of charcoal, oil palm endocarp and unidentified seeds (after performing a log (quantity + 1) transformation of these variables), in order to determine whether they characterized the same types of human activities. To test whether the different transects and test-pits experienced similar anthropogenic disturbance regimes, a linear mixed effect model with six factors (sites, depths, transects within sites, pits within transects, transects depending on depth within sites and pits depending on depth within sites) was performed on charcoal and oil palm endocarps separately (R software 3.2.4, www.r-project.org/). Sites, transects and test-pits were considered as random effects, while depth was defined as a fixed effect. The abundance of charcoal and oil palm endocarps underwent a logarithmic transformation to meet the assumption of normality (Biwolé et al. 2015).

Smaller scale spatial structures were characterized for each variable (within each site) by calculating their spatial autocorrelation using Moran's *I* statistic (Moran, 1948). The latter was computed as follows:

$$I_{ab} = \frac{(x_a - \bar{x})(x_b - \bar{x})}{Var(x)} + \frac{1}{(n-1)}$$

where x_1 and x_2 are, respectively, the values of variable X for samples a and b, while x and $Var(x)$ represent the mean and variance of the variable, respectively. The $1/(n-1)$ term was used to ensure that the average I_{ab} computed for all existing a, b pairs equals zero. Mean Moran's *I* values were computed for 12 to 14 distance intervals and plotted against spatial distance (autocorrelograms) to visually characterize spatial patterns at different scales: within a test-pit (distinguishing adjacent soil layers from layers separated by two to four layers), within a transect and among sites. Mantel tests between the spatial distance matrix and the I_{ab} matrix were performed to determine the significance of the spatial structure of each variable (Vleminckx et al. 2014).

Finally, we tested the Pearson correlation coefficient between each category of botanical remains and the distance to the nearest pottery discovery, in order to determine whether they were related to human settlement. To avoid type I error inflation due to spatial dependence between data points, correlation coefficients were tested by comparing the observed values with a null distribution of coefficients obtained after performing 4999 translations similar to torus-translations (Harms et al. 2001). More precisely, this procedure consisted in randomly shifting test-pits within each transect independently, while preserving the original disposition of the test-pits, except at transect extremities where test-pits were transposed to the opposite extremity (as if test-pits were located along a ring). *P*-values were then obtained as the proportion of correlation values lying outside the 95% confidence envelope. Spatial autocorrelation and torus-translation tests were performed using software Torocor 1.0 (http://ebe.ulb.ac.be/ebe/Software.html, Vleminckx et al. 2014). Input files for the spatial autocorrelations are available in the ***Appendices 1*** (Site 1) and ***2*** (Site 2), and for the torus-translations in the ***Appendices 3*** (Site 1) and ***4*** (Site 2).

4.2.5. Radiocarbon dating

Radiocarbon dating was performed on 50 charred pieces, namely 25 for each study site, including 37 on oil palm endocarps, 1 on an unidentified charred seed and 12 on wood charcoals in the absence of short-lived material (***Table 4.1***). Samples were chosen preferentially on hilltops or flat topographic situations to get reliable data from human sites (Oslisly and White 2003) and to avoid colluvium (Carcaillet 2001b). Two soil profiles up to 150-cm depth were chosen in T3 of Site 1 (plot P3) and T6 of Site 2 (plot P9) as reference profiles to test the age–depth relationship, with five oil palm endocarps dated at regularly spaced depths in each profile (by 20-cm layers in Site 1 and 10-cm layers in Site 2). All dates were obtained from samples with sizes ranging 2- to 4-mm diameter for charcoals, and up to 6-mm diameter for endocarps. Single oil palm endocarps or charcoals in direct contact with potsherds were used to estimate the age of pottery (Bourland et al. 2015). The Poznań Radiocarbon Laboratory (Poz) dated the 50 charcoal samples using Accelerator Mass Spectrometry (AMS). Calibration was performed in the OxCal v4.2.3 program (Bronk Ramsey 2013) set with the IntCal13 atmospheric calibration curve (Reimer et al. 2013). To estimate the temporal distribution of events and to compare the two study sites, we performed a summed probability distribution of the radiocarbon dates calibrated in BP, in combination with a Bayesian model (Bronk Ramsey 2009). Finally, we drew maps of the temporal patterns of each study site by using the same Bayesian distributions of the radiocarbon ages (Bronk Ramsey and Lee 2013) and added the macroremains quantities for each dated plot (***Appendix 5***).

4.3. Results

4.3.1. Charcoal, oil palm endocarps and seeds spatial patterns

Macrobotanical remains were found in all transects (***Figure 4.2***). The summed masses ranged from 5.25 to 11.20 g/L in Site 1 (T3 and T1, respectively) and from 1.62 to 3.73 g/L in Site 2 (T5 and T6, respectively). The remains were present in 76 test-pits out of 88 (Site 1: all test-pits out of 35; in Site 2: 41 test-pits out of 53). They were found at all depths up to 60 cm in both sites. Charcoals were present in 71 test-pits out of 88 (Site 1: all test-pits out of 35; in Site 2: 36 test-pits out of 53) and represented 116.29 g in Site 1, 27.07 g in Site 2, while oil palm endocarps were present in 53 out of the 88 test-pits (Site 1: 32 test-pits out of 35; in Site 2: 36 test-pits out of 53) and represented 17.73 g in Site 1 and 24.91 g in Site 2.

Unidentified seeds were less present as they were found in 34 test-pits out of 88 (Site 1: 14 test-pits out of 35; in Site 2: 20 test-pits out of 53). They represented 2.53 g in Site 1 and 1.41 g in Site 2.

Within each study site, no significant difference was observed for charcoal and oil palm endocarps abundance between transects (***Table 4.2***), while the abundance of unidentified seeds was significantly different between transects of Site 2 (namely more present in T4).

Significant spatial structures were found in both sites for charcoal and oil palm endocarps, while no significant Moran's I values were found for the seeds (***Figure 4.3***). However, spatial autocorrelation was only significant for soil layers separated by 10 to 25 cm for charcoal masses, and among all layers for oil palm endocarps.

4.3.2. Relationship between archaeological findings and the presence of charred botanical remains

Artefacts were found in 11 pits (5 pits in Site 1; 6 in Site 2), identifying the presence of human settlements in both study sites (***Figure 4.2***, ***Table 4.3***). All potsherds were recorded on hilltops or plateaus and/or within 250–500 m of a watercourse. Two opaline–quartz flakes were also discovered in two soil profiles on transect T1 in the soil pit of plot 7 and on T3 in the soil pit of plot 3 between 70- and 80-cm in depth. A grindstone in quarzitic sandstone and a quartz flake were found in Site 2 Transect 4 in a soil pit at 80, and two other flakes at 140-cm depth. Detailed analysis of the archaeological material will be performed in a future study.

The abundance of oil palm endocarps was significantly higher in test-pits where archaeological material was found (***Table 4.4***). However, no significant difference was observed regarding the abundances of charcoal and unidentified seeds. When plotting these abundances against the distance to the nearest pottery finding, we observed a decreasing trend that was more significant for oil palm endocarps than for charcoal or seeds in both sites (***Figure 4.4***). All trends were significant for oil palm endocarps but not for the two other macroremains categories, according to Pearson correlation tests. However, the only strong trend observed ($R^2 = 0.38$) declined ($R^2 \approx 0.06$) when removing the five plots separated by a null value. These five values were also far apart (great variation).

4.3.3. Radiocarbon ages temporal distribution

The 50 radiocarbon ages obtained spanned from 2800 cal. BP (Site 2) and 2350 cal. BP (Site 1) to the present time (***Table 4.1***, ***Figure 4.5***), but with an older date around 10,700 cal. BP in Site 2 (***Table 4.1***). Ages were mainly distributed into two similar time periods, with slight time shifts between the study sites: (1) a first period between 2350 and 1500/1350 cal. BP (Phase A), (2) a second period, with fewer dates between 1500/1350 and 580/300 cal. BP (hiatus) and (3) a third period between 580/300 cal. BP and the present (Phase B).

The age–depth relationship was weak at both sites (see Vleminckx et al. 2014), but with similar patterns. Young dates after 800 cal. BP concentrated in the first 30-cm depth while older dates between 1500 and 2800 cal. BP clustered in the first 40-cm depth. Radiocarbon ages focused on 2300 cal. BP were found deeper than 40 cm (i.e. in the reference soil pits at both sites). The oldest date around 10,700 cal. BP in Site 2 was found between 100 and 110 cm.

Modeled distributions of the radiocarbon ages were mapped at 200-year intervals (***Appendix 5***). The distributions showed the discontinuity of spatial occupation over time and the 2000- to 2800-km spacing between synchronous human activities in a same transect, especially around 1800 BP in both sites. Distances dropped below 2000 km around 1600 BP. The maps also demonstrated a southward displacement of the disturbances over time in Site 2. Charcoal and oil palm endocarps quantities in the dated test-pits showed reverse trends between very spatially close test-pits in the same transect. In addition, potsherds were more often associated with larger quantities of oil palm endocarps.

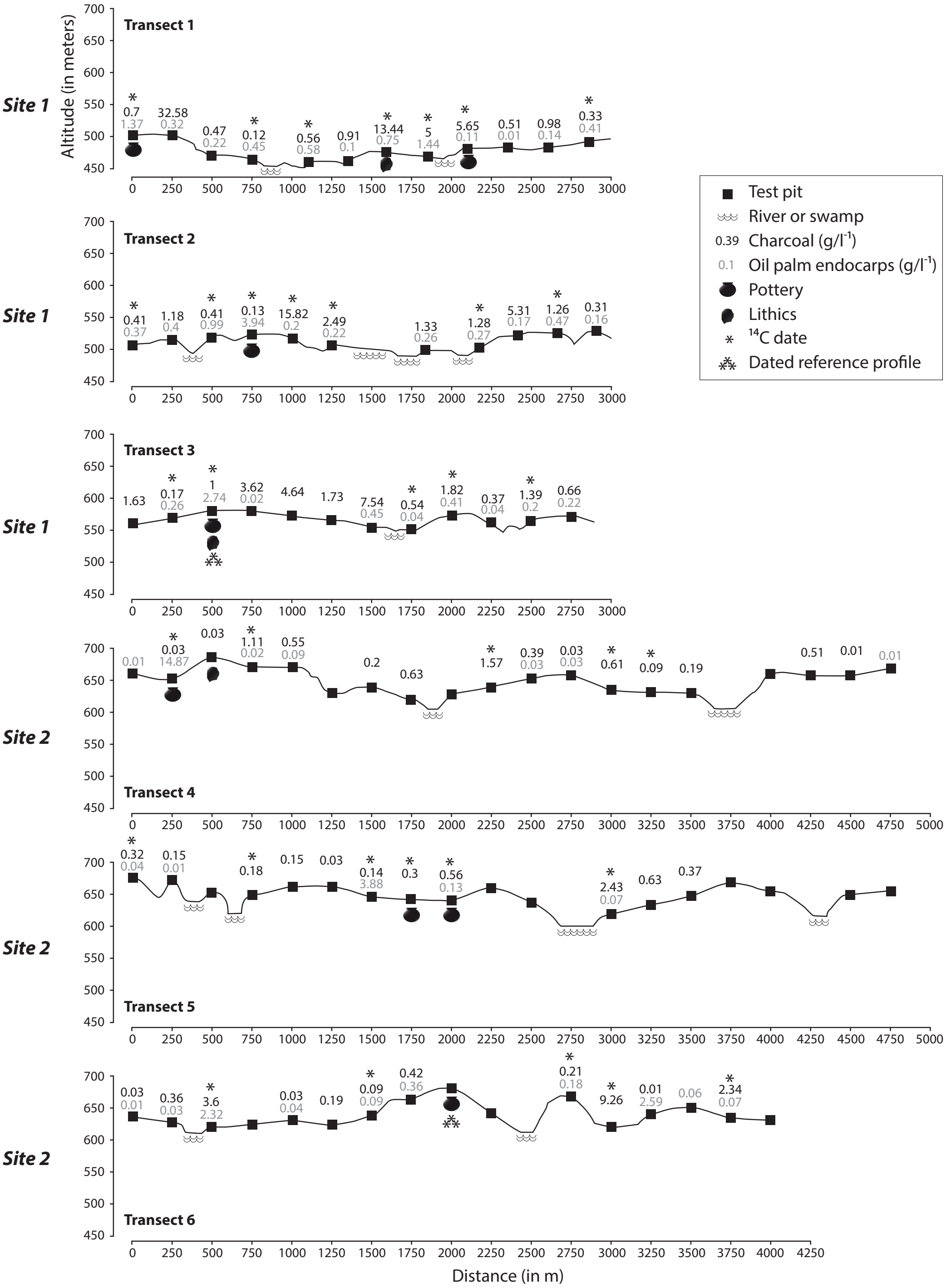

Figure 4.2. The six transects and the 88 test-pits investigated.

The total masses (in grams) of charcoal (in black) and oil palm endocarps (in grey) by test-pit as well as the archaeological findings are reported. Null values and masses of unidentified seeds are not represented.

Table 4.1. The 50 radiocarbon AMS ages classified by site, transect, test-pit and pedological pits and depth. The reference soil profiles are indicated in bold.
DM: dated material; C: Charcoal; CE: Charred endocarp (unidentified taxon); *OPE*: oil palm endocarp *Elaeis guineensis*; A and B: identified archaeological Phase A and Phase B; AMS: Accelerator Mass Spectrometry; BP: Before Present.

Site	Transect	Test-pit	Depth (cm)	DM	Lab code	BP	±	Calibration		Archaeological phases	Associated archaeological findings
								68.2%	95.4%		
1	1	1	10-20	*OPE*	Poz-62641	1805	30	1810/1705	1822/1626	A	.
1	1	4	10-20	*OPE*	Poz-62642	2250	30	2333/2181	2344/2155	A	.
1	1	5	10-20	*OPE*	Poz-62644	2230	30	2316/2160	2333/2153	A	.
1	1	7	20-40	*OPE*	Poz-49335	1540	30	1519/1386	1525/1363	A	.
1	1	8	10-20	*OPE*	Poz-62645	780	30	726/681	741/669	B	.
1	1	9	20-30	C	Poz-49330	145	30	275/9	283/2	B	Pottery
1	1	12	10-20	*OPE*	Poz-62646	1870	30	1868/1740	1877/1724	A	.
1	2	1	10-20	*OPE*	Poz-62647	1810	30	1810/1709	1823/1628	B	.
1	2	3	10-20	*OPE*	Poz-62648	1960	30	1945/1877	1989/1830	A	.
1	2	4	0-20	*OPE*	Poz-49334	150	25	277/8	284/0	B	.
1	2	5	10-20	*OPE*	Poz-62649	1655	30	1599/1530	1688/1420	A	.
1	2	6	10-20	*OPE*	Poz-62650	1705	30	1690/1561	1698/1549	A	.
1	2	8	0-10	*OPE*	Poz-62651	1860	30	1861/1737	1870/1720	A	.
1	2	10	30-40	*OPE*	Poz-49331	1750	35	1707/1616	1775/1560	A	.
1	3	2	20-30	*OPE*	Poz-62653	1865	30	1864/1739	1874/1720	A	.
1	3	3	10-20	*OPE*	Poz-62654	1660	30	1602/1533	1690/1421	A	.
1	**3**	**3**	**0-10**	**C**	**Poz-49323**	**260**	**30**	**421/156**	**431/0**	**B**	**Pottery**
1	**3**	**3**	**30-40**	***OPE***	**Poz-49324**	**1810**	**30**	**1810/1709**	**1823/1628**	**A**	**Pottery**
1	**3**	**3**	**70-80**	***OPE***	**Poz-49327**	**2160**	**30**	**2301/2116**	**2307/2057**	**A**	**.**
1	**3**	**3**	**100-110**	***OPE***	**Poz-49328**	**2005**	**30**	**1991/1926**	**2038/1883**	**A**	**.**
1	**3**	**3**	**140-150**	***OPE***	**Poz-49329**	**2090**	**30**	**2112/2005**	**2144/1991**	**A**	**.**
1	3	8	20-30	*OPE*	Poz-62655	1495	30	1405/1347	1516/1310	A	.
1	3	9	20-30	*OPE*	Poz-62656	625	30	653/559	661/551	B	.
1	3	9	30-40	*OPE*	Poz-49333	1790	30	1805/1628	1817/1620	A	.
1	3	11	0-10	*OPE*	Poz-62657	1720	30	1693/1569	1703/1560	A	.
2	4	2	10-20	*OPE*	Poz-62626	1810	30	1810/1709	1823/1628	A	Pottery
2	4	2	50-60	*OPE*	Poz-62625	1750	30	1705/1619	1729/1565	A	Pottery
2	4	4	10-20	*OPE*	Poz-62627	860	30	791/732	901/695	B	.
2	4	10	10-20	C	Poz-62628	2090	30	2112/2005	2144/1991	A	.
2	4	13	10-20	C	Poz-62629	175	35	285/0	298/0	B	.
2	4	14	0-10	CE	Poz-49337	1825	35	1813/1720	1865/1630	A	.
2	4	14	30-40	C	Poz-49338	2220	30	2310/2159	2324/2152	A	.
2	5	1	10-20	C	Poz-62630	305	30	429/306	462/300	B	.
2	5	4	20-30	C	Poz-62631	1610	35	1552/1417	1568/1407	A	.
2	5	7	30-40	*OPE*	Poz-62632	2265	30	2342/2185	2348/2158	A	.
2	5	8	20-30	C	Poz-49339	1915	30	1888/1825	1935/1742	A	.
2	5	9	0-10	C	Poz-49340	2745	30	2861/2791	2923/2768	A	.
2	5	9	30-40	*OPE*	Poz-49341	1670	35	1610/1538	1695/1423	A	.
2	5	13	20-30	*OPE*	Poz-62634	360	30	484/325	500/315	B	.
2	6	3	20-30	*OPE*	Poz-62635	1775	30	1727/1622	1813/1611	A	.
2	6	7	10-20	*OPE*	Poz-62636	2195	30	2305/2150	2312/2132	A	.
2	**6**	**9**	**0-10**	***OPE***	**Poz-49342**	**2190**	**30**	**2305/2148**	**2310/2127**	**A**	**.**
2	**6**	**9**	**30-40**	***OPE***	**Poz-49343**	**2165**	**30**	**2301/2120**	**2308/2061**	**A**	**.**
2	**6**	**9**	**70-80**	***OPE***	**Poz-49344**	**2250**	**35**	**2335/2180**	**2345/2155**	**A**	**.**
2	**6**	**9**	**100-110**	***OPE***	**Poz-49325**	**9400**	**50**	**10692/10575**	**10748/10507**	**.**	**.**
2	**6**	**9**	**140-150**	***OPE***	**Poz-49345**	**2275**	**30**	**2346/2206**	**2350/2159**	**A**	**.**
2	6	12	10-20	C	Poz-62637	140	30	271/11	281/6	B	.
2	6	13	20-30	C	Poz-62638	260	30	421/156	431/0	B	.
2	6	15	10-20	*OPE*	Poz-62639	1745	30	1700/1618	1720/1565	A	.
2	6	16	10-20	C	Poz-62640	80	30	254/33	260/25	B	.

Table 4.2. Summary of linear mixed effect model with six factors (sites, depths, transects within sites, test-pits within transects, transects depending on depth, test-pits depending on depth) performed on the abundances (grams per liter) of charcoal and oil palm endocarps. Sites, transects and test-pits were considered as random effects, while soil depth was defined as a fixed effect. Significant differences are highlighted in bold.

			Charcoal		**Oil palm endocarps**	
Variables	Effect	DF	*F*	*p*	*F*	*p*
Site	Random	1	**27.99**	**0.004**	5.34	0.067
Depth	Fixed	5	2.17	0.102	1.92	0.140
Transect (Site)	Random	4	0.69	0.604	0.31	0.867
Pits (Site Transect)	Random	82	**4.24**	**0.000**	**3.67**	**0.000**
Transect*Depth (Site)	Fixed	20	1.10	0.345	0.96	0.507
Pits*Depth (Site Transect)	Fixed	410	0.38	0.976	2.25	0.182

DF: degree of freedom; *F*: The *F*-statistic value; *p*: probability value.

Table 4.3. Pottery findings in eight pits from Sites 1 and 2.
Fragment number is indicated by depth.

				Depth (cm)							
	Transect	**Plot**	**Soil profile**	**0-10**	**10-20**	**20-30**	**30-40**	**40-50**	**50-60**	**60-70**	**Total no**
Site 1	1	1	.	.	.	.	3	1	.	.	4
	1	9	.	36	32	7	.	.	1	.	76
	2	4	x	18	21	4	3	.	.	.	46
	3	3	x	7	7	1	.	4	3	1	23
Site 2	4	2	.	.	6	12	11	7	35	7	78
	5	8	.	.	7	.	.	.	.	.	7
	5	8	x	.	.	19	15	18	2	.	54
	5	9	.	.	2	4	.	.	.	.	6

Table 4.4. Mass (g/L) of charcoal, oil palm endocarps (OPE) and unidentified seeds (Un. seeds) in test-pits where an absence or presence of pottery was recorded.
P-values (Wilcoxon test) indicate the significance of the difference between the two cases.

	Absence of pottery	**Presence of pottery**	***P*-value (Wilcoxon test)**
Charcoal	0.34 (± *0.07*)	0.55 (± *0.28*)	0.39
OPE	0.08 (± *0.02*)	0.55 (± *0.25*)	**0.03***
Un. seeds	0.02 (± $5.61\ 10^{-3}$)	$8.29\ 10^{-3}$ (± $3.83\ 10^{-3}$)	0.77

*Significant at 0.05.

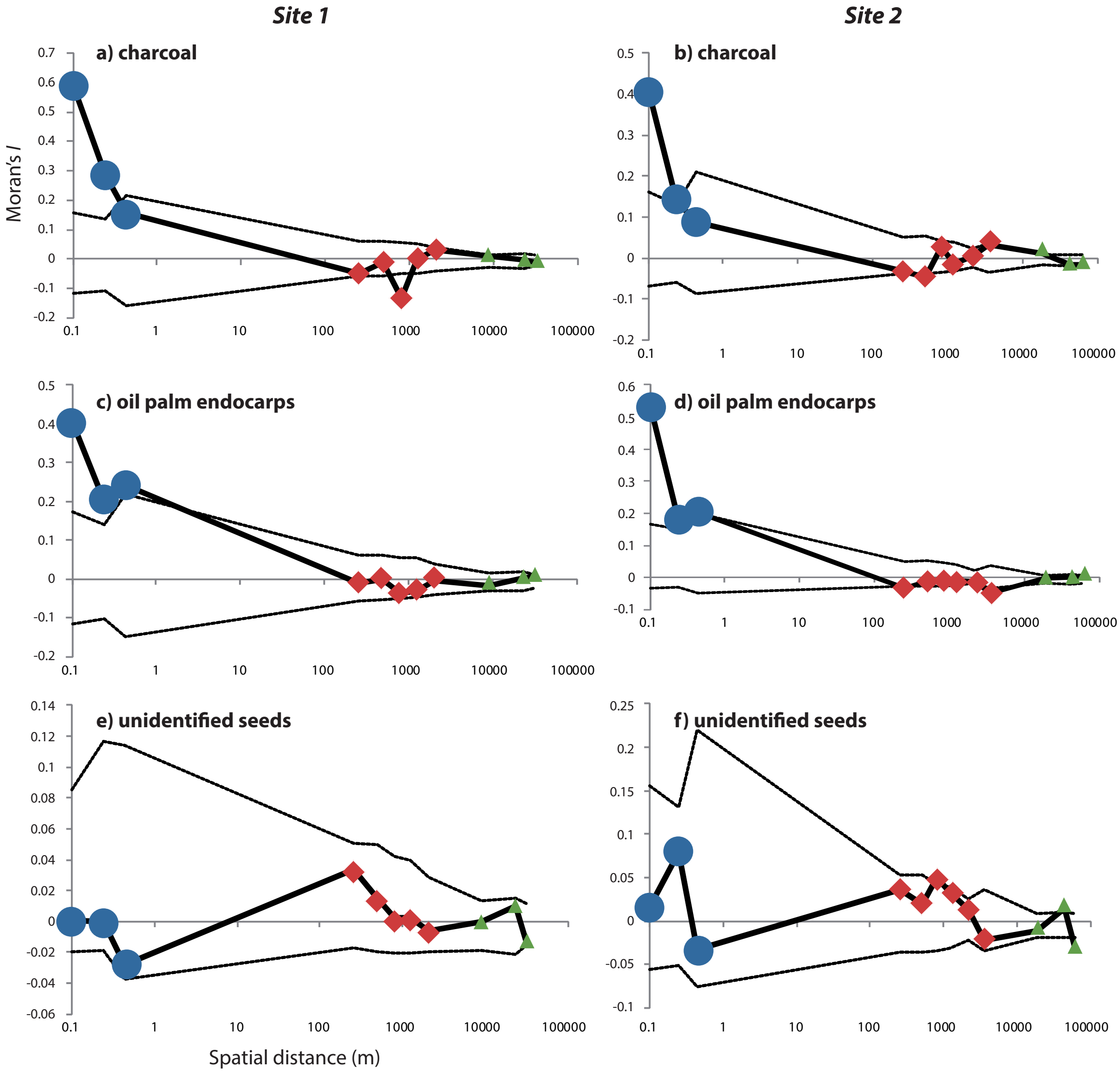

Figure 4.3. Autocorrelograms of charcoal abundance values for each study area: mean Moran's *I* computed for 12 to 14 distance intervals.

On the left side (<1 m), the abscissa for the three first symbols (big blue discs) represent the vertical distance between soil layers from a single test-pit, the first symbol distinguishing adjacent layers, while the second and third symbols distinguish non-adjacent layers separated by 25 and 45 cm, respectively. On the right side (>10 m), the abscissa corresponds to horizontal distance between soil volumes from different test-pits located in different plots from a same transect (between 100 and 5000 m, red lozenges), and from different plots from different transects (>5000 m, green triangles). Symbols above or below the plain lines (95% confidence envelopes) indicate significantly positive or negative Moran's *I* value ($p < 0.05$).

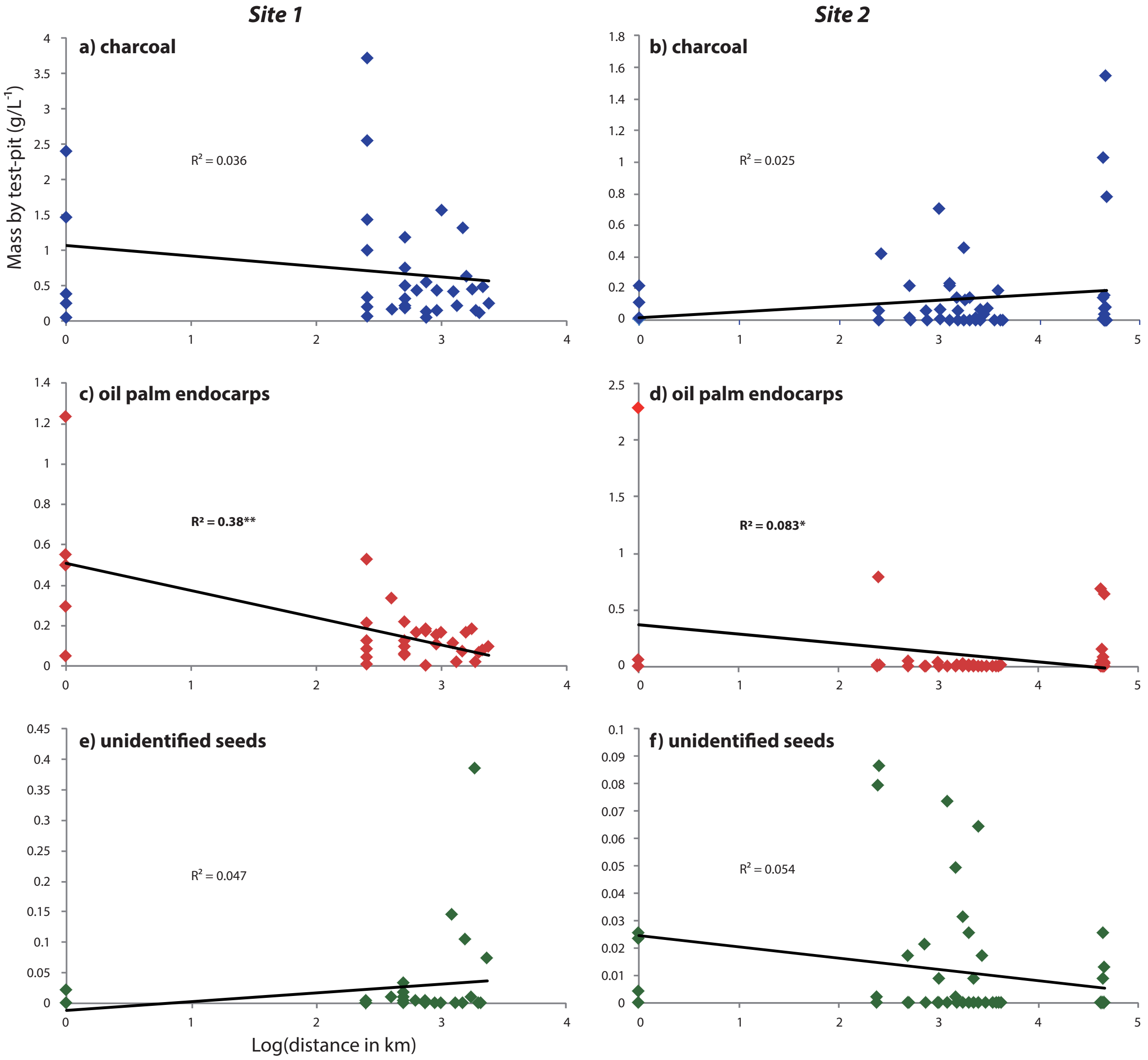

Figure 4.4. Relationship between (1) the abundance of charcoal, oil palm endocarps and unidentified seeds, and (2) the distance to the nearest pottery findings.

Correlation values between the distance to (1) the nearest pottery findings and (2) the abundance of charcoal, oil palm endocarps and unidentified seeds, and their significance according to the torus-translation procedure are indicated on each graph.

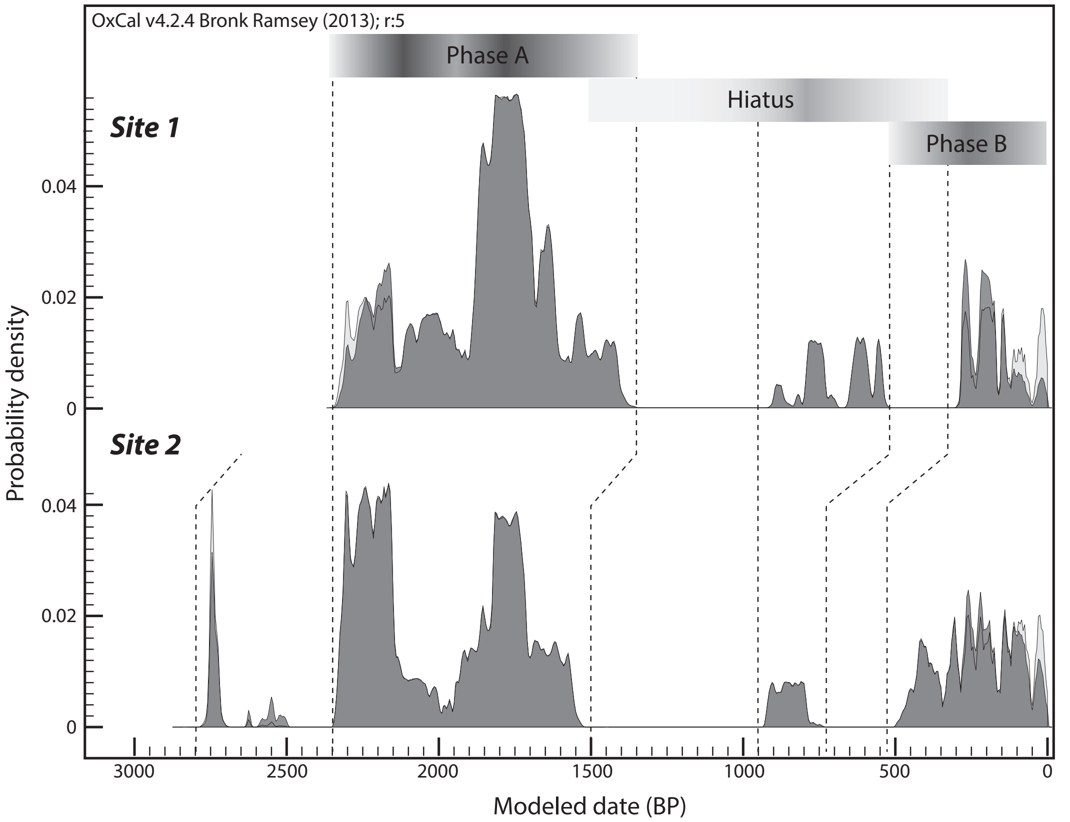

Figure 4.5. Modeled probability density (dark grey) of the 49 radiocarbon dates between 2800 to the present in cal. BP (the oldest date at 10,700 cal. BP is not shown).
Light grey indicates the probability removed from the model. Black dashed lines between the peaks of the curves represented temporal differences between Sites 1 and 2, with an eastward migration. Three periods were delimited: (1) a Phase A (2300–1500/1350 cal. BP), (2) a hiatus phase with less occupation (1500/1350–580/300 cal. BP) and (3) a Phase B (580/300 cal. BP to the present).

4.4. Discussion

In this study, we aimed at characterizing the temporal and spatial patterns of human activity at local scale in the dense forests of southern Cameroon by using a systematic sampling protocol. The majority of charred macrobotanical remains were considered as by-products of human land-use in our study (sensu Glaser 2007). We found evidence of scattered human settlements and activity in the two study sites, which were mainly dated to the late-Holocene (after 2500 BP). Archaeological remains, in the form of artefacts and biomarkers (i.e. charcoals and charred seeds), showed different spatial patterns according to their location along the study transects, revealing two main types of human activities: domestic and agricultural. These results support the relevance of an analysis based on soil charred macrobotanical remains to test spatial patterns of past human land-use in tropical contexts.

4.4.1. Human-induced paleofires

The discrimination between natural and anthropogenic fires since the Holocene remains a complex issue in the absence of archaeological evidence, such as potsherds (Conedera et al. 2009, Scott and Damblon 2010, Théry-Parisot et al. 2010), and more specifically in underexplored regions (Di Pasquale et al. 2008, Hubau et al. 2014, 2015). However, three arguments could allow for the interpretation of charred biomarkers as human-induced in our study sites: (1) their local significance, (2) their scattered distribution both in time and space, and (3) a reduced probability of natural fires during the period considered.

Paleofires were local. To detect the local nature of human activities, we analysed charred botanical remains of ≥ 2 mm. Previous studies on paleofires and experimental work have shown, indeed, that macro charcoals of ≥ 0.4 mm, and most often of ≥ 2 mm, dominated the charcoal records (94% of the mass in Ohlson and Tryterud 2000) and provided information about local fires due to limited transport of this fragment size (Clark 1988, Clark and Patterson 1997, Ohlson and Tryterud 2000, Eckmeier et al. 2007, Conedera et al. 2009, Scott and Damblon 2010). At maximum, charred macroremains derived from within a few hundred metres of the source area of their production (Conedera et al. 2009). Furthermore, the admixture of macro charcoals and macrobotanical remains of different sizes and shapes in our records confirms *in situ* assemblages resulting from local fires (Conedera et al. 2009, Scott 2010). Finally, Hubau et al. (2015) demonstrated that test-pits recorded one burning only or that charcoals were stratified in separate layers. Moreover, when there was only one burning per pit, the same few species have been identified throughout the profile. Charcoal identification is still in progress in our study sites, but preliminary results show the same trends. We can thus be rather confident that macroremains actually captured discreet and very local fire events, despite their vertical dispersion.

Paleofires were scattered. Regarding their distribution, charcoal and charred botanical remains were unearthed everywhere at both sites, with no specific spatial structure, with the exception of the unidentified seeds which were found in greater quantity in transect T4 of Site 2. Spatial structures were only significant for charcoals and oil palm endocarps coming from the same test-pits. This suggests that charred remains were scattered and that there was no relationship between fire events detected in two adjacent or non-adjacent test-pits. This can correspond to a much-localized response of charcoal and oil palm endocarp abundance by depth that also strongly varied between test-pits. Inter-pit variability relative to charcoal concentration has already been demonstrated at local scale (Touflan and Talon 2009). This variability could be linked to biomass differences at the time of burning, which we cannot estimate in the current state of knowledge, because of uncertainties related to biomass estimations for tropical African forests (see, for example, Kearsley et al. 2013). Nonetheless, Brando et al. (2016) recently demonstrated in neotropical forests that fires little affected large trees >30 cm in diameter at breast height (dbh). The fact that we found the same temporal and spatial patterns of scattered fires in our two study sites, corresponding to two contrasting situations in terms of environmental conditions and vegetation, confirms the discontinuity of late-Holocene paleofires. Moreover, the absence of synchronicity of the fires and the local origin of soil charcoals (Whitlock and Larsen 2001, Carcaillet et al. 2009, Conedera et al. 2009) compared with sedimentary charcoals close to our study sites (e.g. the Ntem Interior for Site 1, and Goualougo Lake and Mopo Baï in the Republic of the Congo for Site 2, Brncic et al. 2007, 2009, Tovar et al. 2014) also supports the assumption of scattered fires in southern Cameroon as being a general trend.

Paleofires were rarely natural. The only old age, obtained at Site 2 (Poz-49325, 9400 BP), corresponds to the late-Pleistocene/Holocene transition (Sangen 2012, Sangen et al. 2011). A climate with reduced precipitation has caused the shrinkage of the central African moist forests of the order of 84% (Anhuf et al. 2006). Those drier climatic conditions may have favoured the ignition of natural fires at that time (Hubau et al. 2013, 2015) in the absence of a dense prehistoric and impacting population (Cornelissen 2002). The main body of radiocarbon ages indicates that paleofires concentrated during the late-Holocene (after 2500 BP). This occurred after the First Millennium Rainforest Crisis (Ngomanda et al. 2009b), a strong dry event around 2500 BP in central Africa that has induced forest fragmentation and could have driven agriculturists to expand southwards in the forest (Schwartz 1992, Lanfranchi et al. 1998, Clist 2006). Climate was less dry after this time, reducing the probability of natural fires to occur (Brncic et al. 2009, Maley et al. 2012, Bostoen et al. 2013, Lézine et al. 2013). Indeed, even increased fuel loads in the understory were unlikely to create catastrophic fires outside periods of intense drought (Brando et al. 2016; R. Oslisly pers. com. about extremely rare cases of lightnings in the Lopé reserve in Gabon). But, after 2500 BP, alluvial sediments in the surroundings of both study sites (the Ntem Interior delta, the upper Nyong, Sanaga, Boumba, Dja and Ngoko valleys, Sangen 2012, Sangen et al. 2011, Runge et al. 2014) have recorded an increased erosion coinciding with forest regression (Neumer et al. 2008), coupled with a growing number of archaeological sites and discoveries in southern Cameroon (Wotzka 2006, Höhn et al. 2008, Meister 2008, Sangen 2012, Oslisly et al. 2013a, 2013b, Morin-Rivat et al. 2014, Bourland et al. 2015). We also found much more charcoal in Site 1 than in Site 2, despite the fact that Site 1 receives more rainfall and is thus more humid, supporting the hypothesis of important anthropogenic disturbances in the area. The great amounts of charcoal and macrobotanical remains trapped in the riverbanks have also been interpreted as remnants of slash-and-burn agriculture (Sangen 2012). We do not exclude, however, the possibility of small-scale natural paleofires in periods of severe droughts in relation with ENSO events (Scott 2000, Hammond et al. 2006, Titiz and Sanford Jr 2007, Neumann et al. 2012a, 2012b, Hubau et al. 2015).

4.4.2. Ancient land-use in southern Cameroon

Late-Holocene human occupations. The set of 49 radiocarbon ages, excluding one date (Poz-49325, 9400 BP), clearly concentrates to the late-Holocene (after 2500 BP), in agreement with previous works (Wotzka 2006, Oslisly et al. 2013a, 2013b) that have reported an increase in the number of archaeological sites during this period. Moreover, despite the fact that the two study sites were 350 km apart, the ages were distributed according to the two same well-known archaeological periods: (1) 2300–1500 (Site 2)/1300 (Site 1) BP, and (2) 580 (Site 2)/300 (Site 1) BP to the present. We suggest to use Phases A and B, instead of the too largely used early and late Iron Age (Phillipson 2005), because we cannot be sure of the identity of past populations in our study areas. Pyro-technologies were represented by pottery in both sites and iron metallurgy in the study areas (Eggert et al. 2006, Morin-Rivat et al. 2014), which suggest scattered human settlements. The bimodal pattern of human occupation, characterized by an intermediate hiatus in the radiocarbon ages between 1500 (Site 2)/1300 (Site 1) and 580 (Site 2)/300 (Site 1) BP, has already been reported for central Africa (Oslisly 1995, Oslisly et al. 2013a, 2013b, Wotzka 2006, http://www.pprfth-ac.org/archeologie/) and for southern Cameroon in particular (Morin-Rivat et al. 2014). This hiatus phase has been interpreted as a population collapse (Oslisly 2001). Its definitive explanation is still debated (Wotzka 2006), with propositions related to widespread epidemic diseases (e.g. trypanosomiasis) and famines (Oslisly 2001, Oslisly et al. 2013b) or destructive taphonomic processes of the human settlements (Wotzka 2006). We suggest, however, that the slave trade since the 16th century could partly have an impact on human populations by raiding peoples far into the forest. Especially, the time shift between Site 1 and Site 2 at the end of this hiatus (580/300 BP) could be explained by populations displacements eastwards (see also Wotzka 2006).

Past human activities and land-use management. The absence of correlation between charcoal and oil palm endocarps supports the hypothesis that they did not represent the same types of events and probably of human activities. Moreover, there was a relationship between potsherds and oil palm endocarps, the latter most often associated with potsherds than with charcoal only, and found in higher positions, such as hilltops in the vicinity of watercourses. Rivers are usually considered as aggregation sites for populations in tropical environments (Oslisly and White 2003, Bush and Silman 2007, McMichael et al. 2012). This combination between potsherds and oil palm endocarps thus seems to represent domestic activities in human settlements, as reported in several sites in southern Cameroon (Eggert et al. 2006). By contrast, charcoal and unidentified seeds followed other trends and were less often associated with pottery findings. We suppose that they can represent other signals, more distant to human settlements. Seeds were not numerous but showed various patterns of abundance. Their presence may be interpreted as the burning of wild plant species, either during wild fires or slash-and-burn agricultural activities. In general, charcoal presence may correspond to agricultural practices and to slash-and-burn shifting cultivation in particular, notwithstanding specific domestic contexts (e.g. domestic hearths). We also found that synchronous human activities around 1800 BP could be spaced between 2000 and 2800 m apart. This may correspond to the land needed for a village to thrive. Two centuries later, around 1600 BP, this distance dropped below 2000 m (i.e. 1750 m in average). This may be linked to a peak in human occupation during Phase A (Wotzka 2006, Oslisly et al. 2013a 2013b), which may suggest a peak in human density in both study areas. Distance between contemporaneous activities may thus be reduced with increasing population. People currently walk 2-km distance to go cultivate their fields in southern Cameroon (Carrière 2002). However, we cannot transfer the present situation to the past, even though a traditional land-use as described in southern Cameroon is likely, with shifting fields located in the village lands (Vermeulen and Karsenty 2001). It can be assumed that people moved their villages because of soil exhaustion over generations, or for political purposes, such as alliances (e.g. same family, ethnic group), conflict management (Vermeulen and Karsenty 2001) or because of disease outbreaks (e.g. ebola). All these elements suggest that people may have been a crucial factor in the presence of charcoal. We assumed that these populations, even two millennia ago and up to the 19th century, had a deep knowledge of their long-term land-use and their spatial occupation.

Charcoal for slash-and-burn cultivation. Iron smelting and shifting agriculture yielded large quantities of charcoal (Neumann et al. 2012a, Oslisly et al. 2013a). In our study sites, no metallurgical slags or '*tuyères*' fragments have been discovered so far, which makes the assumption of charcoals as remnants of agricultural practices more likely. Agriculture has been rarely demonstrated in Africa's dense forest in the absence of obvious evidence, for instance pearl millet seeds (*Pennisetum glaucum*), as discovered in southern Cameroon and dated to 2200 BP (Eggert et al. 2006, Kahlheber et al. 2009, Neumann et al. 2012a). The use of late-Holocene soil charcoals is thus of great interest to track past agricultural practices within the African moist forest (Morin-Rivat et al. 2014). In our study, oil palm endocarps add another interesting element of discussion relative to the utilization of wild plant resources by past populations (Clist 1997, Lavachery 2001, Lavachery et al. 2005, Logan and D'Andrea 2012). Recently, Kay and Kaplan (2015) classified similar discoveries from the northern Congo Basin (Morin-Rivat et al. 2014) as originating from 'foragers-horticulturists' rather than from true agriculturists.

4.5. Conclusion

This study has demonstrated the statistical power of using charcoal and charred botanical remains so as to interpret past land-use in tropical contexts. Nonetheless, this does not exclude some limitations. The first one relies on the linear sampling used in this study, which could not afford exhaustive information on human activities, but brought information along great distances. An improvement of this could be a sampling according to a grid. Second, this method needs large soil quantities to collect the charred botanical remains (see Di Pasquale et al. 2008), which could potentially give a lower temporal resolution than in sedimentary charcoals from lakes (Whitlock and Larsen 2001). Even though we reduced the thickness of the soil layers (10 cm versus 25 cm in Di Pasquale et al. 2008) to try to increase the temporal resolution of our records, only weak age–depth relationships emerged, especially in Site 2. Nonetheless, the most recent dates came generally from the topmost 40 cm of the test-pits with increasing age with depth (Vleminckx et al. 2014, Hubau et al. 2015), which is also consistent with previous results on tropical soils (Hammond et al. 2006, Vleminckx et al. 2014). Additional geomorphological and pedological work should be done, however, in order to understand soil formation, accumulation rate and disturbance processes in African tropical soils (Dincauze 2000). Indeed, we cannot exclude likely post-depositional processes in our study sites, such as soil reworking by soil fauna, uprooting, erosion, burrowing and decomposition (Conedera et al. 2009, Théry-Parisot et al. 2010). Finally, attention should be paid to the potential inbuilt ages of the dated charcoal compared with the short-lived endocarps, as they could come from long-lived trees and could thus overestimate the actual ages by several hundreds of years (Gavin 2001, Hammond et al. 2006).

In spite of these limitations, it does not understate the interest of the method in terms of spatial study of past disturbances (Carcaillet 2001a, 2001b), and clear advantages emerged from an approach based on different categories of land-use biomarkers (Ohlson and Tryterud 2000, Di Pasquale et al. 2008, Conedera et al. 2009, Robin et al. 2013). The repetition of our sampling in two different study sites that represented contrasting ecological situations, the large number of replicates in terms of test-pits (88) and soil samples (528), as well as the 50 radiocarbon ages obtained, contribute to the reliability of our results (Gavin et al. 2003, Eckmeier et al. 2007, Conedera et al. 2009, Touflan and Talon 2009). The ubiquity of charcoal and its good preservation in soils over the limited number of suitable sites for palynology and sedimentary charcoal (Robin et al. 2013) make it a highly relevant tool, especially to discover human settlements and activities in areas that have not been archaeologically surveyed. Our results also highlighted agricultural practices that have long been neglected and thus open the way for a very practical archaeology of land-use and landscapes in tropical contexts.

Chapter 5 Present-day central African forest is a legacy of the 19th century human history

Chapters 3 and 4 showed that human activities in the northern Congo Basin were of three kinds: domestic, agricultural, and artisanal (i.e. iron smelting), and were dated to two main time periods: between ~2300 to 1300 BP, and from ~600 BP to the present. **Chapter 5** focuses on this last period, and aims at assessing the consequences of historical anthropogenic disturbances, and in particular on light-demanding species.

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Tête 75 – Véronique LG Morin

Abstract

The populations of light-demanding trees that dominate the canopy of central African forests are now aging. Here, we show that the lack of regeneration of these populations began ~165 ya (around 1850) after major anthropogenic disturbances ceased. Since 1885, less itinerancy and disturbance in the forest has occurred because the colonial administrations concentrated people and villages along the primary communication axes. Local populations formerly gardened the forest by creating scattered openings, which were sufficiently large for the establishment of light-demanding trees. Currently, common logging operations do not create suitable openings for the regeneration of these species, whereas deforestation degrades landscapes. Using an interdisciplinary approach, which included paleoecological, archaeological, historical, and dendrological data, we highlight the long-term history of human activities across central African forests and assess the contribution of these activities to present-day forest structure and composition. The conclusions of this sobering analysis present challenges to current silvicultural practices and to those of the future.

Keywords: central Africa, European colonization, slavery, changes in land-use, light-demanding tree species, tropical forest

5.1. Introduction

Central African forests underwent an unequal history of disturbances during the Holocene (after 10,000 yrs BP) compared with Neotropical forests, which remained relatively stable since the Late Glacial Maximum (LGM, ~13,000–10,000 yrs BP) (Anhuf et al. 2006). Over the last three millennia, significant changes in the vegetation structure and floristic composition were caused by climate fluctuations (Maley et al. 2012, Neumann et al. 2012b, Lézine et al. 2013). Specifically, a dry event around 2500 ya caused forest fragmentation, an event with a more pronounced seasonality. This fragmented forest included patches of savanna (Maley 2002). This dry episode was less severe since 2500 BP, as evidenced at the Mopo Bai site in the Republic of the Congo, where Poaceae pollen severely dropped from 36% to 13% between 2580 and 2400 BP, which is evidence for a retreat of the savannas to the benefit of the forests (Bostoen et al. 2015). After 2000 yrs BP, a relatively wet climate in central Africa favored forest recolonization by light-demanding tree species, with few effects imputable to humans (Brncic et al. 2009, Maley et al. 2012, Lézine et al. 2013, Bostoen et al. 2015). The subsequent climatic variations were less important with little effect on the vegetation (Oslisly et al. 2013b); however, human activities are assumed to have increased in importance, particularly during the most recent centuries (Willis et al. 2004, Brncic et al. 2007, Greve et al. 2011, Oslisly et al. 2013a, 2013b). The abundance of direct (artifacts) and indirect evidence (charred oil palm endocarps) in soils confirms the non-pristine nature of central African forests (Morin-Rivat et al. 2014).

Human activities in the Holocene, and particularly shifting cultivation, have been invoked to partially explain the low diversity of central African forests (Parmentier et al. 2007) and the abundance of light-demanding species in the canopy (White and Oates 1999, van Gemerden et al. 2003, Engone Obiang et al. 2014, Vleminckx et al. 2014, Biwolé et al. 2015). The light-demanding species form, in some places, almost pure 0.5 to 1 ha stands that mirror the size of traditionally cultivated fields (van Gemerden et al. 2003). An example is the Sangha River Interval (SRI) in which the vegetation currently forms a 'corridor' of old-growth semi-deciduous *Celtis* forests (Gond et al. 2013, Fayolle et al. 2014a), with local variations caused by the geological substrate or the forest degradation along roads and close to cities (Fayolle et al. 2012) (***Figure 5.1***). The SRI is a 400-km-wide region, with low endemism between the Lower Guinean and the Congolian subcenters of endemism (White 1983). This area, which is between southeastern Cameroon, southern Central African Republic and northern Congo, may have been a savanna corridor 2500 ya (Maley 2002).

Until the recent studies of Harris (2002), and Gillet and Doucet (2012), the vegetation in the SRI was under sampled, and whether the origin of this corridor is environmental (Fayolle et al. 2012) or historical (Morin-Rivat et al. 2014) remains to be explored. In this study, we assessed the potential impact of historical human activities on central African forests. Specifically, we analyzed the population/age structure of four primary light-demanding timber species across the SRI and examined the synchronism with the paleoenvironmental, archaeological, and historical data in this region (***Figure 5.1***).

5.2. Materials and methods

5.2.1. Study area

The Sangha River Interval (SRI) is a 400-km-wide area in southeastern Cameroon, southern Central African Republic (CAR), and northern Republic of Congo. The extremes that encompass the area are 0°–5° N and 13°–19° E (Gond et al. 2013). The climate is humid tropical to equatorial from north to south and from east to west with alternating wet (May, September-October) and dry seasons (December-February, July; Gillet and Doucet 2012). Mean annual rainfall ranges between 1616 and 1760 mm (Lomié in Cameroon and Impfondo in the Republic of the Congo; www.climatedata.eu). Monthly average temperatures fluctuate around 25°C. The vegetation of the area corresponds to moist forests of the Guineo-Congolian domain (White 1983, Gond et al. 2013, Fayolle et al. 2014b).

5.2.2. Forest inventory data

We used published analyzed forest inventory data (Fayolle et al. 2014a) from 22 sites (i.e. forest concessions) scattered over southeastern Cameroon (n = 6), southwestern Central African Republic (n = 6), and northern Republic of Congo (n = 10) (***Appendix 6***). The forest inventories were conducted between 2000 and 2007 with a systematic sampling of 1% of the concession area. We used a dataset with 1,765,483 inventoried trees with a dbh ≥ 30 cm in 22 sites (i.e. forest concessions before exploitation) that covered six million ha in the SRI (Fayolle et al. 2014a) (***Appendix 6***). We examined the diameter distribution at the genus level for the entire SRI. All trees ≥ 30 cm in diameter at breast height (dbh) were identified and measured in 0.5 ha plots consecutively distributed along parallel and equidistant transects in unlogged forest concessions (Picard and Gourlet-Fleury 2008, Réjou-Méchain et al. 2008, Gourlet-Fleury et al. 2011, Fayolle et al. 2012, 2014a, Gond et al. 2013). The minimum diameter of the trees recorded was 30 cm, which effectively confined our analysis to (sub)canopy trees with reduced mortality and less variation in growth rates (Clark and Clark 1992). Vernacular names were converted into genus-level scientific names, and the trees were assigned to 10-cm-wide diameter at breast height (dbh) classes, with the largest trees with a dbh ≥ 150 cm in a single class (total of 13 classes). Diameter distributions were analyzed for a set of 176 of the inventoried genera for which we were confident of the identification (Fayolle et al. 2014a).

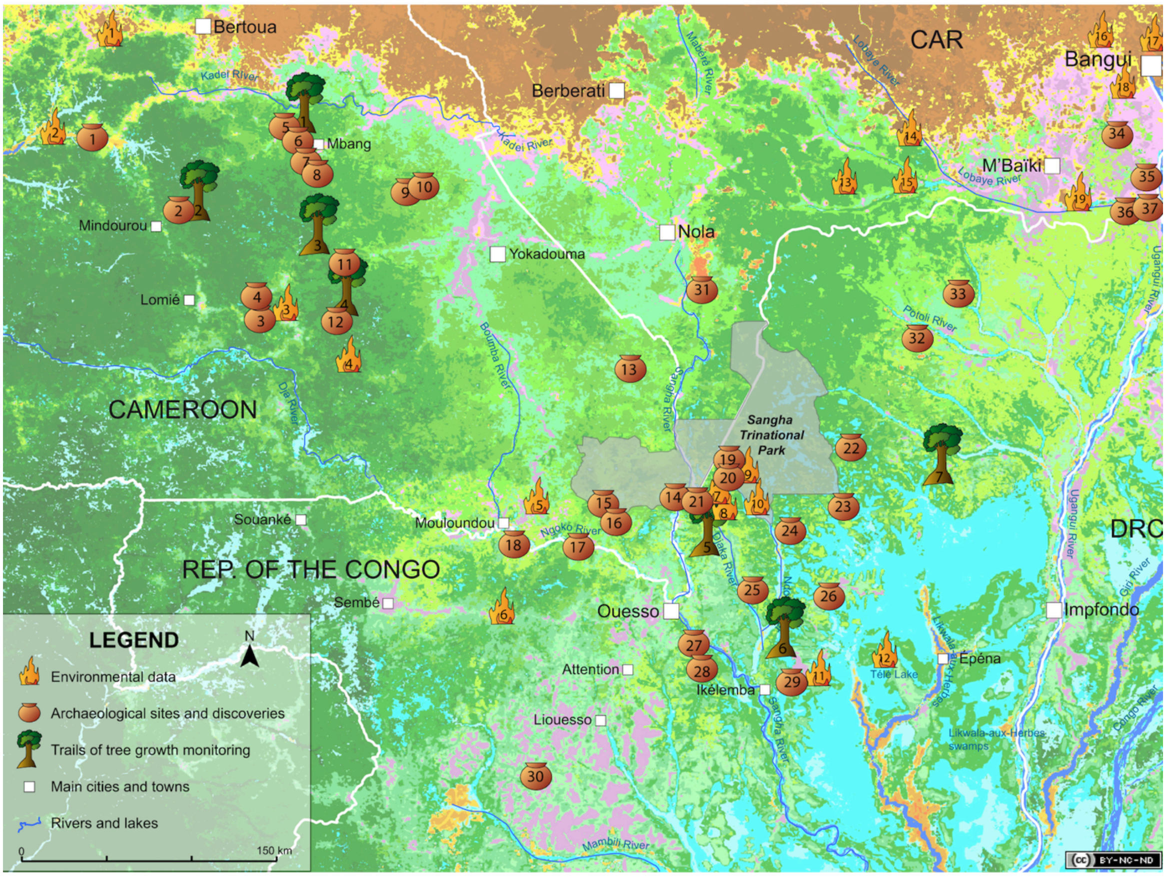

Figure 5.1. Paleoenvironmental changes and human activities in the Sangha River Interval. The 34 sites with paleoenvironmental data (fires) and the 38 dated archaeological sites and discoveries (pots) are indicated on a vegetation map modified from Gond et al. (2013) (http://www.coforchange.eu/ products/maps). The seven sites used to monitor tree growth (trees) are also indicated (see ***Appendices 9***, ***10*** and ***11*** for site names). Brown (three shades): savanna of the Sudano-Guinean domain; orange (three shades): savanna included in dense forest; yellow: savanna-forest edge; purple (two shades): very open forest; blue-green: open semi-deciduous forest; medium green (three shades): dense semi-deciduous forest; dark green (five shades): dense evergreen forest; light green (two shades): open evergreen forest; light blue (two shades): swamp forest and swamp. Map: QGIS 2.14 (http://www.qgis.org), CAD: Illustrator CS4 (https://www.adobe.com).

5.2.3. Analysis of diameter distribution

To detect the main variation in the diameter distribution among the genera, we performed a correspondence analysis (CA) of the genus diameter matrix followed by a clustering based on Euclidian distances and an average agglomeration method. In this study, we focused on four particular genera that are monospecific in the SRI and had a unimodal distribution (***Figure 5.2*** and ***Appendix 6***) and for which we had data on their annual increments of diameter (i.e. *Erythrophleum*, *Pericopsis*, *Terminalia*, and *Triplochiton*). Details on the diameter distribution of the study species at each study site are shown in ***Figure 5.3***. *Terminalia* and *Triplochiton* are characteristic of semi-deciduous *Celtis* spp. forest in the SRI (Fayolle et al. 2014b), whereas *Pericopsis* is an endangered timber species according to the CITES Red List. We later refer to species only (i.e. *Erythrophleum suaveolens* and *Pericopsis elata*, *Terminalia superba*, and *Triplochiton scleroxylon*) as they are monospecific in the study area.

5.2.4. Published age data

We gathered age data for the four study species in tropical Africa from published tree-ring studies (Worbes et al. 2003, De Ridder et al. 2013a, 2013b, 2014) (***Appendix 7***) to identify the growth models that provided reliable age estimations (***Figure 5.4*** and ***Appendices 7* and 8**). All trees were measured at dbh (130 cm in height). In ***Figure 5.4***, the age/diameter relationships are shown.

5.2.5. Growth data

Repeated diameter measurements of 982 monitored trees of the four study species were obtained on seven trails (n = 4 in Cameroon; n = 3 in the Republic of the Congo) used for the permanent monitoring of tree growth (Picard and Gourlet-Fleury 2008). We calculated the mean annual increment in diameter (MAI_d) for n = 367 *E. suaveolens*; n = 199 *P. elata*; n = 152 *T. superba*; and n = 264 *T. scleroxylon*.

5.2.6. Growth models

To account for the ontogenic variation in growth generally identified for tropical tree species (Hérault et al. 2011), six growth models (i.e. Canham, Gompertz, Verhulst, Power, Power mult, and Lognormal) relating tree diameter (DBH) to growth (MAI_d) were fitted to the growth and diameter data for all study species. Linear and Mean models were additionally fitted for comparison (***Appendix 8*** and ***Figure 5.4***). We used the Bayesian Information Criterion (BIC) for assessing the performance of the models.

5.2.7. Age estimation

Ordinary differential equations were solved numerically to obtain the relationship between tree diameter and time (age) (***Figure 5.4***). We finally estimated the age of trees at the mode of the diameter distribution based on the Mean Annual Increment of diameter (MAI_d) and converted these ages into dates using the inventory date of AD 2000 as the reference date (***Appendix 9***).

5.2.8. Synthesis of paleoenvironmental changes

We documented the paleoenvironmental changes in the SRI for the last 1000 years (***Appendix 10***) (Laraque et al 1998, DeMenocal et al. 2000, Runge and Fimbel 2001, Harris 2002, Runge and Nguimalet 2005, Brncic et al. 2007, 2009, Neumer et al. 2008, Runge 2008, Sangen et al. 2011, Sangen 2012, Aleman et al. 2013, Runge et al. 2014, Tovar et al. 2014, Lupo et al. 2015). We acquired paleoenvironmental data from 34 sites, either terra firme, swamp, lake or marine sites, that provided data on the past climate (SSTs and atmospheric dust signal), vegetation (phytoliths, $\delta^{13}C$, pollen) and anthropogenic disturbances (charcoal influxes, alluvial discharges through grain size and chemical elements analyses). Site locations are shown in ***Figure 5.1***, and the data are synthesized in ***Figure 5.5***. The degree of frequency of a proxy was determined regarding all similar curves in the identical study (e.g. *E. guineensis* pollen curve ~ all pollen curves in Brncic et al. 2009), and the cutoffs were evenly set from the minimum to the maximum values.

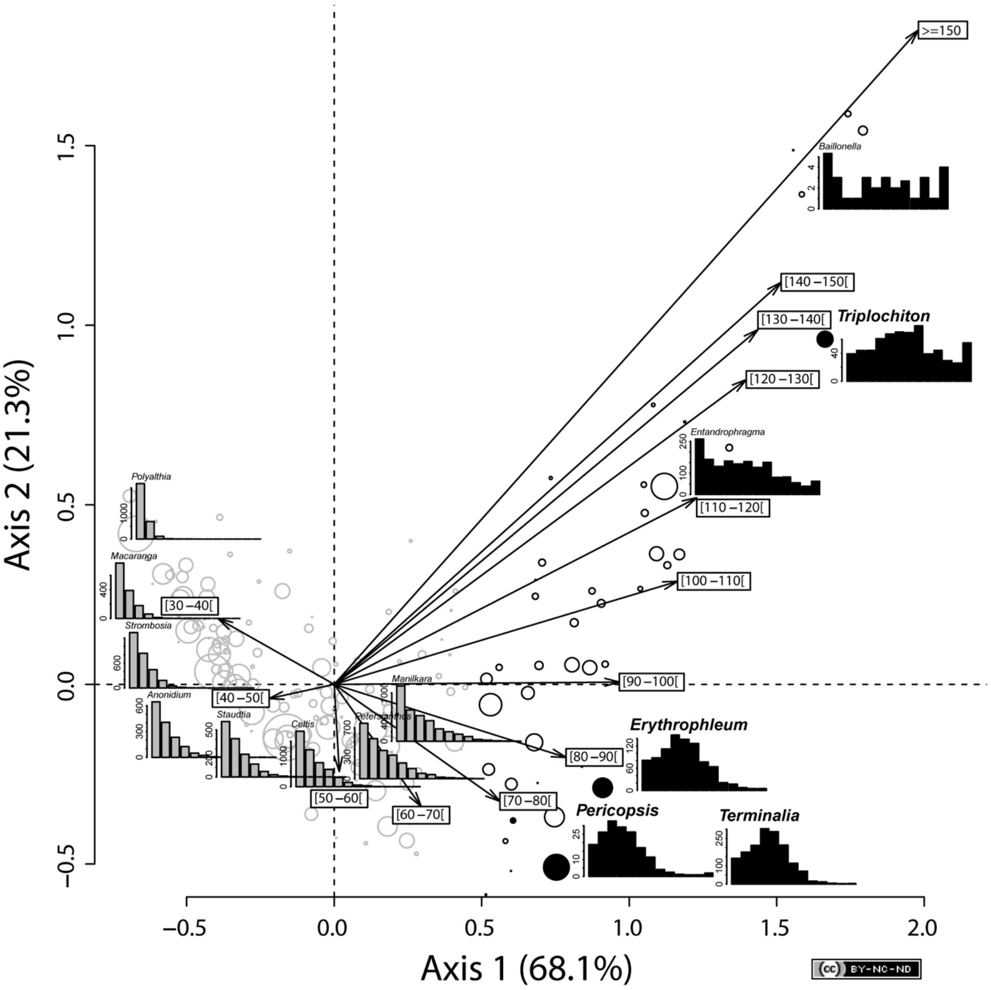

Figure 5.2. Variation in tree diameter distribution among the 176 genera across the SRI. Projection of the genera and the 10-cm-wide diameter classes in the ordination space defined by the first two axes of a correspondence analysis of the abundance matrix, as defined by 176 genera and 13 diameter classes. The size of the circles is proportional to the square root of the genus abundance. The color of the symbol corresponds to the two groups identified with a clustering analysis (based on Euclidean distances and an average agglomeration method) on the species score on the first factorial axis. Genera that showed a reverse-J diameter distribution (n = 134) are indicated in gray and those genera that showed a deviation from the reverse-J distribution (n = 42) in black (e.g. *Baillonella*). Black filled circles indicate the four genera that are monospecific in the SRI and used for the age estimations. Diameter distribution of the 10 most abundant genera is shown in addition to that of the four selected genera: *Celtis* (gray), *Polyalthia* (gray), *Strombosia* (gray), *Petersianthus* (gray), *Manilkara* (gray), *Entandrophragma* (black), *Terminalia* (black), *Anonidium* (gray), *Staudtia* (gray), and *Macaranga* (gray). Statistics: R (https://www.r-project.org/), CAD: Illustrator CS4 (https://www.adobe.com).

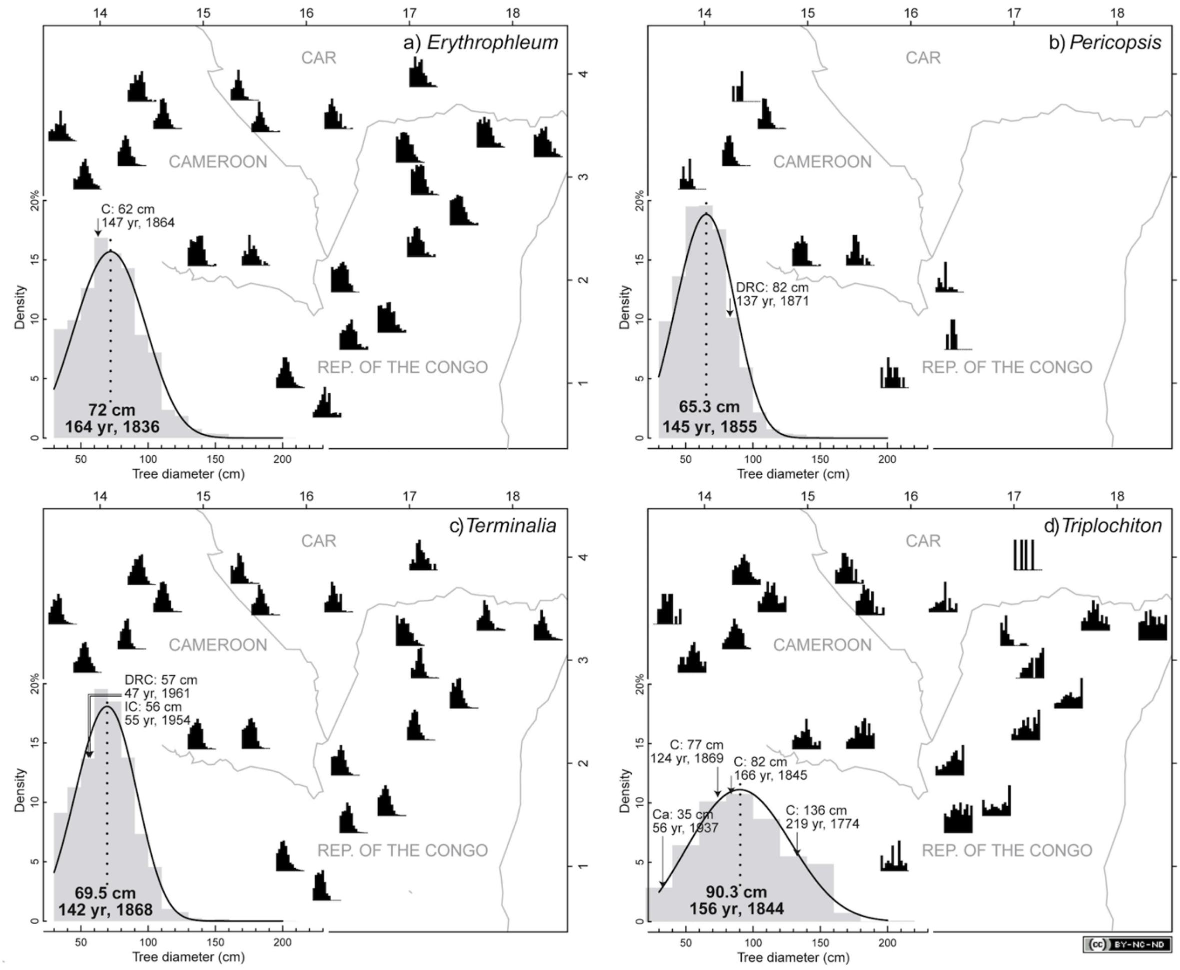

Figure 5.3. Distribution of diameters of the four study species in the 22 study sites (black). The solid lines on the average diameter distributions (gray) correspond to the fitted parametric diameter distribution (Weibull), which was used to estimate the mode and corresponding age. Ages and dates (AD) in the Sangha River Interval were estimated using the mean annual increment of diameter of a) 367 *Erythrophleum suaveolens*, b) 199 *Pericopsis elata*, c) 152 *Terminalia superba* and d) 265 *Triplochiton scleroxylon*. Age estimations were confirmed using published tree-ring data for these four species in natural forests in Cameroon (C), the Democratic Republic of Congo (DRC) and the Ivory Coast (IC) (values indicated by arrows; ***Appendix 7***). Maps: QGIS 2.14 (http://www.qgis.org), CAD: Illustrator CS4 (https://www.adobe.com).

5.2.9. Synthesis of human activities

We used 63 uncalibrated traditional and accelerator mass spectrometry (AMS) radiocarbon dates and two optically stimulated luminescence (OSL) dates from 52 archaeological sites and punctual discoveries that covered the last 1000 years (***Appendix 11***) (Fay 1997, Lanfranchi et al. 1998, Brncic 2003, Moga 2008, Meyer et al. 2009, Oslisly et al. 2013b, Morin-Rivat et al. 2014, 2016, Lupo et al. 2015). A total of 22 published dates from 21 sites in Cameroon, 15 dates from 13 sites in the Republic of the Congo, and 28 dates from 18 sites in the Central African Republic were acquired. The site locations are shown in ***Figure 5.1***.

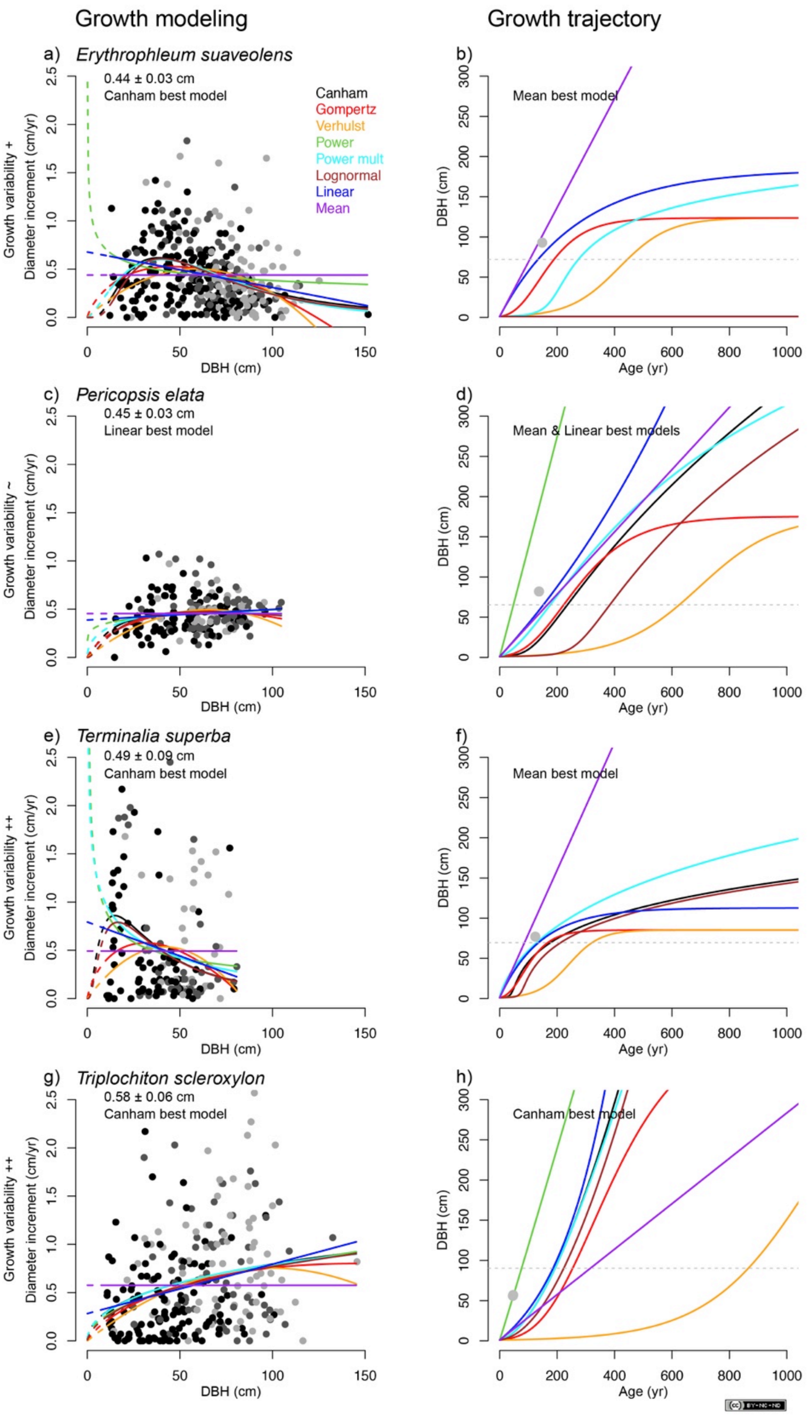

Figure 5.4. Growth models (a, c, e and g) and growth trajectories (b, d, f and h) for the four study species based on tree-ring data.

Eight growth models (i.e. Canham, Gompertz, Verhulst, Power, Power mult, Lognormal, Linear and Mean) were fitted to the data. Age estimations were obtained with numerical solutions to ordinary differential equations (ODE). Solid lines correspond to the model prediction on the observed range of diameters. Dashed lines correspond to the predictions for small trees (below the inventory threshold of ≤ 10 cm). For growth models, the color of symbols indicates access to light (light gray = emergent and dominant trees, Dawkins 5; gray = canopy and codominant trees, Dawkins 4; black = lower canopy and understory dominated trees, Dawkins ≤ 3). For growth trajectories, age/diameter values based on published tree-ring data that are indicated by light gray dots. Statistics: R (https://www.r-project.org/), CAD: Illustrator CS4 (https://www.adobe.com).

5.2.10. Bayesian analysis of the radiocarbon dates

The analyses on dates were performed using the OxCal v.4.2 program (Bronk Ramsey 2013) with the IntCal13 atmospheric calibration curve (Reimer et al. 2013). All dates were tested using an outlier analysis (Bronk Ramsey 2009). To provide an estimate of the temporal trends of human activities in the SRI, we performed a summed probability distribution of the 63 available radiocarbon dates calibrated in yrs BP in combination with a Bayesian model (Bayliss 2009, Bronk Ramsey 2009) (***Figure 5.5***). Chronological Query Language (CQL) codes used are indicated in the ***Appendix 12***.

5.2.11. Synthesis of the historical data

After reviewing the historical literature, we selected 12 references that illustrate key dates and events from the beginning of the 15th century to the present, which influenced directly or indirectly human populations in the SRI (***Appendix 13***) (Vennetier 1963, Robineau 1967, Kaspi 1971, Burnham 1996, Copet-Rougier 1998, Coquery-Vidrovitch 1998, Freed 2010, Giles-Vernick 2000, Manning and Akyeampong 2006, Laporte et al. 2007, Gendreau 2010, Stock 2013). All cited localities are indicated in ***Figure 5.1***.

5.3. Results

5.3.1. Forest composition

The 1,765,483 inventoried trees were studied at the genus level, and included 176 genera (***Appendix 6***). The five most represented genera were *Celtis* (Ulmaceae), *Polyalthia* (Annonaceae), *Strombosia* (Olacaceae), *Petersianthus* (Lecythidaceae), and *Manilkara* (Sapotaceae).

Most of the genera included shade-bearers (n = 71 genera), which were followed by the pioneers (n = 47), and the non-pioneer light-demanding species (NPLD, n = 37). We had no information for 21 genera. Regarding leaf phenology, 108 genera were evergreen, versus 50 deciduous. No information was available for 16 genera.

Wood density ranged from 0.22 g.cm^3 for *Ricinodendron* (Euphorbiaceae) to 0.88 g.cm^3 for *Bobgunnia* (Fabaceae). Mean density was 0.58 g.cm^3. Mean diameters ranged from 31.62 cm to 93.46 cm in dbh for *Meiocarpidium* (Annonaceae) and *Autranella* (Sapotaceae), respectively, with a mean for all genera of 47.45 cm in dbh. Mean basal area ranged from 0.12 m^2/ha to 0.92 m^2/ha for *Lasiodiscus* (Rhamnaceae) and *Ceiba* (Malvaceae), respectively, with a mean for all genera of 0.30 m^2/ha.

5.3.2. Forest structure

Among the inventoried trees, we identified two groups of genera: (i) those that showed a reverse-J shape distribution (***Figure 5.2*** and ***Appendix 6***) with many small and young trees (most of the genera, n = 134, 76%), and (ii) those for which distributions deviated from this pattern (n = 42, 24%), including flat (e.g. *Baillonella*) and unimodal distributions of diameter. Among these, we identified four primary canopy genera (i.e. *Erythrophleum* and *Pericopsis* (Fabaceae), *Terminalia* (Combretaceae), and *Triplochiton* (Malvaceae)) with unimodal diameter distributions (***Figure 5.3***).

These genera are monospecific in the SRI (*Pericopsis elata*, *Terminalia superba*, *Erythrophleum suaveolens*, and *Triplochiton scleroxylon*), and share similar functional traits (i.e. deciduous, emergent, pioneer light-demanding trees). Combined, these four species represented 4.3% of the inventoried trees, reaching a maximum of 8.62% in one site in Cameroon.

5.3.3. Diameter distribution of the four studied species

The dbh ranged from 10.6 cm (*T. superba*) to 151.6 cm (*E. suaveolens*) (***Appendix 9***). The mode of the diameter distribution differed between the four studied light-demanding species, with 65.3 cm for *P. elata*, 69.8 cm for *T. superba*, 72 cm for *E. suaveolens*, and 90.3 cm for *T. scleroxylon*. Weibull distributions indicated modes comprised between 65.3 cm in dbh for *P. elata*, and 90.3 cm in dbh for *T. scleroxylon*. The modes for *T. superba* and *E. suaveolens* were 69.5 cm and 72 cm in dbh, respectively.

5.3.4. Tree-ring data

Four studies provided growth and age data, which were based on tree-ring analysis (***Appendix 7***). We found data for 83 discs (*P. elata* = 24; *T. superba* = 41; *T. scleroxylon* = 18) from four locations in the Democratic Republic of Congo, the Ivory Coast, and Cameroon. Data for *E. suaveolens* were not available. Mean ring width ranged from 0.298 ± 0.54 (standard deviation, SD) cm for *P. elata* to 0.719 ± 0.267 (SD) for *T. superba*. It was 0.620 ± 0.28 (SD) cm for *T. scleroxylon*.

5.3.5. Mean annual increment in diameter (MAI$_d$)

In the study sites, the MAI$_d$ of the monitored trees ranged from 0.44 ± 0.033 (standard error, SE) cm/y for *E. suaveolens* (367 stems) to 0.58 ± 0.061 (SE) cm/y for the fast-growing *T. scleroxylon* (265 stems). It was 0.45 ± 0.026 (SE) cm/y and 0.53 ± 0.112 (SE) cm/y for *P. elata* (199 stems) and *T. superba* (152 stems), respectively (***Appendix 9***).

5.3.6. Performance of the growth models

Results of tree modeling (***Figure 5.4*** and ***Appendix 8***) indicated that the Canham model was the best model to explain tree growth in *E. suaveolens* (BIC = 196.6), *T. superba* (BIC = 256.1), and *T. scleroxylon* (BIC = 372.1), whereas only the Mean model best explained tree growth in *P. elata* (BIC = 99.1). The performance of the models remained, however, very low.

5.3.7. Growth/age relationship

According to the age data from published tree-ring studies (***Appendix 7***), we found that estimations based on mean growth were likely to be more reliable than those based on growth models (***Figure 5.4***). In particular, the performances of the Canham and Lognormal models were low, as well as, to a lesser extent, that of the unimodal distributions (sigmoidal growth trajectory). Based on mean growth estimates, the age of the canopy trees was only a few centuries, with a mode dated to between 142 and 164 ya, which corresponds to the years AD 1836 and 1858 (mean AD 1850) (***Figure 5.2***).

5.3.8. Chronology of paleoenvironmental changes

Climate of the last 1000 years was documented by sea surface temperatures (SSTs) and the atmospheric dust signal from the marine core ODP 659, taken off the West African coast, and sediments from Mopo Bai and Goualogou Lake in the Republic of the Congo. Climate oscillated between wet and dry periods (***Figure 5.5*** and ***Appendix 10***). Typically, climate was dry until ~AD 1200, between AD 1250 and 1450, and since AD 1850, with intermediate wet periods, in particular a long one between ~AD 1450 and 1850.

The erosion curve included data related to grain size and chemical elements from the banks of the Nyong, Boumba, Dja, Ngoko rivers in Cameroon and in the Republic of the Congo, and the Mbaéré valley and the Sadika alluvial fan in the Central African Republic. This signal did not overlap climate data, as erosion was high between ~AD 1350 and 1950, with a slight drop dated to between AD 1500 and 1650.

The history of vegetation change derived from $\delta^{13}C$ values obtained at the same sites as those documenting erosion. Results indicated two main time periods: a first one until ~AD 1200 dominated by forest vegetation (C3 dominant, values > 25‰), and a second one from ~AD 1600 until today dominated by grass cover (C4 dominant, values < 25‰).

Pollen data of light-demanding species (i.e. *T. scleroxylon*, *E. suaveolens*, *Macaranga* spp., *Myrianthus/Musanga* type and *E. guineensis*) were obtained at Lake Télé, Mopo Bai and Goualogou Lake in the Republic of the Congo, and at sites in the northern Lobaye in the Central African Republic. They were more present between ~AD 1300 and 1400, then between ~AD 1600 and 1850.

Paleofires were documented by macro- and microcharcoal data from Mopo Bai and Goualogou Lake in the Republic of the Congo, and the Lobaye area (in the Rep. of the Congo and the Central African Republic). Indicators of paleofires slightly increased between ~AD 1300 and 1400. They were more substantial, however, between ~AD 1550 and 1850.

5.3.9. Chronology of human activities

Evidence of human activities was identified during two main periods: the first one around AD 1000, and the second between ~AD 1400 and 1850 (***Figure 5.5*** and ***Appendix 11***). The main discoveries comprised potsherds associated with settlements, iron slags and tuyères related to iron smelting, or were located in places where salt was exploited (e.g. Ngoko River). Most of the artifacts were found between ~AD 1600 and 1800. Focusing on the pottery only, dates were distributed into three periods: (i) between ~AD 800 and 1100, (ii) between AD 1300 and 1600, and (iii) between AD 1700 and 1800. Smelting activities were documented at a few sites only, especially in the southern Central African Republic (i.e. Bagbaya, Ngara, and Lingbangbo), which were in use during short time periods: between ~AD 1000–1100, AD 1300–1400, AD 1500–1700, and AD 1700–1900.

5.3.10. Radiocarbon chronology

The results of the Bayesian analysis of the radiocarbon dates indicated a weak radiocarbon signal until ~AD 1200, which increased from ~AD 1200 (***Figure 5.5*** and ***Appendix 12***). Main peaks were centered on ~AD 1350, 1550, and 1750. The signal strongly decreased after ~AD 1800, with a last small peak around AD 1950-1964 related to the nuclear activities of the mi-twentieth century.

5.3.11. Historical events

Key events emerged within the historical chronology (***Appendix 13***). Firstly, the slave-raiding leaded by the Fulbe people, and particularly the period between AD 1480 and 1600, profoundly destabilized the area. During the following centuries (17th-18th centuries), the Triangular Trade pushed other populations to flee southward in the forest.

The second key event is the beginning of the colonization of Africa, which put a stop to the Fulbe's activities. The exploration of the SRI that began after AD 1875, and the permanent presence of the European colonists since then, deeply disturbed the spatial distribution of the local populations, as well as their activities (e.g. enrolment in the concession companies, education, diseases, etc.). During this period, the conflicts that opposed France and Germany (i.e. the 1870 War, and the First and Second World Wars) were also transferred to the African territories.

Finally, the region experienced a massive rural exodus since the 1930s, which was amplified since the independences (Cameroon, Republic of the Congo, and Central African Republic the same year: 1960).

5.4. Discussion

5.4.1. Generalized decline of light-demanding tree populations

The reverse-J-shape distribution of diameters, characteristic of most genera, is typical of 'active' tree populations with many small and young trees (***Figure 5.3***). By contrast, the unimodal distribution of diameters could represent a generalized limited number of young trees (i.e. a lack of regeneration) and indicate the widespread decline of the tree populations. This type of distribution was characteristic of four primary canopy genera (i.e. *Erythrophleum* and *Pericopsis* (Fabaceae), *Terminalia* (Combretaceae), and *Triplochiton* (Malvaceae)), which we studied further. Historical factors were previously invoked to explain such distributions for *E. suaveolens* and *T. superba* in eastern Cameroon (Durrieu de Madron and Forni 1997). Similarly, a unimodal distribution of diameters was reported for the light-demanding timber species *Aucoumea klaineana* in Gabon, which could not be explained only by demography.

Ontogenic variations in growth are well described for tropical tree species, and unimodal growth trajectories are widely reported (Hérault et al. 2011). The low performance of the models to estimate tree age is explained by the slow growth of young trees (dbh 10 cm) and the great uncertainty regarding the time a tree remains in the small diameter classes (***Figure 5.4*** and ***Appendix 8***). Indeed, a linear relationship between tree diameter and age is acceptable for tropical tree species of a larger size (Worbes et al. 2003). Most suppressed individuals were destined to die, and therefore, only the trees with vigorous growth are able to reach the canopy and could be thus included in this type of analysis. The tree-ring approach, including information for the growth of small trees, remains therefore essential for age estimation (Worbes et al. 2003), but studies are only sporadic for central African forests.

Based on mean growth estimates, canopy trees in the SRI were aged to only a few centuries, with a mode dated to AD 1850 in average. This age range is consistent with the estimated ages of canopy trees in Nigeria (van Gemerden et al. 2003) and in Cameroon (Worbes et al. 2003). Moreover, the population decline of A. klaineana in Gabon is attributed to a shift in the disturbance regime two to three centuries ago (Engone Obiang et al. 2014). The argument for a regional trend is supported by these age estimates and the general pattern we reported across the SRI. We assumed that the unimodal population/age structure of the light-demanding tree species was linked to the recent human history. Specifically, we postulated that the decrease in anthropogenic disturbances and the generalized land abandonment from ~165 ya were less favorable to the regeneration of light-demanding tree species (van Gemerden et al. 2003, Brncic et al. 2007, Greve et al. 2011, Biwolé et al. 2015). Additionally, the present-day natural gap size has been shown to be insufficient for the regeneration of most of these species (van Gemerden et al. 2003).

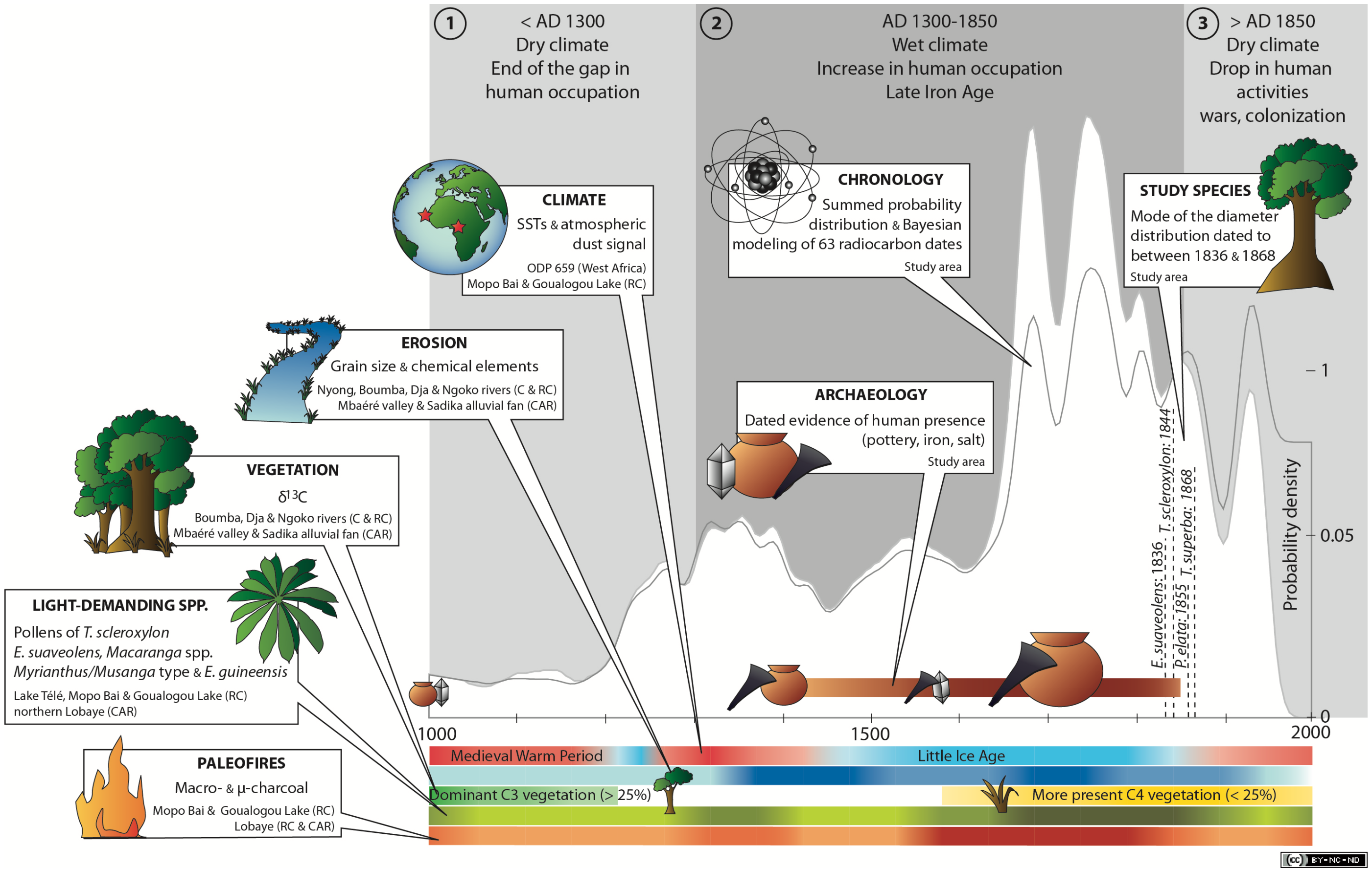

Figure 5.5. Chronology of paleoenvironmental changes and human activities in the Sangha River Interval.
We compiled data on climate, erosion, vegetation types, light-demanding species and paleofires for the last 1000 years from 34 paleoenvironmental sites and data from 38 dated archaeological sites and discoveries with 63 related radiocarbon dates. The summed probability distribution of the radiocarbon ages showed fluctuations in the signal of human activities through time. Three primary time periods were identified: (a) before AD 1300; (b) from AD 1300 to 1850; and (c) after AD 1850. Color scales (four levels) were assigned depending on the proxy influx on the curve: light = present but rare; light-medium = present; medium = frequent; and dark = very frequent. Abbreviations: AD = Anno Domini (= calendar dates); C = Cameroon; RC = Republic of the Congo; CAR = Central African Republic; SSTs = Sea Surface Temperatures; C3/C4 plants = woody species (below 25‰)/herbs (above 25‰); *E. guineensis* = the oil palm *Elaeis guineensis* (***Appendices 10*** and ***11***).
CAD: Illustrator CS4 (https://www.adobe.com).

5.4.2. The regional history of human activities

All proxies converged toward the identical regional history that is divided into three primary periods: (i) a dry period between AD 950 and 1300 with almost no human activity recorded; (ii) a wet period between AD 1300 and 1850 with large-scale human activities and a high disturbance regime that led to a forest-savanna mosaic; and (iii) a forest aging period from AD 1850 to the present. The aging period corresponded to a shift in the disturbance regime that was most likely caused by a depopulation of the forest with the beginning of the European colonization (Robineau 1967, Copet-Rougier 1998, Coquery-Vidrovitch 1998).

The first time period before AD 1300 corresponds to a dry climate, consistent with the higher latitude Medieval Warm Period (DeMenocal et al. 2000), with only scarce pollen of pioneer and light-demanding species (Brncic et al. 2007, 2009). The vegetation was composed of forest tree species according to $\delta^{13}C$ values between 30.6 and 25.8‰ (White et al. 2000), Sangen 2012). In southeastern Cameroon, alluvial records indicate a growing human impact on forests between AD 1000 and 1200, particularly because of shifting cultivation and the associated increase in erosional processes (Sangen 2012, Runge et al. 2014). Charcoal (related to natural fires and anthropogenic burning) in lake sediments and soils were recorded only at the end of this period, which corresponds to the end of the hiatus phase in human activities (massive depopulation) previously documented for central Africa (Wotzka 2006, Oslisly et al. 2013a, 2013b) and specifically for the SRI (Morin-Rivat et al. 2014). Surveys have been carried out, but the poor surface visibility can underestimate true human presence (see Morin-Rivat et al. 2016, for an example of methodology). Sometimes no archaeological research has been carried out in certain regions covered by dense forest (B. Clist, pers. comment, but see referenced archaeological sites on: http://www.pprfth-ac.org/archeologie/). Notably, at this time, human populations were only indicated at a few sites that were dedicated to iron metallurgy (southern CAR near Bangui and Nola and the site of Ngombé in the Rep. of the Congo, approximately AD 1300) and to salt exploitation (Ngoko River, approximately AD 1000).

From AD 1300 to 1850, pollen sequences indicated a relatively wet climatic period. Nevertheless, burning increased, and this burning is attributed to human activities because the moisture content of the vegetation was too high for fires to often occur naturally (Vennetier 1963, Brncic et al. 2007, 2009). The Mbaéré valley and the Sadika alluvial fan (Gadzi-Carnot sandstones in CAR) recorded intensive erosion and relatively high $\delta^{13}C$ values after AD 1200, indicating forest regression and the formation of a forest-savanna mosaic (Sangen 2012, Runge et al. 2014). In southeastern Cameroon, the anthropogenic erosion culminated at approximately AD 1200–1400 (Sangen 2012, Runge et al. 2014). The decrease in the run-off with an increased rate of sedimentation between AD 1400 and 1600 corresponds to the climatic period of the Little Ice Age (Brncic et al. 2007, 2009), in combination with an increase in the frequency of El-Niño events between AD 1200 and 1500 (Sangen 2012). Since then, despite a more humid period following the Little Ice Age, maximal incidence of human activities have been recorded in the SRI, which opened the forest cover and favored the pioneers. Nonetheless, we must remain cautious regarding the interpretation of the archaeological data, as there is a huge gap of knowledge in the SRI, especially in the area between Souanké and Berberati (***Figure 5.1***). In the state of the art, it is not possible to interpret the spatial distribution of human settlements and activities. In particular, iron-smelting sites are only few, they are concentrated in the southern Central African Republic, and were in use during short periods. The volume of charcoal used and, by extension, the associated deforestation, should have been important for feeding the furnaces, as shown by Pinçon (1990). However, the debate is still alive about estimating the volume of wood needed for metallurgy (Lupo et al. 2015), compared to the volume of trees logged for shifting agriculture (Goucher 1981).

The period of ~AD 1850 to the present marked a decrease in the disturbance regime (***Figure 5.5***). The pollen of naturally grown oil palms and pioneer trees became rare or absent. In southeastern Cameroon and in the CAR, pollen, phytoliths, soil charcoal and $\delta^{13}C$ values indicate little disturbance during the past 100–150 years, with the recolonization of the savannas by forest trees (Runge et al. 2014, Lupo et al. 2015). The anthropogenic burning persisted, as indicated by charcoal particles found in sites located along rivers (Brncic et al. 2007, 2009, Tovar et al. 2014), which might document either the colluvium of charcoals downslope or the concentration of human activities on the riverbanks. During this period, less evidence of human activities is reported (Oslisly 2013b, Morin-Rivat et al. 2014). In the 1960s, young secondary forests (i.e. with *Musanga cecropioides*) constituted only 1% of the forest types and were located along the main roads (Vennetier 1963). Despite the drying of the 20th century, confirmed by low flow regimes in the primary rivers, the Sangha, Ubangui, Lobaye, and Likwala-aux-Herbes (Runge and Nguimalet 2005, Aleman et al. 2013), and the increase in anthropogenic activities in recent years (e.g. mining, industrial logging from the 1970s, burning, and cultivation) that induced very localized, degraded landscapes (Laporte et al. 2007, Sangen 2012, Gond et al. 2013), forests apparently extended naturally in central Africa (Sangen 2012).

5.4.3. Recent and generalized land abandonment

Although precise historical information is not available before the mid-19th century for central Africa (Robineau 1967, Burnham 1996) (see ***Appendix 13*** for a detailed chronology), we observed a drop in the radiocarbon signal between AD 1480 and 1650 (***Figure 5.5***) that we assigned to the inland impacts of the Triangular trade, with a fled of whole populations within the forest in the late 16th century (Gendreau 2010). Indeed, between AD 1550 and 1850, the Fulbe populations coming from northern Cameroon (Burnham 1996) organized the slave-raiding for Europeans and induced the flight of populations southward into the forest (Vennetier 1963), explaining the increase in human presence and activities (i.e. agriculture and smelting) in the region. The successive ebb (~1480-1600 AD) and flow of groups until the 18th century explain the numerous interethnic wars in the Upper-Sangha (e.g. the Fang invasion since the 14th century), for land control and cultural supremacy (Copet-Rougier 1998).

Based on the large dataset that we gathered, human activities clearly decreased after ~AD 1850, which corresponds to the beginning of the regeneration shortage of light-demanding tree populations. In the last decades of the 19th century, Savorgnan de Brazza reported that the SRI was densely populated (Copet-Rougier 1998), which seems now unlikely given the low density of human populations (less than one inhabitant per km^2). We hypothesize that the European colonization deeply disturbed the spatial organization of the local populations in central Africa, as demonstrated in Gabon (Pourtier 1989, Engone Obiang et al. 2014). Colonization stopped the migrations and the interethnic warfare and forced entire groups to settle along rivers and roads for administrative and commercial purposes (Vennetier 1963, Robineau 1967). However, the process of village redistribution during the colonial times strongly varied from one place to another, according to the settlement of the colonial posts, and the borders between the French and German possessions (Pourtier 1989: e.g. of the Fang villages in Gabon). Additional factors can also be invoked to explain the emptying of the forests, including the involvement of local populations in the Franco-German conflicts during their respective colonial expansions and the two World Wars, the forced or voluntarily labor in concession companies, the deadly repression of riots, and the increased mortality because of diseases (e.g. trypanosomiasis along the Ubangui and the Sangha rivers) (Robineau 1967, Runge and Nguimalet 2005, Runge 2008, Runge et al. 2014). Furthermore, because of the land abandonment caused by the new relationships established between the local peoples and the colonists (Giles-Vernick 2000), the Mpiemu tales of the late 19th century relate to the regrowth of the forest.

From the 1930s and after the independence (1960), the abandonment of the forests was amplified because the access to education contributed to an increase in the rural exodus to the main towns and capitals in a search for valued wage labor in administration or trade (Vennetier 1963, Robineau 1967). From this period, deep demographic disparities emerged between towns and rural areas: most working-age people went to cities (e.g. Ouesso, Impfondo and Brazzaville in Congo, Yokadouma and Bertoua in Cameroon, and Berberati and Bangui in CAR), while children and the elderly people were left in villages. Thus, less labor force was available for forest clearing and cultivation (Vennetier 1963).

5.5. Conclusion

For the first time in the Sangha River Interval, a convergent body of evidence shows the effect of past changes in the disturbance regime on forest structure and composition. Consistent with previous observations in Nigeria (White and Oates 1999, van Gemerden et al. 2003), in Gabon (Engone Obiang et al. 2014), and in southwestern Cameroon (Biwolé et al. 2015), the population decline of light-demanding tree species that now dominate the canopy is explained by the decrease in anthropogenic disturbances. Caution is nevertheless required regarding the interpretation of the radiocarbon signal. Large-scale historical events, such as the interethnic wars and the European colonization of Africa, contributed to reduce human pressure on the forest. Former agricultural activities such as shifting cultivation, which were scattered in the forest areas between AD 1300 and 1850, likely had an indirect positive influence on the regeneration of these species. Past local populations of 'foragers-horticulturists' (Kay and Kaplan 2015) gardened the forest by preserving useful light wooded trees (e.g. *T. scleroxylon*, typically dependent of slash-and-burn agriculture for their regeneration; R. Oslisly pers. com.) or dense wooded trees (e.g. *P. elata* and *E. suaveolens*) in the fields during forest clearing, and therefore created favorable conditions for their recruitment by maintening the openings created since the 2500 BP-episode of forest fragmentation (Carrière et al. 2002). Since ~AD 1850, the reduced disturbance regime has apparently hindered the regeneration of most species of light-demanding trees (Carrière et al. 2002, van Gemerden et al. 2003, Willis et al. 2004, Brncic et al. 2007). The current lack of regeneration and the general aging of the populations threaten both their viability and the sustainability of logging (Hall et al. 2003, van Gemerden et al. 2003). Thus, based on these results, a renewed interest in silvicultural practices (Doucet et al. 2004) that create larger openings in the canopy should be inspired. Complementary liberation, thinning treatments, and population enforcement, may also contribute to maintain these timber species (Fayolle et al. 2014a).

Third part Conclusions

Chapter 6 General conclusion

The reaches opened before us and closed behind, as if the forest had stepped leisurely across the water to bar the way for our return. We penetrated deeper and deeper into the heart of darkness. It was very quiet there. At night sometimes the roll of drums behind the curtain of trees would run up the river and remain sustained faintly, as if hovering in the air high over our heads, till the first break of day. Whether it meant war, peace, or prayer we could not tell. The dawns were heralded by the descent of a chill stillness; the woodcutters slept, their fires burned low; the snapping of a twig would make you start. We were wanderers on a prehistoric earth, on an earth that wore the aspect of an unknown planet.

Joseph Conrad – *Heart of Darkness* – 1899

This last chapter sums up the main elements observed during this PhD, in terms of chronology of the archaeological evidence, methodology of sampling, and interdisciplinary research regarding past human impacts on central Africa's tropical forests. Finally, it presents the remaining gaps of knowledge and targets the potential for additional research and methodological improvement, in order to better document the relationship between man and his environment during the Holocene.

Le bois bleu – Véronique LG Morin

6.1. Introduction

In this PhD thesis, we aimed at evaluating the long-term dynamics of central African moist forests in relationship with human activities. Past anthropogenic disturbances may have contributed to the expansion and maintenance of light-demanding tree species during the late-Holocene (i.e. after 2500 BP). Some of these light-demanding species are exploited for their timber, but currently suffer from a lack of regeneration that threatens both their viability and the sustainability of logging.

In the framework of this research, we focused on the anthropogenic impacts and thus determined three research questions related to: 1) the chronology of human presence in the northern Congo Basin, 2) the types, magnitude, and severity of past human activities, and 3) the potential influence of land-use changes in the current depletion of light-demanding tree populations. The main objective of this study was thus to understand the impact of past human disturbances on the structure and composition of central African moist forests during the late-Holocene. Our hypothesis was that human activity had a local and recurrent impact on vegetation that maintained light-demanding tree species during the last two millennia. Land-use changes occurred, however, since the European colonization, which modified the type and location of human-driven disturbances on the forest cover.

Numerous questions remain unresolved, however, regarding the relationship between man and his environment in central Africa during the Holocene, in terms of spatial distribution, human activity has been insufficiently documented in areas covered by dense forest, especially in the northern Congo Basin. The corollary of this situation was that the temporal dimension of human activity in that region was characterized by many knowledge gaps, especially regarding the most recent periods. Indeed, previous archaeological literature focused on food-producers settlements after the 2500-BP dry climatic event, but had little interest in the depopulation phases during the Atlantic slave trade or the colonial era. It was, therefore, particularly difficult to make the link between old to recent events of anthropogenic disturbance and the current state of vegetation.

The mean we found to reconcile those different aspects –space and time, and human and nature– was to analyze several biomarkers of land-use in several sites, spreading from southwestern Cameroon to the northern Republic of the Congo. In particular, we study charred botanical remains, because they combined these spatial and temporal dimensions: (i) those materials can be found everywhere in forest soils, and (ii) they can be dated by the radiocarbon method. We detailed these particular methodological aspects in **Chapter 2**. These biomarkers thus drew a line between archaeology and ecology, because both human and nature can produce them. This places itself in the context of the contradictory debate raised between Bayon et al. (2012a), one hand, and Neumann et al. (2012b) and Maley et al. (2012), the other hand, regarding the impact of human-induced *vs* climate-induced disturbances on central African moist forests. One of the main conclusions we have drawn from that debate is that the scale of observation, both in terms of space and time, remain crucial to understand the respective influence of human or climatic drivers. This particularity was taken into consideration in our research by analyzing our materials and data at different spatial scale: regional, inter-site, and intra-site.

6.2. Main results and research contributions

6.2.1. Chronology of human presence in the Congo Basin

Regarding the chronology, Chapter 3 presented a regional study focused on the Sangha River Interval, an underexplored area covering southeastern Cameroon, southern Central African Republic and the northern Republic of the Congo. It exposed the state of the art of archaeology, along with new data regarding the spatial and temporal patterns of human occupation in this area. The empty spaces were partially filled in by the gathering of 43 unpublished dated charred seeds and charcoal pieces, corresponding to 36 archaeological sites and discoveries.

In addition, we found charred botanical remains to be ubiquitous in soils. Among the remains, charcoal was by far the most present, which confirmed the non-pristine nature of the central African moist forests and the occurrence of past fire-events. The incidence of the naturally-growing oil palm, in the form of charred endocarps, still raises the question of an ancient exploitation and/or management of this staple resource by forest people. In support for a presence of human in the moist forest, we found artifacts, mainly in the form of potsherds, but also some lithics made on quartz.

One of the main contributions of this study was the bimodal temporal pattern of the summed radiocarbon ages. Indeed, we documented two periods of human activity in the study area that matched to two well-known archaeological periods: a) a Phase A from 2300 to 1300 BP, corresponding broadly to the Early Iron Age, and b) a Phase B from 670 BP to the present, corresponding to the Late Iron Age, with a still intriguing phase of depopulation between these two phases. This hiatus may be due to a more humid climate and subsequent epidemics (e.g. the trypanosomiasis), or still due to a lack of archaeological investigation in the region (B. Clist pers. com.), which is unlikely with regard to the numerous available archaeological sites in the region that support the hiatus hypothesis (http://www.pprfth-ac.org/archeologie/). The time periods we defined, and in the state of current knowledge, add nonetheless support to the pattern of human occupation already documented in central Africa.

6.2.2. Identifying past human activities within the forest

Based on this spatial and temporal framework, **the objective of Chapter 4 was to determine the types of activities people practiced during the past**. This study narrowed down the observation scale, and addressed the need of precise indicators at local scale. We thus presented a site-focused and systematic methodology based on land-used biomarkers: artifacts and charred botanical remains. This study was performed in two contrasted sites in terms of ecology, located in southwestern and southeastern Cameroon, and distant of 400 km apart.

Among the main results, we found at both sites the same temporal pattern as that presented in **Chapter 3**, with two archaeological phases dated to the late-Holocene, with an intermediate hiatus phase in terms of human settlements and activities. We also found in southeastern Cameroon unpublished occurrences of Early Iron Age potsherds decorated with comb-stamped circles.

We demonstrated that charcoal were likely deriving from human activities as they were local, scattered and produced during a rather wet period. We showed that the different types of charred botanical remains can represent distinct signals of human activities with: a) oil palm endocarps associated with potsherds corresponding to domestic activities (i.e.

villages), and b) charcoal corresponding to agricultural activities (i.e. slash-and-burn cultivation). The latter were mostly found in the two first kilometers from the villages, which are the daily distance people currently walk to cultivate their field.

By using a spatial Bayesian analysis of the radiocarbon ages, we showed that the distance between two contemporaneous activities tended to be greater than two kilometers apart (e.g. around 1800 BP). This distance was reduced around 1600 BP, parallel to a peak in human density, indicating, therefore, a short-term response of people to such change (Dincauze 2000). We thus assumed, as a work hypothesis, that past forest populations had a deep knowledge of land-use, and adapted their management to alliances and conflicts between groups.

Finally, we stressed that the methodology proposed was performed with simple tools, even during fieldwork, and can be applied to other tropical contexts, especially in remote areas covered by dense forest.

6.2.3. Linking ancient land-use with the current state of light-demanding tree populations

Finally, **Chapter 5 addressed the question of the age of current light-demanding tree populations and the causes of their current depletion**. This last paper gave the opportunity to combine big datasets embracing palaeoecology, archaeology, history, dendrochronology and botanical inventories in the Sangha River Interval. Their analysis drew several lines of evidence towards an anthropogenic impact on forests that shaped their structure and composition. More specifically, they favored the natural regeneration of light-demanding tree populations by creating recurrent and scattered gaps in the canopy. Several populations of these light-demanding trees currently show a unimodal distribution of their diameter. This particular pattern usually occurs for species with a lack of regeneration, the latter threatening both their viability and the sustainability in case of timber exploitation.

We showed that recent land-use changes occurred since the mid-19th century, affecting the disturbance regime due to human activities within the forest. After a period characterized a high population density up to the 19th century, the co-occurring slave-raiding, inter-ethnic wars and European colonization in central Africa caused a drop in this density and the inherent anthropogenic disturbances. People died from wars or epidemics, or were settled along the main road axes for administrative purposes. Rural exodus to main cities amplified the phenomenon of socioeconomic disruption and forest depopulation during the 20th century. Today, human population density is less than one inhabitant/km², which allows the shade tolerant species to naturally regenerate at the expense of the light-demanding tree species that need more open areas to naturally root and grow.

Our results stressed the need for silvicultural strategies reproducing certain effects of past anthropogenic disturbances and enhancing the recruitment of the targeted tree species, in order to ensure the sustainability of these light-demanding tree populations.

6.3. Potential for additional research

In this work, we addressed various archaeological questions, which revealed, however, several lacks in terms of chronology (Chapter 3), archaeological cultures and human activities (Chapter 4), and effects of land-use on current forests (Chapter 5).

6.3.1. Towards a more precise archaeological chronology

Regarding the archaeological chronology, the number and reliability of existing radiocarbon ages remain too weak, and holes still persisted, even in defined archaeological phases, such as the Early and Late Iron Age. In particular, the sampling of to-be-dated materials seems problematic. Concerning sample collection, protocols exist for archaeological sites, but are missing for off-site contexts. The latter are still despised by archaeologists, because of the absence of clear stratigraphy and its inherent relative chronology. This off-site dated soil charcoal could, however, offer great opportunities to date past fire events, either natural or anthropogenic, and thus to document the local environment in the vicinity of ancient human settlements.

Accurate chronologies of past events, either natural or anthropogenic, constitute the foundation of any diachronic analysis. In particular, the so-called hiatus phase between ca. 1300 and 600 BP should be investigated in order to determine its exact causes, or even if this not derives from a research artifact, i.e. a restricted number of archaeological prospections within this region (B. Clist pers. com.) Nonetheless, we are still speculative about soil accumulation rates in central Africa, which leads to an uncertainty regarding the reliability of the temporal framework of human presence within the forest. Precise geomorphological fieldwork studies along with an experimental design (e.g. monitored sediment traps) and a computer-based modeling of the potential soil processes (e.g. accumulation, erosion, and colluvium) could help deciphering the deep and unfortunately often uniform yellow or red soil profiles (see e.g. Thiéblemont et al. 2013).

Statistical analyses of radiocarbon ages currently know increasing improvement, notably by using the last updates of the OxCal sofware. Nonetheless, the use of cumulated calibrated ages should be done with caution (B. Clist, pers. com.), especially when it includes both archaeological and off-sites ages, and in the absence of well-defined archaeological frameworks related to local cultures. Applications of Bayesian research on the datasets, as done in **Chapters 4 and 5**, should also benefit from strict research questions, so as to better define the temporal range and spatial extent of the analyses (i.e. prior and posterior likelihood). A further research direction could be, therefore, the overhaul of our previous analyses, with the addition of new radiocarbon ages, in a better-defined archaeological framework.

6.3.2. Knowing past forest cultures

However, archaeological cultures and related activities and technologies are still insufficiently investigated in the dense forests of central Africa, especially in the northern Congo Basin. For instance, in the Sangha River Interval, no data are available along a diagonal from Souanké, in the Republic of the Congo, to Berberti in Cameroon. New findings could fill in the gaps in the archaeological records, and push the limits of our knowledge about human cultures and lifestyles deeper within the forest. Culture, in the sense of the archaeological research, reassembles material remains (i.e. artifacts), stylistic repertoires (e.g. pottery shapes and decoration), and specific practices (e.g. smelting) (Chouquer 2008). Nonetheless, several aspects are still missing, especially those related to the location of the pottery and iron production centers, and the related trade. Therefore, a harmonized and adjustable protocol for systematic archaeological surveys is needed. This archaeological protocol could easily be combined with the fieldwork methodology we set up for the collection of charred botanical remains (see ***Chapter 4***). In 2013, we identified in the FMU 10.056 at SFID-Mbang a suitable site for this purpose. This site provided great amounts of pottery presenting Early Iron Age decorations, along with several well-preserved dump-pits with charred oil palm endocarps. We propose a full excavation of this unpublished site. Moreover, a systematic radial sampling from this archaeological site could help finding evidence for burnt vegetation related to agriculture.

Beyond the harvest of new archaeological information and material, important collections, especially of potsherds, are still pending in the caves of universities and museums. Ceramic, indeed, is insufficiently known in central Africa. Its study could provide new technological and cultural elements related to the Iron Age in the northern Congo Basin, in particular. Specialists are only a handful, however. Tight collaborations with our colleagues of African institutions are more than necessary, especially in the universities of the countries we work in (i.e. Cameroon and the Republic of the Congo, in particular) in order to study these dormant collections.

In addition, a collaborative platform, which could take the form of a GIS, could allow a better identification of the archaeologically blanks, little investigated areas, or areas under research programs. A first step could be seen in the ACACIA initiative (University of Lausanne, Switzerland, http://arve.unil.ch/research/land-use-in-iron-age-africa/), which is currently establishing temporal (i.e. time-slices covering ~3800–400 BP) and cultural maps of archaeological findings in west and central Africa based on socioeconomic systems (i.e. hunter-gatherers, fishers, small-scale cultivators, desert pastoralists without cattle, savanna pastoralists with cattle, extensive early farmers, extensive diversified farmers, intensive diversified farmers, wetland farmers, upland rice farmers; Kay and Kaplan 2015). These ten categories are not mutually exclusive. The question of the classification of human practices, on the basis of the material culture, deserves to be addressed with both caution and enthusiasm.

6.3.3. Evaluating land-use during the late-Holocene

The magnitude, severity and actual impacts of land-use on the forest cover deeply depend on population density and lifestyles, including food acquisition. It seems difficult to define the notion of territory, whose limits move both in time and space (Chouquer 2008). The human settlement forms its core, surrounded by two concentric circles, the food-producing territory, followed by the supply territory (Leroi-Gourhan 1964 and 1965; see Kay and Kaplan 2015 for an application). **Chapter 4** constituted a first attempt to attest the likely use of small-scale slash-and-burn shifting cultivation up to two millennia ago in southern Cameroon, probably performed in the vicinity of the human settlements. Our first observations described scattered occupations that could correspond to punctual and random human pressure on the forest in the same range as the Ntumu's current agricultural practices in southern Cameroon (Carrière 1999, 2002, Carrière et al. 2002). Only a charcoal quantification applied to more sampling sites could support the decreasing pattern of agricultural pressure we detected in **Chapter 4** by using a distance analysis.

Land-use evaluation could also go through the identification of the macrobotanical remains (i.e. charred seeds and charcoals) we have already collected in southern Cameroun and in the northern Republic of the Congo. Regarding macrobotanical remains identification, several studies have been published for central Africa (e.g. Oslisly 1999), Höhn and Neumann 2012, Hubau 2013, Hubau et al. 2013, 2014, 2015, Tshibamba 2015, Tshibamba et al. 2013, Mbayu et al. 2016). They provide new and crucial insights into vegetation evolution over time (Demoule et al. 2002) with regard to human activities. Hubau et al. (2012) usefully proposed a first identification protocol for ligneous species in DRC, using the wood descriptions gathered in the InsideWood platform (InsideWood 2004-onwards, Wheeler 2011). Nonetheless, charcoal identification in species-rich biomes deeply depends on numerous anatomical descriptions, made according to the IAWA list of anatomical features (IAWA Committee 1989). This long-term task needs the support of important wood collections (e.g. the Tervuren Xylarium; MRAC 2007), and research projects (e.g. Xylaredd and Herba-Xylaredd). These new anatomical descriptions could be included in an updated version of Hubau et al. (2012) identification protocol. Charred seeds are under analysis (L. Champion, Univ. College London) and charcoal identifications will be soon published with the contribution of W. Hubau (MRAC).

The last aspect concerns the documentation of land-use changes during the last four centuries. As stressed by Kiahtipes (2016), there is a lack of archaeological interest for the most recent times, though they bridge the gap between human history and current forest landscapes. There is thus necessary to dive into the historical and colonial archives in order to know more about the populations who lived in central Africa during this period. The presence of such archives (e.g. texts, maps, testimonies) has already been identified at several places in Belgium and France (i.e. IGN, Institut de Géographie, and BNF (digitalized resources of the Gallica platfom) in Paris, MRAC in Tervuren, and the Royal Archives in Brussels). They could add support to our interpretations of land-use changes during Phase B (Late Iron Age and after). They could also help apprehending spatial patterns and recent changes in human settlement with regard to past conflicts and colonial activities. Nevertheless, it is very important to keep in mind not to model a modern vision, including a commercial and utilitarian logic, on past environments using these textual archives (Lewuillon 2004, Chouquer 2008).

6.4. Concluding remarks

This multidisciplinary work attempted to tend a line between archaeology and ecology, past and present, regional and local scales. The originality of this work is that, using several big datasets, the archaeological approach contributes to characterize different kinds of land-use that were only anticipated by the ecological and ethnographical approaches. This work provided evidence for tight man-environment interactions in the northern Congo Basin, especially since the late-Holocene, which affected forest structure and composition. In particular, anthropogenic disturbances created gaps in the canopy that favored the maintenance of light-demanding tree populations. However, land-use changes occurred since the colonial era, which deeply disrupted traditional practices (i.e. shifting agriculture and iron smelting), and led to a human depopulation since the mid-19th century that generate a rapid forest recovery.

Nonetheless, our research did not abound in the direction of Bayon et al. (2012a) who postulated that anthropogenic disturbances were mainly responsible for an intensified weathering of tropical soils in Africa, as a consequence of agricultural practices. We found local impacts of human activities during the last two millennia in southern Cameroon and in the northern Republic of the Congo, though their magnitude and severity remain difficult to quantify accurately in the current state of our knowledge.

Recent joint actions and multidisciplinary projects linking paleoecology, archaeology and current ecology (e.g. DFG program *"Dynamics of forest ecosystems in central Africa during the Holocene"*, Runge 2014, CoForChange 2010-2014, and current C3A and AFRIFORD research program) have proven their necessity by amplifying research in central Africa. This PhD only constitutes a satellite in the orbit of these broader multidisciplinary projects, which contribute to the emergence of new and inspiring research for the future management and preservation of Africa's tropical environments.

21 March 2017

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Appendices

Appendix 1

Chapter 4 – Dataset used to test the spatial autocorrelations of pedoanthracological variables at Site 1 (Wijma)

torocor	#grids	#variables	Missing data										
210	0	6	NA										
13	15	35	55	310	600	1000	1500	3000	6000	12000	25000	50000	100000
plot	X	Y	log.Charcoal0	log.Palm0	log.seeds	log(min)	depth	tot-charcoal	tot-Palm	tot-seeds			
p319	659659.8056	254532.5521	0.004321374	0.004321374	0	0	1	0	0	0			
p320	659669.8056	254532.5521	0.008600172	0.089905111	0	0	2	0	0	0			
p321	659679.8056	254532.5521	0.206825876	0.204119983	0	0	3	0	0	0			
p322	659689.8056	254532.5521	0.017033339	0.155336037	0	0	4	0	0	0			
p323	659699.8056	254532.5521	0.004321374	0	0	0	5	0	0	0			
p324	659709.8056	254532.5521	0.004321374	0.041392685	0	0	6	0.245423508	0.495075191	0			
p325	659465.0378	254375.8183	1.22762965	0	0	2.399673652	1	0	0	0			
p326	659475.0378	254375.8183	1.070037867	0	0	2.399673652	2	0	0	0			
p327	659485.0378	254375.8183	0.322219295	0.120573931	0	2.399673652	3	0	0	0			
p328	659495.0378	254375.8183	0.45331834	0	0	2.399673652	4	0	0	0			
p329	659505.0378	254375.8183	0.580924976	0	0	2.399673652	5	0	0	0			
p330	659515.0378	254375.8183	0.075546961	0	0	2.399673652	6	3.729677088	0.120573931	0			
p331	659270.2699	254219.0845	0.004321374	0.008600172	0	2.699837724	1	0	0	0			
p332	659280.2699	254219.0845	0.071882007	0.004321374	0	2.699837724	2	0	0	0			
p333	659290.2699	254219.0845	0	0.033423755	0	2.699837724	3	0	0	0			
p334	659300.2699	254219.0845	0.029383778	0	0	2.699837724	4	0	0	0			
p335	659310.2699	254219.0845	0.075546961	0.045322979	0	2.699837724	5	0	0	0			
p336	659320.2699	254219.0845	0.008600172	0	0	2.699837724	6	0.189734292	0.09166828	0			
p337	659075.5021	254062.3507	0.004321374	0.004321374	0.004321374	2.875639913	1	0	0	0			
p338	659085.5021	254062.3507	0.008600172	0.045322979	0	2.875639913	2	0	0	0			
p339	659095.5021	254062.3507	0.021189299	0.053078443	0	2.875639913	3	0	0	0			
p340	659105.5021	254062.3507	0.012837225	0.064457989	0	2.875639913	4	0	0	0			

p341	659115.5021	254062.3507	0.004321374	0.004321374	0	2.875639913	5	0	0	0			
p342	659125.5021	254062.3507	0	0.012837225	0	2.875639913	6	0.051269443	0.184339384	0.004321374			
p343	658802.8271	253842.9233	0.071882007	0.158362492	0	2.699837724	1	0	0	0			
p344	658812.8271	253842.9233	0.136720567	0.012837225	0	2.699837724	2	0	0	0			
p345	658822.8271	253842.9233	0.004321374	0.041392685	0.004321374	2.699837724	3	0	0	0			
p346	658832.8271	253842.9233	0	0	0	2.699837724	4	0	0	0			
p347	658842.8271	253842.9233	0	0.004321374	0	2.699837724	5	0	0	0			
p348	658852.8271	253842.9233	0	0	0	2.699837724	6	0.212923948	0.216913776	0.004321374			
p349	658608.0593	253686.1895	0	0	0	2.399673787	1	0	0	0			
p350	658618.0593	253686.1895	0	0	0	2.399673787	2	0	0	0			
p351	658628.0593	253686.1895	0.004321374	0.004321374	0	2.399673787	3	0	0	0			
p352	658638.0593	253686.1895	0.017033339	0.025305865	0.004321374	2.399673787	4	0	0	0			
p353	658648.0593	253686.1895	0.11058971	0.008600172	0	2.399673787	5	0	0	0			
p354	658658.0593	253686.1895	0.195899652	0.004321374	0	2.399673787	6	0.327844076	0.042548785	0.004321374			
p355	658413.2914	253529.4557	0.776701184	0	0	0	1	0	0	0			
p356	658423.2914	253529.4557	0.658964843	0.008600172	0	0	2	0	0	0			
p357	658433.2914	253529.4557	0.719331287	0	0	0	3	0	0	0			
p358	658443.2914	253529.4557	0.136720567	0.103803721	0	0	4	0	0	0			
p359	658453.2914	253529.4557	0.086359831	0.10720997	0	0	5	0	0	0			
p360	658463.2914	253529.4557	0.029383778	0.071882007	0	0	6	2.407461489	0.29149587	0			
p361	658218.5236	253372.7219	0.086359831	0.017033339	0	2.399673652	1	0	0	0			
p362	658228.5236	253372.7219	0.320146286	0.017033339	0	2.399673652	2	0	0	0			
p363	658238.5236	253372.7219	0.068185862	0.033423755	0	2.399673652	3	0	0	0			
p364	658248.5236	253372.7219	0.195899652	0.096910013	0	2.399673652	4	0	0	0			
p365	658258.5236	253372.7219	0.463892989	0.178976947	0	2.399673652	5	0	0	0			
p366	658268.5236	253372.7219	0.309630167	0.181843588	0	2.399673652	6	1.444114787	0.525220982	0			
p367	658023.7557	253215.9881	0.523746467	0	0	0	1	0	0	0			
p368	658033.7557	253215.9881	0.488550717	0	0	0	2	0	0	0			
p369	658043.7557	253215.9881	0.113943352	0.004321374	0	0	3	0	0	0			
p370	658053.7557	253215.9881	0.06069784	0.017033339	0	0	4	0	0	0			
p371	658063.7557	253215.9881	0.201397124	0.008600172	0	0	5	0	0	0			

p372	658073.7557	253215.9881	0.075546961	0.017033339	0	0	6	1.463882462	0.046988224	0			
p373	657828.9879	253059.2543	0	0	0	2.399673652	1	0	0	0			
p374	657838.9879	253059.2543	0.004321374	0	0	2.399673652	2	0	0	0			
p375	657848.9879	253059.2543	0.1430148	0	0	2.399673652	3	0	0	0			
p376	657858.9879	253059.2543	0.025305865	0	0	2.399673652	4	0	0	0			
p377	657868.9879	253059.2543	0.008600172	0.004321374	0	2.399673652	5	0	0	0			
p378	657878.9879	253059.2543	0.012837225	0	0	2.399673652	6	0.194079436	0.004321374	0			
p379	657634.22	252902.5205	0.021189299	0	0	2.699837724	1	0	0	0			
p380	657644.22	252902.5205	0.004321374	0	0	2.699837724	2	0	0	0			
p381	657654.22	252902.5205	0.008600172	0.017033339	0	2.699837724	3	0	0	0			
p382	657664.22	252902.5205	0.264817823	0.033423755	0	2.699837724	4	0	0	0			
p383	657674.22	252902.5205	0.008600172	0.008600172	0	2.699837724	5	0	0	0			
p384	657684.22	252902.5205	0.017033339	0	0	2.699837724	6	0.324562179	0.059057267	0			
p385	657439.4522	252745.7867	0	0.012837225	0	2.875639913	1	0	0	0			
p386	657449.4522	252745.7867	0.004321374	0.064457989	0	2.875639913	2	0	0	0			
p387	657459.4522	252745.7867	0.096910013	0.06069784	0	2.875639913	3	0	0	0			
p388	657469.4522	252745.7867	0.012837225	0.017033339	0	2.875639913	4	0	0	0			
p389	657479.4522	252745.7867	0.017033339	0.004321374	0	2.875639913	5	0	0	0			
p390	657489.4522	252745.7867	0	0.008600172	0	2.875639913	6	0.131101951	0.167947939	0			
p391	674551.7326	269211.9614	0	0.008600172	0	2.954724756	1	0	0	0			
p392	674561.7326	269211.9614	0.017033339	0.008600172	0	2.954724756	2	0	0	0			
p393	674571.7326	269211.9614	0	0.017033339	0	2.954724756	3	0	0	0			
p394	674581.7326	269211.9614	0.012837225	0.012837225	0	2.954724756	4	0	0	0			
p395	674591.7326	269211.9614	0.004321374	0.017033339	0	2.954724756	5	0	0	0			
p396	674601.7326	269211.9614	0.123851641	0.086359831	0	2.954724756	6	0.158043579	0.150464078	0			
p397	674779.7949	269365.6252	0.004321374	0	0	2.796574314	1	0	0	0			
p398	674789.7949	269365.6252	0.004321374	0	0.004321374	2.796574314	2	0	0	0			
p399	674799.7949	269365.6252	0.029383778	0	0	2.796574314	3	0	0	0			
p400	674809.7949	269365.6252	0.193124598	0.071882007	0	2.796574314	4	0	0	0			
p401	674819.7949	269365.6252	0.053078443	0.068185862	0	2.796574314	5	0	0	0			
p402	674829.7949	269365.6252	0.146128036	0.021189299	0	2.796574314	6	0.430357603	0.161257168	0.004321374			

p403	674966.3914	269491.3501	0.025305865	0	0.004321374	2.603144332	1	0	0	0			
p404	674976.3914	269491.3501	0.008600172	0.017033339	0	2.603144332	2	0	0	0			
p405	674986.3914	269491.3501	0.037426498	0.255272505	0	2.603144332	3	0	0	0			
p406	674996.3914	269491.3501	0.049218023	0.06069784	0	2.603144332	4	0	0	0			
p407	675006.3914	269491.3501	0.017033339	0	0	2.603144332	5	0	0	0			
p408	675016.3914	269491.3501	0.033423755	0	0.004321374	2.603144332	6	0.171007652	0.333003685	0.008642748			
p409	675298.1184	269714.8611	0.004321374	0.149219113	0.008600172	0	1	0	0	0			
p410	675308.1184	269714.8611	0.012837225	0.045322979	0	0	2	0	0	0			
p411	675318.1184	269714.8611	0.008600172	0.390935107	0.004321374	0	3	0	0	0			
p412	675328.1184	269714.8611	0.017033339	0.283301229	0	0	4	0	0	0			
p413	675338.1184	269714.8611	0.004321374	0.198657087	0	0	5	0	0	0			
p414	675348.1184	269714.8611	0.008600172	0.164352856	0.008600172	0	6	0.055713655	1.23178837	0.021521717			
p415	675505.4478	269854.5555	0.584331224	0.017033339	0	2.39967374	1	0	0	0			
p416	675515.4478	269854.5555	1.03702788	0.029383778	0	2.39967374	2	0	0	0			
p417	675525.4478	269854.5555	0.367355921	0	0	2.39967374	3	0	0	0			
p418	675535.4478	269854.5555	0.330413773	0.037426498	0	2.39967374	4	0	0	0			
p419	675545.4478	269854.5555	0.170261715	0	0	2.39967374	5	0	0	0			
p420	675555.4478	269854.5555	0.056904851	0	0	2.39967374	6	2.546295365	0.083843615	0			
p421	675712.7772	269994.2499	0.075546961	0.033423755	0.008600172	2.699837745	1	0	0	0			
p422	675722.7772	269994.2499	0.421603927	0.004321374	0	2.699837745	2	0	0	0			
p423	675732.7772	269994.2499	0.079181246	0.041392685	0	2.699837745	3	0	0	0			
p424	675742.7772	269994.2499	0.11058971	0.012837225	0	2.699837745	4	0	0	0			
p425	675752.7772	269994.2499	0.041392685	0	0	2.699837745	5	0	0	0			
p426	675762.7772	269994.2499	0.029383778	0	0	2.699837745	6	0.757698307	0.091975039	0.008600172			
p427	676044.5042	270217.7609	0	0.021189299	0	2.954724783	1	0	0	0			
p428	676054.5042	270217.7609	0.008600172	0	0	2.954724783	2	0	0	0			
p429	676064.5042	270217.7609	0	0	0	2.954724783	3	0	0	0			
p430	676074.5042	270217.7609	0.021189299	0	0	2.954724783	4	0	0	0			
p431	676084.5042	270217.7609	0.290034611	0.037426498	0	2.954724783	5	0	0	0			
p432	676094.5042	270217.7609	0.117271296	0.049218023	0	2.954724783	6	0.437095378	0.10783382	0			
p433	676314.0324	270399.3636	0	0.021189299	0.008600172	3.08849046	1	0	0	0			

p434	676324.0324	270399.3636	0	0	0.008600172	3.08849046	2	0	0	0			
p435	676334.0324	270399.3636	0.017033339	0	0.004321374	3.08849046	3	0	0	0			
p436	676344.0324	270399.3636	0.28780173	0.06069784	0.123851641	3.08849046	4	0	0	0			
p437	676354.0324	270399.3636	0.068185862	0.025305865	0	3.08849046	5	0	0	0			
p438	676364.0324	270399.3636	0.053078443	0.004321374	0	3.08849046	6	0.426099374	0.111514378	0.145373358			
p439	676521.3618	270539.058	0.012837225	0.008600172	0	3.169086352	1	0	0	0			
p440	676531.3618	270539.058	0.572871602	0	0	3.169086352	2	0	0	0			
p441	676541.3618	270539.058	0.401400541	0	0	3.169086352	3	0	0	0			
p442	676551.3618	270539.058	0.033423755	0	0	3.169086352	4	0	0	0			
p443	676561.3618	270539.058	0.012837225	0	0	3.169086352	5	0	0	0			
p444	676571.3618	270539.058	0.281033367	0.06069784	0	3.169086352	6	1.314403715	0.069298012	0			
p445	676749.4242	270692.7218	0	0.004321374	0	3.243286151	1	0	0	0			
p446	676759.4242	270692.7218	0.033423755	0	0	3.243286151	2	0	0	0			
p447	676769.4242	270692.7218	0.190331698	0	0.004321374	3.243286151	3	0	0	0			
p448	676779.4242	270692.7218	0.173186268	0.127104798	0	3.243286151	4	0	0	0			
p449	676789.4242	270692.7218	0.053078443	0.025305865	0	3.243286151	5	0	0	0			
p450	676799.4242	270692.7218	0.004321374	0.025305865	0.004321374	3.243286151	6	0.454341539	0.182037903	0.008642748			
p451	676956.7536	270832.4162	0	0	0	3.301247096	1	0	0	0			
p452	676966.7536	270832.4162	0.008600172	0	0	3.301247096	2	0	0	0			
p453	676976.7536	270832.4162	0	0	0	3.301247096	3	0	0	0			
p454	676986.7536	270832.4162	0.053078443	0	0	3.301247096	4	0	0	0			
p455	676996.7536	270832.4162	0.064457989	0.064457989	0	3.301247096	5	0	0	0			
p456	677006.7536	270832.4162	0	0	0	3.301247096	6	0.126136604	0.064457989	0			
p457	683335.8784	271644.6249	0.004321374	0	0.033423755	2.699837759	1	0	0	0			
p458	683345.8784	271644.6249	0.357934847	0	0	2.699837759	2	0	0	0			
p459	683355.8784	271644.6249	0.033423755	0.053078443	0	2.699837759	3	0	0	0			
p460	683365.8784	271644.6249	0.008600172	0	0	2.699837759	4	0	0	0			
p461	683375.8784	271644.6249	0.089905111	0	0	2.699837759	5	0	0	0			
p462	683385.8784	271644.6249	0.004321374	0	0	2.699837759	6	0.498506633	0.053078443	0.033423755			
p463	683564.9736	271744.7017	0	0.004321374	0	2.399673868	1	0	0	0			
p464	683574.9736	271744.7017	0	0.064457989	0	2.399673868	2	0	0	0			

p465	683584.9736	271744.7017	0.017033339	0	0	2.399673868	3	0	0	0			
p466	683594.9736	271744.7017	0.008600172	0	0	2.399673868	4	0	0	0			
p467	683604.9736	271744.7017	0.012837225	0	0	2.399673868	5	0	0	0			
p468	683614.9736	271744.7017	0.033423755	0.012837225	0	2.399673868	6	0.071894491	0.081616588	0			
p469	683794.0689	271844.7786	0.012837225	0.195899652	0	0	1	0	0	0			
p470	683804.0689	271844.7786	0.037426498	0	0	0	2	0	0	0			
p471	683814.0689	271844.7786	0.181843588	0	0	0	3	0	0	0			
p472	683824.0689	271844.7786	0.025305865	0	0	0	4	0	0	0			
p473	683834.0689	271844.7786	0.075546961	0.012837225	0	0	5	0	0	0			
p474	683844.0689	271844.7786	0.045322979	0.340444115	0	0	6	0.378283116	0.549180992	0			
p475	684023.1641	271944.8554	0.041392685	0.008600172	0	2.39967364	1	0	0	0			
p476	684033.1641	271944.8554	0.51851394	0	0	2.39967364	2	0	0	0			
p477	684043.1641	271944.8554	0.214843848	0	0	2.39967364	3	0	0	0			
p478	684053.1641	271944.8554	0.025305865	0.004321374	0	2.39967364	4	0	0	0			
p479	684063.1641	271944.8554	0.06069784	0.195899652	0	2.39967364	5	0	0	0			
p480	684073.1641	271944.8554	0.136720567	0	0	2.39967364	6	0.997474746	0.208821198	0			
p481	684252.2593	272044.9323	0.025305865	0	0.017033339	2.699837679	1	0	0	0			
p482	684262.2593	272044.9323	0.029383778	0	0	2.699837679	2	0	0	0			
p483	684272.2593	272044.9323	0.025305865	0.071882007	0	2.699837679	3	0	0	0			
p484	684282.2593	272044.9323	0.201397124	0.049218023	0	2.699837679	4	0	0	0			
p485	684292.2593	272044.9323	0.561101384	0	0	2.699837679	5	0	0	0			
p486	684302.2593	272044.9323	0.346352974	0	0	2.699837679	6	1.188846991	0.12110003	0.017033339			
p487	684481.3545	272145.0092	0	0	0	2.875639902	1	0	0	0			
p488	684491.3545	272145.0092	0.012837225	0	0	2.875639902	2	0	0	0			
p489	684501.3545	272145.0092	0.068185862	0	0	2.875639902	3	0	0	0			
p490	684511.3545	272145.0092	0.350248018	0	0	2.875639902	4	0	0	0			
p491	684521.3545	272145.0092	0.06069784	0	0	2.875639902	5	0	0	0			
p492	684531.3545	272145.0092	0.056904851	0	0	2.875639902	6	0.548873796	0	0			
p493	684710.4498	272245.086	0.004321374	0	0	3.000434071	1	0	0	0			
p494	684720.4498	272245.086	0.257678575	0	0	3.000434071	2	0	0	0			
p495	684730.4498	272245.086	0.136720567	0	0	3.000434071	3	0	0	0			

p496	684740.4498	272245.086	0.795880017	0.161368002	0	3.000434071	4	0	0	0			
p497	684750.4498	272245.086	0.245512668	0	0	3.000434071	5	0	0	0			
p498	684760.4498	272245.086	0.127104798	0	0	3.000434071	6	1.567217999	0.161368002	0			
p499	684985.364	272365.1783	0.025305865	0	0	3.114277279	1	0	0	0			
p500	684995.364	272365.1783	0.041392685	0	0	3.114277279	2	0	0	0			
p501	685005.364	272365.1783	0.041392685	0.017033339	0	3.114277279	3	0	0	0			
p502	685015.364	272365.1783	0.075546961	0	0	3.114277279	4	0	0	0			
p503	685025.364	272365.1783	0.004321374	0	0	3.114277279	5	0	0	0			
p504	685035.364	272365.1783	0.033423755	0	0	3.114277279	6	0.221383326	0.017033339	0			
p505	685214.4593	272465.2551	0.11058971	0.004321374	0	3.190611796	1	0	0	0			
p506	685224.4593	272465.2551	0.281033367	0	0.103803721	3.190611796	2	0	0	0			
p507	685234.4593	272465.2551	0.06069784	0.049218023	0	3.190611796	3	0	0	0			
p508	685244.4593	272465.2551	0.139879086	0.079181246	0	3.190611796	4	0	0	0			
p509	685254.4593	272465.2551	0.021189299	0.033423755	0	3.190611796	5	0	0	0			
p510	685264.4593	272465.2551	0.017033339	0	0	3.190611796	6	0.630422643	0.166144398	0.103803721			
p511	685489.3735	272585.3473	0.045322979	0	0.385606274	3.267406399	1	0	0	0			
p512	685499.3735	272585.3473	0.049218023	0	0	3.267406399	2	0	0	0			
p513	685509.3735	272585.3473	0.037426498	0	0	3.267406399	3	0	0	0			
p514	685519.3735	272585.3473	0.017033339	0.017033339	0	3.267406399	4	0	0	0			
p515	685529.3735	272585.3473	0	0	0	3.267406399	5	0	0	0			
p516	685539.3735	272585.3473	0.004321374	0	0	3.267406399	6	0.153322212	0.017033339	0.385606274			
p517	685718.4688	272685.4242	0.240549248	0.079181246	0	3.322426052	1	0	0	0			
p518	685728.4688	272685.4242	0.155336037	0	0	3.322426052	2	0	0	0			
p519	685738.4688	272685.4242	0.049218023	0	0	3.322426052	3	0	0	0			
p520	685748.4688	272685.4242	0	0	0	3.322426052	4	0	0	0			
p521	685758.4688	272685.4242	0.033423755	0	0	3.322426052	5	0	0	0			
p522	685768.4688	272685.4242	0.008600172	0	0	3.322426052	6	0.487127236	0.079181246	0			
p523	685947.564	272785.5011	0	0	0.008600172	3.371252628	1	0	0	0			
p524	685957.564	272785.5011	0	0	0.064457989	3.371252628	2	0	0	0			
p525	685967.564	272785.5011	0	0	0	3.371252628	3	0	0	0			
p526	685977.564	272785.5011	0.021189299	0.017033339	0	3.371252628	4	0	0	0			

p527	685987.564	272785.5011	0.079181246	0.025305865	0	3.371252628	5	0	0	0			
p528	685997.564	272785.5011	0.149219113	0.049218023	0	3.371252628	6	0.249589658	0.091557227	0.073058161			

Appendix 2

Chapter 4 – Dataset used to test the spatial autocorrelations of pedoanthracological variables at Site 2 (SFID-Mbang)

torocor	#grids	#variables	Missing data										
318	0	8	NA										
13	15	35	55	310	600	1000	1500	3000	6000	12000	25000	50000	100000
plot	X	Y	log.Charcoal0	log.Palm0	log.seeds	log(min)	depth	tot-charcoal	tot-Palm	tot-seeds			
p1	408600.3	446023.9	0	0	0	2.386423308	1	0	0	0			
p2	408610.3	446023.9	0	0	0	2.386423308	2	0	0	0			
p3	408620.3	446023.9	0	0.002166062	0	2.386423308	3	0	0	0			
p4	408630.3	446023.9	0	0	0.002166062	2.386423308	4	0	0	0			
p5	408640.3	446023.9	0	0	0	2.386423308	5	0	0	0			
p6	408650.3	446023.9	0	0	0	2.386423308	6	0	0.002166062	0.002166062			
p7	408636.1	445784.1	0.010723865	0.1430148	0.006466042	0	1	0	0	0			
p8	408646.1	445784.1	0	0.733197265	0.01911629	0	2	0	0	0			
p9	408656.1	445784.1	0	0.991226076	0	0	3	0	0	0			
p10	408666.1	445784.1	0	0.120573931	0	0	4	0	0	0			
p11	408676.1	445784.1	0	0	0	0	5	0	0	0			
p12	408686.1	445784.1	0	0.290034611	0	0	6	0.010723865	2.278046684	0.025582333			
p13	408710.4	445535	0	0	0.02325246	0	1	0	0	0			
p14	408720.4	445535	0	0	0	0	2	0	0	0			
p15	408730.4	445535	0.012837225	0	0	0	3	0	0	0			
p16	408740.4	445535	0	0	0	0	4	0	0	0			
p17	408750.4	445535	0	0	0	0	5	0	0	0			
p18	408760.4	445535	0	0	0	0	6	0.012837225	0	0.02325246			
p19	408767.4	445284.9	0	0	0	2.410799457	1	0	0	0			

p20	408777.4	445284.9	0.06069784	0.008600172	0.008600172	2.410799457	2	0	0	0			
p21	408787.4	445284.9	0	0	0.031408464	2.410799457	3	0	0	0			
p22	408797.4	445284.9	0.133538908	0	0	2.410799457	4	0	0	0			
p23	408807.4	445284.9	0.130333768	0	0.012837225	2.410799457	5	0	0	0			
p24	408817.4	445284.9	0.096910013	0	0.033423755	2.410799457	6	0.42148053	0.008600172	0.086269616			
p25	408807	445053.9	0	0.010723865	0	2.69170226	1	0	0	0			
p26	408817	445053.9	0.053078443	0	0.012837225	2.69170226	2	0	0	0			
p27	408827	445053.9	0	0.006466042	0	2.69170226	3	0	0	0			
p28	408837	445053.9	0.117271296	0.021189299	0	2.69170226	4	0	0	0			
p29	408847	445053.9	0.021189299	0	0	2.69170226	5	0	0	0			
p30	408857	445053.9	0.02325246	0	0.004321374	2.69170226	6	0.214791498	0.038379207	0.017158598			
p31	408841	444792.8	0	0	0	2.87771842	1	0	0	0			
p32	408851	444792.8	0	0	0	2.87771842	2	0	0	0			
p33	408861	444792.8	0	0	0	2.87771842	3	0	0	0			
p34	408871	444792.8	0	0	0	2.87771842	4	0	0	0			
p35	408881	444792.8	0	0	0	2.87771842	5	0	0	0			
p36	408891	444792.8	0	0	0	2.87771842	6	0	0	0			
p37	408890.9	444550.9	0	0	0	3.000658064	1	0	0	0			
p38	408900.9	444550.9	0.008600172	0	0.008600172	3.000658064	2	0	0	0			
p39	408910.9	444550.9	0	0	0	3.000658064	3	0	0	0			
p40	408920.9	444550.9	0	0	0	3.000658064	4	0	0	0			
p41	408930.9	444550.9	0	0	0	3.000658064	5	0	0	0			
p42	408940.9	444550.9	0	0	0	3.000658064	6	0.008600172	0	0.008600172			
p43	408940.2	444313.9	0	0	0.033423755	3.094658017	1	0	0	0			
p44	408950.2	444313.9	0.071882007	0	0	3.094658017	2	0	0	0			
p45	408960.2	444313.9	0.152288344	0	0.033423755	3.094658017	3	0	0	0			
p46	408970.2	444313.9	0.002166062	0	0	3.094658017	4	0	0	0			
p47	408980.2	444313.9	0	0	0.006466042	3.094658017	5	0	0	0			
p48	408990.2	444313.9	0.010723865	0	0	3.094658017	6	0.237060279	0	0.073313553			
p49	408992.5	444058.8	0	0	0.049218023	3.177222652	1	0	0	0			
p50	409002.5	444058.8	0	0	0	3.177222652	2	0	0	0			

p51	409012.5	444058.8	0	0	0	3.177222652	3	0	0	0			
p52	409022.5	444058.8	0	0	0	3.177222652	4	0	0	0			
p53	409032.5	444058.8	0	0	0	3.177222652	5	0	0	0			
p54	409042.5	444058.8	0	0	0	3.177222652	6	0	0	0.049218023			
p55	409021.9	443824.9	0.079181246	0	0	3.240359225	1	0	0	0			
p56	409031.9	443824.9	0.372912003	0	0	3.240359225	2	0	0	0			
p57	409041.9	443824.9	0.004321374	0	0	3.240359225	3	0	0	0			
p58	409051.9	443824.9	0	0	0	3.240359225	4	0	0	0			
p59	409061.9	443824.9	0	0	0	3.240359225	5	0	0	0			
p60	409071.9	443824.9	0	0	0	3.240359225	6	0.456414623	0	0			
p61	409069.6	443567.3	0	0.012837225	0	3.301294177	1	0	0	0			
p62	409079.6	443567.3	0	0	0.025305865	3.301294177	2	0	0	0			
p63	409089.6	443567.3	0.1430148	0	0	3.301294177	3	0	0	0			
p64	409099.6	443567.3	0	0	0	3.301294177	4	0	0	0			
p65	409109.6	443567.3	0	0	0	3.301294177	5	0	0	0			
p66	409119.6	443567.3	0	0	0	3.301294177	6	0.1430148	0.012837225	0.025305865			
p67	409110.6	443322.8	0	0.010723865	0	3.35201028	1	0	0	0			
p68	409120.6	443322.8	0.012837225	0	0.008600172	3.35201028	2	0	0	0			
p69	409130.6	443322.8	0	0	0	3.35201028	3	0	0	0			
p70	409140.6	443322.8	0	0	0	3.35201028	4	0	0	0			
p71	409150.6	443322.8	0	0	0	3.35201028	5	0	0	0			
p72	409160.6	443322.8	0	0	0	3.35201028	6	0.012837225	0.010723865	0.008600172			
p73	409165.7	443076.7	0	0	0.064457989	3.39813234	1	0	0	0			
p74	409175.7	443076.7	0.045322979	0	0	3.39813234	2	0	0	0			
p75	409185.7	443076.7	0.021189299	0	0	3.39813234	3	0	0	0			
p76	409195.7	443076.7	0	0	0	3.39813234	4	0	0	0			
p77	409205.7	443076.7	0	0	0	3.39813234	5	0	0	0			
p78	409215.7	443076.7	0	0	0	3.39813234	6	0.066512278	0	0.064457989			
p79	409202.5	442832.6	0	0	0.017033339	3.438991389	1	0	0	0			
p80	409212.5	442832.6	0	0	0	3.438991389	2	0	0	0			
p81	409222.5	442832.6	0	0	0	3.438991389	3	0	0	0			

p82	409232.5	442832.6	0.037426498	0	0	3.438991389	4	0	0	0			
p83	409242.5	442832.6	0	0	0	3.438991389	5	0	0	0			
p84	409252.5	442832.6	0	0	0	3.438991389	6	0.037426498	0	0.017033339			
p85	409253.7	442584.5	0.037426498	0	0	3.477281073	1	0	0	0			
p86	409263.7	442584.5	0.017033339	0	0	3.477281073	2	0	0	0			
p87	409273.7	442584.5	0.004321374	0	0	3.477281073	3	0	0	0			
p88	409283.7	442584.5	0	0	0	3.477281073	4	0	0	0			
p89	409293.7	442584.5	0	0	0	3.477281073	5	0	0	0			
p90	409303.7	442584.5	0.01911629	0	0	3.477281073	6	0.077897501	0	0			
p91	409335.3	442080.4	0	0	0	3.545512946	1	0	0	0			
p92	409345.3	442080.4	0	0	0	3.545512946	2	0	0	0			
p93	409355.3	442080.4	0	0	0	3.545512946	3	0	0	0			
p94	409365.3	442080.4	0	0	0	3.545512946	4	0	0	0			
p95	409375.3	442080.4	0	0	0	3.545512946	5	0	0	0			
p96	409385.3	442080.4	0	0	0	3.545512946	6	0	0	0			
p97	409389.4	441827.2	0	0	0	3.576394233	1	0	0	0			
p98	409399.4	441827.2	0	0	0	3.576394233	2	0	0	0			
p99	409409.4	441827.2	0	0	0	3.576394233	3	0	0	0			
p100	409419.4	441827.2	0	0	0	3.576394233	4	0	0	0			
p101	409429.4	441827.2	0.161368002	0	0	3.576394233	5	0	0	0			
p102	409439.4	441827.2	0.025305865	0	0	3.576394233	6	0.186673867	0	0			
p103	409411.8	441588.5	0	0	0	3.603073355	1	0	0	0			
p104	409421.8	441588.5	0	0	0	3.603073355	2	0	0	0			
p105	409431.8	441588.5	0	0	0	3.603073355	3	0	0	0			
p106	409441.8	441588.5	0	0	0	3.603073355	4	0	0	0			
p107	409451.8	441588.5	0	0	0	3.603073355	5	0	0	0			
p108	409461.8	441588.5	0.002166062	0	0	3.603073355	6	0.002166062	0	0			
p109	409448.8	441347	0	0.004321374	0	3.628756309	1	0	0	0			
p110	409458.8	441347	0	0	0	3.628756309	2	0	0	0			
p111	409468.8	441347	0	0	0	3.628756309	3	0	0	0			
p112	409478.8	441347	0	0	0	3.628756309	4	0	0	0			

p113	409488.8	441347	0	0	0	3.628756309	5	0	0	0			
p114	409498.8	441347	0	0	0	3.628756309	6	0	0.004321374	0			
p115	413033.4	428163.8	0.045322979	0.008600172	0	3.246362413	1	0	0	0			
p116	413043.4	428163.8	0.079181246	0	0.031408464	3.246362413	2	0	0	0			
p117	413053.4	428163.8	0.004321374	0	0	3.246362413	3	0	0	0			
p118	413063.4	428163.8	0	0	0	3.246362413	4	0	0	0			
p119	413073.4	428163.8	0	0.008600172	0	3.246362413	5	0	0	0			
p120	413083.4	428163.8	0	0	0	3.246362413	6	0.128825599	0.017200344	0.031408464			
p121	413067	427918.3	0	0	0	3.180710197	1	0	0	0			
p122	413077	427918.3	0.049218023	0	0	3.180710197	2	0	0	0			
p123	413087	427918.3	0	0	0	3.180710197	3	0	0	0			
p124	413097	427918.3	0.004321374	0	0	3.180710197	4	0	0	0			
p125	413107	427918.3	0	0.002166062	0	3.180710197	5	0	0	0			
p126	413117	427918.3	0.006466042	0	0	3.180710197	6	0.060005439	0.002166062	0			
p127	413140.7	427646.4	0	0	0	3.091719192	1	0	0	0			
p128	413150.7	427646.4	0	0	0	3.091719192	2	0	0	0			
p129	413160.7	427646.4	0	0	0	3.091719192	3	0	0	0			
p130	413170.7	427646.4	0	0	0	3.091719192	4	0	0	0			
p131	413180.7	427646.4	0	0	0	3.091719192	5	0	0	0			
p132	413190.7	427646.4	0	0	0	3.091719192	6	0	0	0			
p133	413154.3	427414.4	0	0	0	3.002104849	1	0	0	0			
p134	413164.3	427414.4	0	0	0	3.002104849	2	0	0	0			
p135	413174.3	427414.4	0.071882007	0	0	3.002104849	3	0	0	0			
p136	413184.3	427414.4	0	0	0	3.002104849	4	0	0	0			
p137	413194.3	427414.4	0	0	0	3.002104849	5	0	0	0			
p138	413204.3	427414.4	0	0	0	3.002104849	6	0.071882007	0	0			
p139	413213	427149.7	0	0	0	2.865546247	1	0	0	0			
p140	413223	427149.7	0	0	0	2.865546247	2	0	0	0			
p141	413233	427149.7	0	0	0	2.865546247	3	0	0	0			
p142	413243	427149.7	0	0	0	2.865546247	4	0	0	0			
p143	413253	427149.7	0	0	0	2.865546247	5	0	0	0			

p144	413263	427149.7	0.06069784	0	0.021189299	2.865546247	6	0.06069784	0	0.021189299			
p145	413260.9	426915.6	0	0	0	2.6944277	1	0	0	0			
p146	413270.9	426915.6	0	0	0	2.6944277	2	0	0	0			
p147	413280.9	426915.6	0	0	0	2.6944277	3	0	0	0			
p148	413290.9	426915.6	0	0	0	2.6944277	4	0	0	0			
p149	413300.9	426915.6	0.004321374	0	0	2.6944277	5	0	0	0			
p150	413310.9	426915.6	0.008600172	0	0	2.6944277	6	0.012921546	0	0			
p151	413319.3	426675	0.033423755	0.012837225	0.079181246	2.393530174	1	0	0	0			
p152	413329.3	426675	0	0	0	2.393530174	2	0	0	0			
p153	413339.3	426675	0	0	0	2.393530174	3	0	0	0			
p154	413349.3	426675	0.025305865	0.660865478	0	2.393530174	4	0	0	0			
p155	413359.3	426675	0	0.093421685	0	2.393530174	5	0	0	0			
p156	413369.3	426675	0	0.012837225	0	2.393530174	6	0.058729621	0.779961613	0.079181246			
p157	413361.7	426432.2	0	0	0	0	1	0	0	0			
p158	413371.7	426432.2	0	0	0	0	2	0	0	0			
p159	413381.7	426432.2	0.113943352	0	0	0	3	0	0	0			
p160	413391.7	426432.2	0	0	0	0	4	0	0	0			
p161	413401.7	426432.2	0	0	0	0	5	0	0	0			
p162	413411.7	426432.2	0	0	0	0	6	0.113943352	0	0			
p163	413402	426176.3	0	0.012837225	0	0	1	0	0	0			
p164	413412	426176.3	0.079181246	0	0	0	2	0	0	0			
p165	413422	426176.3	0.11058971	0	0	0	3	0	0	0			
p166	413432	426176.3	0.025305865	0.037426498	0	0	4	0	0	0			
p167	413442	426176.3	0.002166062	0.004321374	0	0	5	0	0	0			
p168	413452	426176.3	0	0	0.004321374	0	6	0.217242883	0.054585096	0.004321374			
p169	413446.2	425937.5	0	0	0	2.387133604	1	0	0	0			
p170	413456.2	425937.5	0	0	0	2.387133604	2	0	0	0			
p171	413466.2	425937.5	0	0	0	2.387133604	3	0	0	0			
p172	413476.2	425937.5	0	0	0	2.387133604	4	0	0	0			
p173	413486.2	425937.5	0	0	0	2.387133604	5	0	0	0			
p174	413496.2	425937.5	0	0	0	2.387133604	6	0	0	0			

p175	413490.8	425681	0	0	0	2.702600522	1	0	0	0			
p176	413500.8	425681	0	0	0	2.702600522	2	0	0	0			
p177	413510.8	425681	0	0	0	2.702600522	3	0	0	0			
p178	413520.8	425681	0	0	0	2.702600522	4	0	0	0			
p179	413530.8	425681	0	0	0	2.702600522	5	0	0	0			
p180	413540.8	425681	0	0	0	2.702600522	6	0	0	0			
p181	413587.2	425204.3	0	0.010723865	0	2.995848451	1	0	0	0			
p182	413597.2	425204.3	0.037426498	0	0	2.995848451	2	0	0	0			
p183	413607.2	425204.3	0.278753601	0.017033339	0	2.995848451	3	0	0	0			
p184	413617.2	425204.3	0.387389826	0	0	2.995848451	4	0	0	0			
p185	413627.2	425204.3	0	0	0	2.995848451	5	0	0	0			
p186	413637.2	425204.3	0	0	0	2.995848451	6	0.703569925	0.027757205	0			
p187	413626.1	424961.3	0	0	0	3.092192068	1	0	0	0			
p188	413636.1	424961.3	0	0	0	3.092192068	2	0	0	0			
p189	413646.1	424961.3	0.004321374	0	0	3.092192068	3	0	0	0			
p190	413656.1	424961.3	0.195899652	0	0	3.092192068	4	0	0	0			
p191	413666.1	424961.3	0	0	0	3.092192068	5	0	0	0			
p192	413676.1	424961.3	0.021189299	0	0	3.092192068	6	0.221410325	0	0			
p193	413683.9	424724.3	0.004321374	0	0.002166062	3.17029451	1	0	0	0			
p194	413693.9	424724.3	0	0	0	3.17029451	2	0	0	0			
p195	413703.9	424724.3	0	0	0	3.17029451	3	0	0	0			
p196	413713.9	424724.3	0.02325246	0	0	3.17029451	4	0	0	0			
p197	413723.9	424724.3	0.113943352	0	0	3.17029451	5	0	0	0			
p198	413733.9	424724.3	0	0	0	3.17029451	6	0.141517186	0	0.002166062			
p199	413727.8	424455.3	0	0	0	3.243674608	1	0	0	0			
p200	413737.8	424455.3	0	0	0	3.243674608	2	0	0	0			
p201	413747.8	424455.3	0	0	0	3.243674608	3	0	0	0			
p202	413757.8	424455.3	0	0	0	3.243674608	4	0	0	0			
p203	413767.8	424455.3	0	0	0	3.243674608	5	0	0	0			
p204	413777.8	424455.3	0	0	0	3.243674608	6	0	0	0			
p205	413782.8	424220.5	0	0	0	3.299622036	1	0	0	0			

p206	413792.8	424220.5	0	0	0	3.299622036	2	0	0	0			
p207	413802.8	424220.5	0	0	0	3.299622036	3	0	0	0			
p208	413812.8	424220.5	0	0	0	3.299622036	4	0	0	0			
p209	413822.8	424220.5	0	0	0	3.299622036	5	0	0	0			
p210	413832.8	424220.5	0	0	0	3.299622036	6	0	0	0			
p211	413832.76	423957.6133	0	0	0	3.354322859	1	0	0	0			
p212	413842.76	423957.6133	0	0	0	3.354322859	2	0	0	0			
p213	413852.76	423957.6133	0	0	0	3.354322859	3	0	0	0			
p214	413862.76	423957.6133	0	0	0	3.354322859	4	0	0	0			
p215	413872.76	423957.6133	0	0	0	3.354322859	5	0	0	0			
p216	413882.76	423957.6133	0	0	0	3.354322859	6	0	0	0			
p217	413882.72	423694.7267	0	0	0	3.402898349	1	0	0	0			
p218	413892.72	423694.7267	0	0	0	3.402898349	2	0	0	0			
p219	413902.72	423694.7267	0	0	0	3.402898349	3	0	0	0			
p220	413912.72	423694.7267	0	0	0	3.402898349	4	0	0	0			
p221	413922.72	423694.7267	0	0	0	3.402898349	5	0	0	0			
p222	413932.72	423694.7267	0	0	0	3.402898349	6	0	0	0			
p223	422992.4	385260.9	0	0	0	4.623511307	1	0	0	0			
p224	423002.4	385260.9	0.004321374	0	0	4.623511307	2	0	0	0			
p225	423012.4	385260.9	0	0	0	4.623511307	3	0	0	0			
p226	423022.4	385260.9	0	0.004321374	0	4.623511307	4	0	0	0			
p227	423032.4	385260.9	0.008600172	0	0	4.623511307	5	0	0	0			
p228	423042.4	385260.9	0	0	0	4.623511307	6	0.012921546	0.004321374	0			
p229	423017.7	385018.5	0	0.012837225	0	4.626002813	1	0	0	0			
p230	423027.7	385018.5	0	0	0	4.626002813	2	0	0	0			
p231	423037.7	385018.5	0.008600172	0	0	4.626002813	3	0	0	0			
p232	423047.7	385018.5	0.021189299	0	0	4.626002813	4	0	0	0			
p233	423057.7	385018.5	0.11058971	0	0	4.626002813	5	0	0	0			
p234	423067.7	385018.5	0	0	0	4.626002813	6	0.140379181	0.012837225	0			
p235	423029.6	384767.6	0.447158031	0	0	4.628533884	1	0	0	0			
p236	423039.6	384767.6	0.004321374	0	0	4.628533884	2	0	0	0			

p237	423049.6	384767.6	0.113943352	0.06069784	0	4.628533884	3	0	0	0			
p238	423059.6	384767.6	0.334453751	0.170261715	0	4.628533884	4	0	0	0			
p239	423069.6	384767.6	0.025305865	0.413299764	0	4.628533884	5	0	0	0			
p240	423079.6	384767.6	0.103803721	0.041392685	0	4.628533884	6	1.028986095	0.685652005	0			
p241	423122.9	384507.9	0	0	0	4.631324844	1	0	0	0			
p242	423132.9	384507.9	0	0	0	4.631324844	2	0	0	0			
p243	423142.9	384507.9	0	0	0	4.631324844	3	0	0	0			
p244	423152.9	384507.9	0	0	0	4.631324844	4	0	0	0			
p245	423162.9	384507.9	0	0	0	4.631324844	5	0	0	0			
p246	423172.9	384507.9	0	0	0	4.631324844	6	0	0	0			
p247	423167.1	384240	0.006466042	0	0	4.634066173	1	0	0	0			
p248	423177.1	384240	0	0	0	4.634066173	2	0	0	0			
p249	423187.1	384240	0	0	0	4.634066173	3	0	0	0			
p250	423197.1	384240	0	0	0	4.634066173	4	0	0	0			
p251	423207.1	384240	0.004321374	0.006466042	0	4.634066173	5	0	0	0			
p252	423217.1	384240	0	0.008600172	0	4.634066173	6	0.010787416	0.015066214	0			
p253	423223.2	384010.2	0	0	0	4.636445335	1	0	0	0			
p254	423233.2	384010.2	0	0	0	4.636445335	2	0	0	0			
p255	423243.2	384010.2	0.075546961	0	0	4.636445335	3	0	0	0			
p256	423253.2	384010.2	0	0	0	4.636445335	4	0	0	0			
p257	423263.2	384010.2	0	0	0	4.636445335	5	0	0	0			
p258	423273.2	384010.2	0	0	0	4.636445335	6	0.075546961	0	0			
p259	423279.1	383771.5	0	0	0	4.638897548	1	0	0	0			
p260	423289.1	383771.5	0	0.004321374	0	4.638897548	2	0	0	0			
p261	423299.1	383771.5	0.037426498	0	0	4.638897548	3	0	0	0			
p262	423309.1	383771.5	0	0.021189299	0	4.638897548	4	0	0	0			
p263	423319.1	383771.5	0	0.012837225	0	4.638897548	5	0	0	0			
p264	423329.1	383771.5	0	0	0	4.638897548	6	0.037426498	0.038347898	0			
p265	423348.1	383516.1	0	0.004321374	0.006466042	4.641526757	1	0	0	0			
p266	423358.1	383516.1	0	0.002166062	0	4.641526757	2	0	0	0			
p267	423368.1	383516.1	0	0	0	4.641526757	3	0	0	0			

p268	423378.1	383516.1	0.133538908	0.049218023	0	4.641526757	4	0	0	0			
p269	423388.1	383516.1	0	0.033423755	0	4.641526757	5	0	0	0			
p270	423398.1	383516.1	0.025305865	0.056904851	0.01911629	4.641526757	6	0.158844774	0.146034065	0.025582333			
p271	423386.7	383278.8	0	0	0	4.643898383	1	0	0	0			
p272	423396.7	383278.8	0	0	0	4.643898383	2	0	0	0			
p273	423406.7	383278.8	0	0	0	4.643898383	3	0	0	0			
p274	423416.7	383278.8	0	0	0	4.643898383	4	0	0	0			
p275	423426.7	383278.8	0	0	0	4.643898383	5	0	0	0			
p276	423436.7	383278.8	0	0	0	4.643898383	6	0	0	0			
p277	423460.9	383039.6	0	0	0	4.646354476	1	0	0	0			
p278	423470.9	383039.6	0	0	0	4.646354476	2	0	0	0			
p279	423480.9	383039.6	0	0	0	4.646354476	3	0	0	0			
p280	423490.9	383039.6	0	0	0	4.646354476	4	0	0	0			
p281	423500.9	383039.6	0	0	0	4.646354476	5	0	0	0			
p282	423510.9	383039.6	0	0	0	4.646354476	6	0	0	0			
p283	423563.4	382544.8	0	0.071882007	0	4.651279252	1	0	0	0			
p284	423573.4	382544.8	0.037426498	0	0	4.651279252	2	0	0	0			
p285	423583.4	382544.8	0.045322979	0	0.008600172	4.651279252	3	0	0	0			
p286	423593.4	382544.8	0.002166062	0	0	4.651279252	4	0	0	0			
p287	423603.4	382544.8	0	0	0	4.651279252	5	0	0	0			
p288	423613.4	382544.8	0	0	0	4.651279252	6	0.084915538	0.071882007	0.008600172			
p289	423606.8	382318.9	0	0	0	4.653501801	1	0	0	0			
p290	423616.8	382318.9	0	0	0	4.653501801	2	0	0	0			
p291	423626.8	382318.9	0.888740961	0	0	4.653501801	3	0	0	0			
p292	423636.8	382318.9	0.481442629	0	0.012837225	4.653501801	4	0	0	0			
p293	423646.8	382318.9	0.173186268	0	0	4.653501801	5	0	0	0			
p294	423656.8	382318.9	0	0	0	4.653501801	6	1.543369858	0	0.012837225			
p295	423666.5	382085.8	0.002166062	0	0	4.65581577	1	0	0	0			
p296	423676.5	382085.8	0	0	0	4.65581577	2	0	0	0			
p297	423686.5	382085.8	0	0.017033339	0	4.65581577	3	0	0	0			
p298	423696.5	382085.8	0	0.517195898	0	4.65581577	4	0	0	0			

p299	423706.5	382085.8	0	0.100370545	0	4.65581577	5	0	0	0			
p300	423716.5	382085.8	0	0	0	4.65581577	6	0.002166062	0.634599782	0			
p301	423741.9	381828.1	0	0	0	4.658380027	1	0	0	0			
p302	423751.9	381828.1	0	0.006466042	0	4.658380027	2	0	0	0			
p303	423761.9	381828.1	0	0.012837225	0	4.658380027	3	0	0	0			
p304	423771.9	381828.1	0	0	0	4.658380027	4	0	0	0			
p305	423781.9	381828.1	0	0.004321374	0	4.658380027	5	0	0	0			
p306	423791.9	381828.1	0	0	0	4.658380027	6	0	0.023624641	0			
p307	423799.4	381588.7	0.338456494	0	0	4.6607217	1	0	0	0			
p308	423809.4	381588.7	0.146128036	0	0	4.6607217	2	0	0	0			
p309	423819.4	381588.7	0.053078443	0	0	4.6607217	3	0	0	0			
p310	423829.4	381588.7	0.136720567	0.029383778	0	4.6607217	4	0	0	0			
p311	423839.4	381588.7	0.049218023	0	0	4.6607217	5	0	0	0			
p312	423849.4	381588.7	0.056904851	0	0	4.6607217	6	0.780506414	0.029383778	0			
p313	423861.7	381347.4	0	0	0	4.663078561	1	0	0	0			
p314	423871.7	381347.4	0	0	0	4.663078561	2	0	0	0			
p315	423881.7	381347.4	0	0	0	4.663078561	3	0	0	0			
p316	423891.7	381347.4	0	0	0	4.663078561	4	0	0	0			
p317	423901.7	381347.4	0	0	0	4.663078561	5	0	0	0			
p318	423911.7	381347.4	0	0	0	4.663078561	6	0	0	0			

Appendix 3

Chapter 4 – Dataset for testing the correlation between variables using torus translations at Site 1 (Wijma)

torocor	#grids	#variables	Missing data								
35	3	7	NA						Mean charcoal	Mean oil palm endocarps	Mean other seeds
0									-0.189752292	-0.620757152	0.216521119
plot	X	Y	Grid	x	y	log.Charcoal0	log.Palm0	log(min)	tot-charcoal	tot-Palm	tot-seeds
p324	659709.8056	254532.5521	D	1	1	0.004321374	0.041392685	0	0.245423508	0.495075191	0
p330	659515.0378	254375.8183	D	2	1	0.075546961	0	2.399673652	3.729677088	0.120573931	0
p336	659320.2699	254219.0845	D	3	1	0.008600172	0	2.699837724	0.189734292	0.09166828	0
p342	659125.5021	254062.3507	D	4	1	0	0.012837225	2.875639913	0.051269443	0.184339384	0.004321374
p348	658852.8271	253842.9233	D	5	1	0	0	2.699837724	0.212923948	0.216913776	0.004321374
p354	658658.0593	253686.1895	D	6	1	0.195899652	0.004321374	2.399673787	0.327844076	0.042548785	0.004321374
p360	658463.2914	253529.4557	D	7	1	0.029383778	0.071882007	0	2.407461489	0.29149587	0
p366	658268.5236	253372.7219	D	8	1	0.309630167	0.181843588	2.399673652	1.444114787	0.525220982	0
p372	658073.7557	253215.9881	D	9	1	0.075546961	0.017033339	0	1.463882462	0.046988224	0
p378	657878.9879	253059.2543	D	10	1	0.012837225	0	2.399673652	0.194079436	0.004321374	0
p384	657684.22	252902.5205	D	11	1	0.017033339	0	2.699837724	0.324562179	0.059057267	0
p390	657489.4522	252745.7867	D	12	1	0	0.008600172	2.875639913	0.131101951	0.167947939	0
p396	674601.7326	269211.9614	E	1	1	0.123851641	0.086359831	2.954724756	0.158043579	0.150464078	0
p402	674829.7949	269365.6252	E	2	1	0.146128036	0.021189299	2.796574314	0.430357603	0.161257168	0.004321374
p408	675016.3914	269491.3501	E	3	1	0.033423755	0	2.603144332	0.171007652	0.333003685	0.008642748
p414	675348.1184	269714.8611	E	4	1	0.008600172	0.164352856	0	0.055713655	1.23178837	0.021521717
p420	675555.4478	269854.5555	E	5	1	0.056904851	0	2.39967374	2.546295365	0.083843615	0
p426	675762.7772	269994.2499	E	6	1	0.029383778	0	2.699837745	0.757698307	0.091975039	0.008600172
p432	676094.5042	270217.7609	E	7	1	0.117271296	0.049218023	2.954724783	0.437095378	0.10783382	0
p438	676364.0324	270399.3636	E	8	1	0.053078443	0.004321374	3.08849046	0.426099374	0.111514378	0.145373358
p444	676571.3618	270539.058	E	9	1	0.281033367	0.06069784	3.169086352	1.314403715	0.069298012	0
p450	676799.4242	270692.7218	E	10	1	0.004321374	0.025305865	3.243286151	0.454341539	0.182037903	0.008642748
p456	677006.7536	270832.4162	E	11	1	0	0	3.301247096	0.126136604	0.064457989	0

p462	683385.8784	271644.6249	F	1	1	0.004321374	0	2.699837759	0.498506633	0.053078443	0.033423755
p468	683614.9736	271744.7017	F	2	1	0.033423755	0.012837225	2.399673868	0.071894491	0.081616588	0
p474	683844.0689	271844.7786	F	3	1	0.045322979	0.340444115	0	0.378283116	0.549180992	0
p480	684073.1641	271944.8554	F	4	1	0.136720567	0	2.39967364	0.997474746	0.208821198	0
p486	684302.2593	272044.9323	F	5	1	0.346352974	0	2.699837679	1.188846991	0.12110003	0.017033339
p492	684531.3545	272145.0092	F	6	1	0.056904851	0	2.875639902	0.548873796	0	0
p498	684760.4498	272245.086	F	7	1	0.127104798	0	3.000434071	1.567217999	0.161368002	0
p504	685035.364	272365.1783	F	8	1	0.033423755	0	3.114277279	0.221383326	0.017033339	0
p510	685264.4593	272465.2551	F	9	1	0.017033339	0	3.190611796	0.630422643	0.166144398	0.103803721
p516	685539.3735	272585.3473	F	10	1	0.004321374	0	3.267406399	0.153322212	0.017033339	0.385606274
p522	685768.4688	272685.4242	F	11	1	0.008600172	0	3.322426052	0.487127236	0.079181246	0
p528	685997.564	272785.5011	F	12	1	0.149219113	0.049218023	3.371252628	0.249589658	0.091557227	0.073058161

Appendix 4

Chapter 4 – Dataset for testing the correlation between variables using torus translations at Site 2 (SFID-Mbang)

torocor	#grids	#variables	Missing data						Mean charcoal	Mean oil palm endocarps	Mean other seeds
53	3	7	NA								
0									0.159128123	-0.288594855	-0.231690464
plot	X	Y	Grid	x	y	log.Charcoal0	log.Palm0	log(min)	tot-charcoal	tot-Palm	tot-seeds
p6	408650.3	446023.9	A	1	1	0	0	2.386423308	0	0.002166062	0.002166062
p12	408686.1	445784.1	A	2	1	0	0.290034611	0	0.010723865	2.278046684	0.025582333
p18	408760.4	445535	A	3	1	0	0	0	0.012837225	0	0.02325246
p24	408817.4	445284.9	A	4	1	0.096910013	0	2.410799457	0.42148053	0.008600172	0.086269616
p30	408857	445053.9	A	5	1	0.02325246	0	2.69170226	0.214791498	0.038379207	0.017158598
p36	408891	444792.8	A	6	1	0	0	2.87771842	0	0	0
p42	408940.9	444550.9	A	7	1	0	0	3.000658064	0.008600172	0	0.008600172
p48	408990.2	444313.9	A	8	1	0.010723865	0	3.094658017	0.237060279	0	0.073313553
p54	409042.5	444058.8	A	9	1	0	0	3.177222652	0	0	0.049218023
p60	409071.9	443824.9	A	10	1	0	0	3.240359225	0.456414623	0	0
p66	409119.6	443567.3	A	11	1	0	0	3.301294177	0.1430148	0.012837225	0.025305865
p72	409160.6	443322.8	A	12	1	0	0	3.35201028	0.012837225	0.010723865	0.008600172
p78	409215.7	443076.7	A	13	1	0	0	3.39813234	0.066512278	0	0.064457989
p84	409252.5	442832.6	A	14	1	0	0	3.438991389	0.037426498	0	0.017033339
p90	409303.7	442584.5	A	15	1	0.01911629	0	3.477281073	0.077897501	0	0
p96	409385.3	442080.4	A	16	1	0	0	3.545512946	0	0	0
p102	409439.4	441827.2	A	17	1	0.025305865	0	3.576394233	0.186673867	0	0
p108	409461.8	441588.5	A	18	1	0.002166062	0	3.603073355	0.002166062	0	0
p114	409498.8	441347	A	19	1	0	0	3.628756309	0	0.004321374	0
p120	413083.4	428163.8	B	1	1	0	0	3.246362413	0.128825599	0.017200344	0.031408464
p126	413117	427918.3	B	2	1	0.006466042	0	3.180710197	0.060005439	0.002166062	0
p132	413190.7	427646.4	B	3	1	0	0	3.091719192	0	0	0
p138	413204.3	427414.4	B	4	1	0	0	3.002104849	0.071882007	0	0

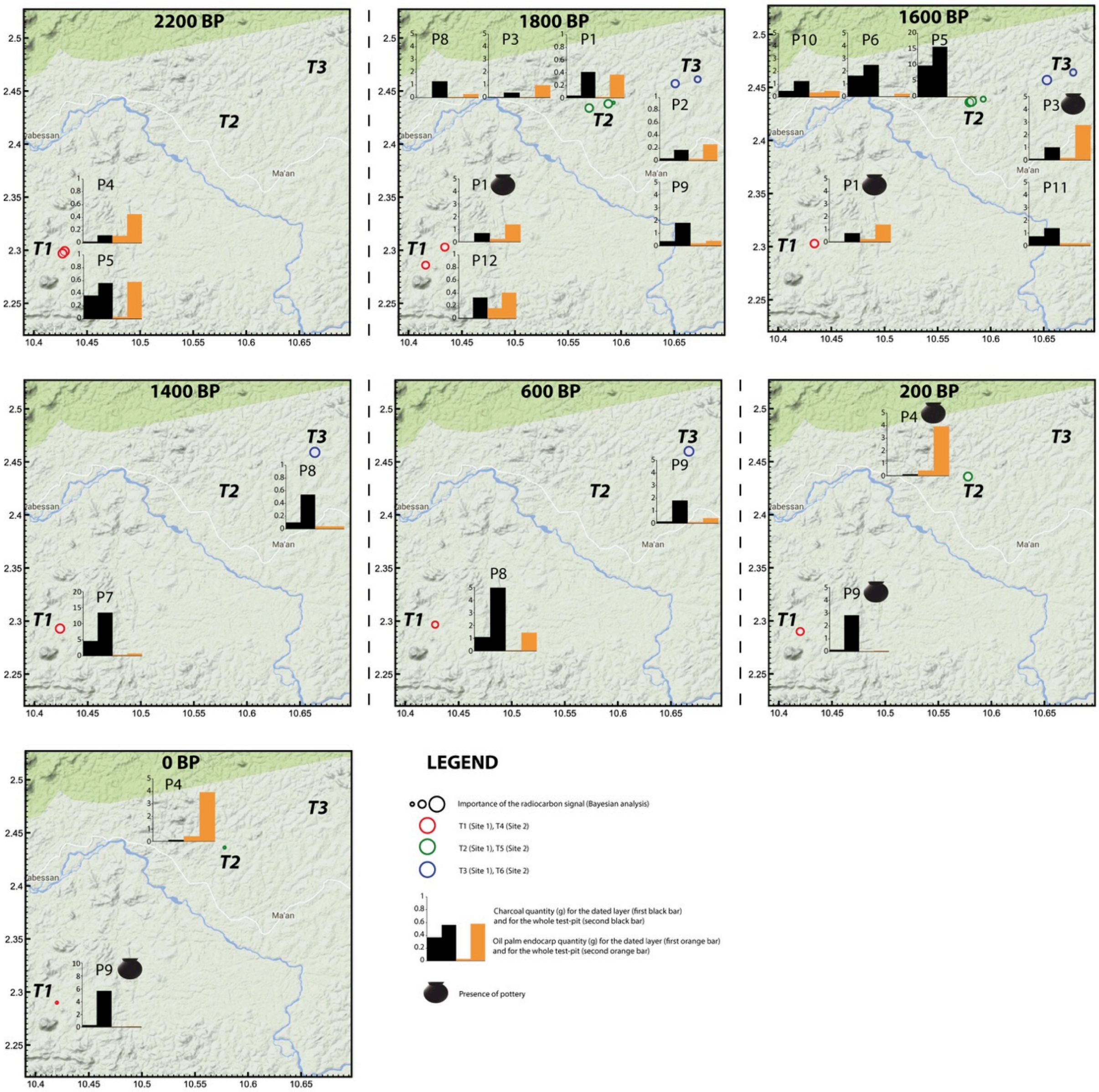
p144	413263	427149.7	B	5	1	0.06069784	0	2.865546247	0.06069784	0	0.021189299
p150	413310.9	426915.6	B	6	1	0.008600172	0	2.6944277	0.012921546	0	0
p156	413369.3	426675	B	7	1	0	0.012837225	2.393530174	0.058729621	0.779961613	0.079181246
p162	413411.7	426432.2	B	8	1	0	0	0	0.113943352	0	0
p168	413452	426176.3	B	9	1	0	0	0	0.217242883	0.054585096	0.004321374
p174	413496.2	425937.5	B	10	1	0	0	2.387133604	0	0	0
p180	413540.8	425681	B	11	1	0	0	2.702600522	0	0	0
p186	413637.2	425204.3	B	12	1	0	0	2.995848451	0.703569925	0.027757205	0
p192	413676.1	424961.3	B	13	1	0.021189299	0	3.092192068	0.221410325	0	0
p198	413733.9	424724.3	B	14	1	0	0	3.17029451	0.141517186	0	0.002166062
p204	413777.8	424455.3	B	15	1	0	0	3.243674608	0	0	0
p210	413832.8	424220.5	B	16	1	0	0	3.299622036	0	0	0
p216	413882.76	423957.6133	B	17	1	0	0	3.354322859	0	0	0
p222	413932.72	423694.7267	B	18	1	0	0	3.402898349	0	0	0
p228	423042.4	385260.9	C	1	1	0	0	4.623511307	0.012921546	0.004321374	0
p234	423067.7	385018.5	C	2	1	0	0	4.626002813	0.140379181	0.012837225	0
p240	423079.6	384767.6	C	3	1	0.103803721	0.041392685	4.628533884	1.028986095	0.685652005	0
p246	423172.9	384507.9	C	4	1	0	0	4.631324844	0	0	0
p252	423217.1	384240	C	5	1	0	0.008600172	4.634066173	0.010787416	0.015066214	0
p258	423273.2	384010.2	C	6	1	0	0	4.636445335	0.075546961	0	0
p264	423329.1	383771.5	C	7	1	0	0	4.638897548	0.037426498	0.038347898	0
p270	423398.1	383516.1	C	8	1	0.025305865	0.056904851	4.641526757	0.158844774	0.146034065	0.025582333
p276	423436.7	383278.8	C	9	1	0	0	4.643898383	0	0	0
p282	423510.9	383039.6	C	10	1	0	0	4.646354476	0	0	0
p288	423613.4	382544.8	C	11	1	0	0	4.651279252	0.084915538	0.071882007	0.008600172
p294	423656.8	382318.9	C	12	1	0	0	4.653501801	1.543369858	0	0.012837225
p300	423716.5	382085.8	C	13	1	0	0	4.65581577	0.002166062	0.634599782	0
p306	423791.9	381828.1	C	14	1	0	0	4.658380027	0	0.023624641	0
p312	423849.4	381588.7	C	15	1	0.056904851	0	4.6607217	0.780506414	0.029383778	0
p318	423911.7	381347.4	C	16	1	0	0	4.663078561	0	0	0

Appendix 5

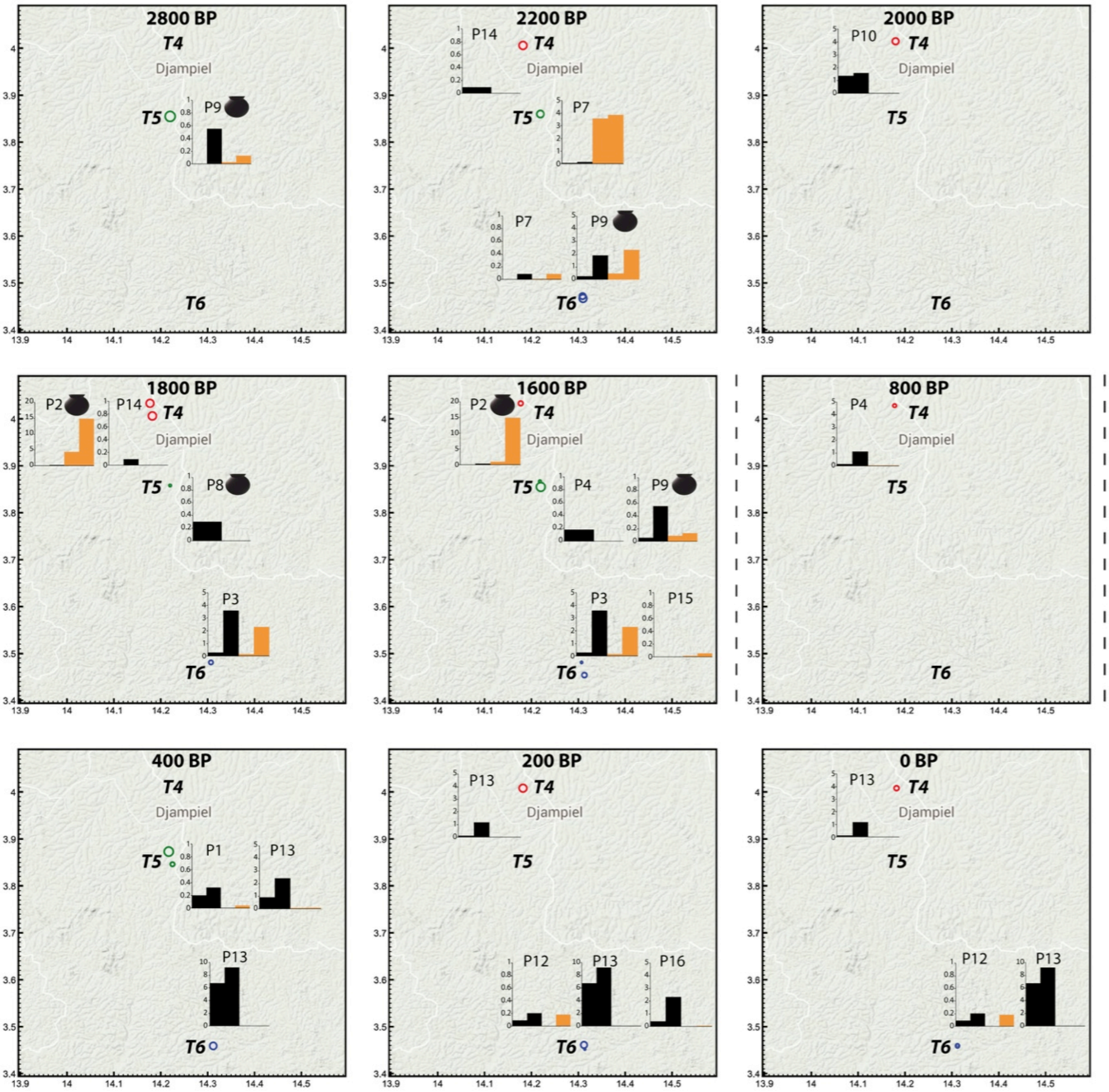
Chapter 4 – Modeled distributions of the radiocarbon dates in BP at 200-years intervals across the six transects, with mention of the macroremains quantities: a) Site 1 (Wijma) and b) Site 2 (SFID-Mbang).

Circle sizes increase with increasing probability distribution of the radiocarbon signal, according to a Bayesian model. Maps show the discontinuity of spatial occupation over time and the spacing between synchronous human activities in a same transect. Age-intervals with no radiocarbon signal are not represented. Macroremains quantities (in g) by dated test-pit (P1 to P16) are represented by type: charcoal (black) and oil palm endocarps (orange), and by dated level (first bar) and for the whole test-pit (second bar).

a) Site 1



b) Site 2


2800 BP
T4
Djampiel
T5
P9
T6
2200 BP
P14
P7
P7
P9
2000 BP
P10
1800 BP
P2
P14
P8
P3
1600 BP
P2
P4
P9
P3
P15
800 BP
P4
400 BP
P1
P13
P13
200 BP
P13
P12
P13
P16
0 BP
P13
P12
P13
13.9
14
14.1
14.2
14.3
14.4
14.5
3.4
3.5
3.6
3.7
3.8
3.9
4

Appendix 6

Chapter 5 – Trait information and characteristics of the diameter distribution for the 176 study genera across the SRI.

Botanical family was extracted from the African Plant Database of the Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria (http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php). Trait information, including regeneration guild sensu Hawthorne (1995) (P = pioneers; NPLD = non-pioneer light-demanders; SB = shade-bearers), leaf phenology (deci = deciduous; ever = evergreen) and wood basic density, was extracted from Fayolle et al. (2014b). Diameter distribution was studied across the SRI using an ordination followed by a clustering (***Figure 5.2***). Total number of stems, mean diameter (in cm) and basal area (in m^2) are given. The four genera that are monospecific in the SRI and were used for age estimations are highlighted.

		Trait (extracted from Fayolle et al. 2014b)			**Diameter distribution (computed from forest inventory data)**			
Genus	**Family**	**Regeneration guild**	**Leaf phenology**	**Wood density (g.cm^{-3})**	**Type of diameter distribution**	**# of stems**	**mean D**	**mean G**
Afzelia	Fabaceae	NPLD	deci	0.614	1. reverse-J shape	3479	43.50	0.231
Allanblackia	Clusiaceae	SB	ever	0.524	1. reverse-J shape	2647	36.61	0.179
Alstonia	Apocynaceae	P	deci	0.298	2. deviation from reverse-J	19968	63.77	0.459
Amphimas	Fabaceae	NPLD	deci	0.711	2. deviation from reverse-J	6661	58.60	0.396
Angylocalyx	Fabaceae	SB	ever	0.612	1. reverse-J shape	28982	39.63	0.216
Annona	Annonaceae			0.529	1. reverse-J shape	148	42.03	0.229
Anonidium	Annonaceae	SB	ever	0.529	1. reverse-J shape	32741	40.87	0.237
Anopyxis	Rhizophoraceae	P	ever	0.725	2. deviation from reverse-J	6914	58.23	0.376
Anthocleista	Loganiaceae	P	ever	0.586	1. reverse-J shape	720	38.96	0.180
Antiaris	Moraceae	P	deci	0.378	2. deviation from reverse-J	2390	60.74	0.434
Antidesma	Euphorbiaceae	SB	ever	0.640	1. reverse-J shape	350	32.86	0.148
Antrocaryon	Anacardiaceae	P	deci	0.445	2. deviation from reverse-J	1902	56.07	0.351
Aoranthe	Rubiaceae	P	ever	0.745	1. reverse-J shape	521	34.18	0.152
Autranella	Sapotaceae	NPLD	deci	0.782	2. deviation from reverse-J	1691	93.46	0.914
Baillonella	Sapotaceae	NPLD	deci	0.658	2. deviation from reverse-J	71	81.27	0.754
Balanites	Zygophyllaceae	NPLD	ever	0.586	2. deviation from reverse-J	603	64.71	0.489
Barteria	Passifloraceae	NPLD	deci	0.640	1. reverse-J shape	167	38.26	0.192
Beilschmiedia	Lauraceae	SB	ever	0.586	1. reverse-J shape	11902	47.80	0.280
Berlinia	Fabaceae	SB	ever	0.614	1. reverse-J shape	3367	41.48	0.264
Blighia	Sapindaceae	SB	ever	0.632	1. reverse-J shape	15223	46.63	0.266
Bobgunnia	Fabaceae	NPLD	ever	0.876	1. reverse-J shape	894	47.35	0.253
Bombax	Malvaceae	P	deci	0.382	2. deviation from reverse-J	1447	67.30	0.507
Brenania	Rubiaceae	P	ever	0.586	1. reverse-J shape	1342	44.30	0.240
Bridelia	Euphorbiaceae	P		0.640	1. reverse-J shape	821	41.35	0.196
Canarium	Burseraceae	P	deci	0.418	2. deviation from reverse-J	1973	66.60	0.493
Carapa	Meliaceae	SB	ever	0.702	1. reverse-J shape	1162	36.49	0.168
Cassia	Fabaceae			0.614	1. reverse-J shape	494	44.01	0.221
Ceiba	Malvaceae	P	deci	0.275	2. deviation from reverse-J	4020	92.32	0.916
Celtis	Ulmaceae	NPLD	deci	0.602	1. reverse-J shape	109557	44.43	0.341
Chionanthus	Oleaceae			0.586	2. deviation from reverse-J	48	57.50	0.335
Chlamydocola	Malvaceae	SB	ever	0.484	1. reverse-J shape	84	41.43	0.339
Christiana	Malvaceae			0.484	1. reverse-J shape	309	35.31	0.173
Chrysophyllum	Sapotaceae	SB	ever	0.658	1. reverse-J shape	28439	47.18	0.287
Citropsis	Rutaceae	SB	ever	0.507	1. reverse-J shape	41	33.41	0.143

Coelocaryon	Myristicaceae	SB	ever	0.446	1. reverse-J shape	10577	38.75	0.206
Cola	Malvaceae	SB	ever	0.484	1. reverse-J shape	13209	38.83	0.203
Copaifera	Fabaceae	NPLD	ever	0.614	2. deviation from reverse-J	2421	71.51	0.548
Cordia	Boraginaceae	P	deci	0.586	2. deviation from reverse-J	1976	62.04	0.450
Croton	Euphorbiaceae	P	deci	0.640	1. reverse-J shape	6928	44.64	0.274
Dacryodes	Burseraceae	NPLD	ever	0.541	1. reverse-J shape	3695	38.91	0.200
Daniellia	Fabaceae	SB	deci	0.614	2. deviation from reverse-J	1081	67.23	0.535
Desplatsia	Malvaceae	SB	ever	0.484	1. reverse-J shape	4250	34.59	0.161
Detarium	Fabaceae	P	deci	0.565	2. deviation from reverse-J	2212	76.90	0.641
Dialium	Fabaceae	SB	ever	0.614	1. reverse-J shape	26618	43.70	0.271
Diospyros	Ebenaceae	SB	ever	0.658	1. reverse-J shape	26809	40.70	0.244
Discoglypremna	Euphorbiaceae	P	deci	0.337	1. reverse-J shape	7031	37.09	0.176
Dracaena	Liliaceae	NPLD	ever	0.586	2. deviation from reverse-J	1853	58.92	0.427
Drypetes	Euphorbiaceae	SB	ever	0.640	1. reverse-J shape	24888	39.27	0.214
Duboscia	Malvaceae	NPLD	ever	0.484	1. reverse-J shape	25736	49.55	0.305
Elaeis	Arecaceae	P	ever	0.586	1. reverse-J shape	365	34.11	0.351
Endodesmia	Clusiaceae		ever	0.635	1. reverse-J shape	153	40.52	0.189
Entandrophragma	Meliaceae	NPLD	deci	0.494	2. deviation from reverse-J	35442	74.67	0.643
Eribroma	Malvaceae	SB	deci	0.484	1. reverse-J shape	11965	49.08	0.289
Erismadelphus	Vochysiaceae		ever	0.568	1. reverse-J shape	218	48.35	0.294
Erythrina	Fabaceae	P	deci	0.612	2. deviation from reverse-J	72	53.47	0.327
Erythrophleum	Fabaceae	P	deci	0.774	2. deviation from reverse-J	19518	67.36	0.488
Fernandoa	Bignoniaceae	P	deci	0.586	1. reverse-J shape	1640	42.15	0.207
Ficus	Moraceae	P		0.547	2. deviation from reverse-J	5740	70.57	0.558
Fillaeopsis	Fabaceae	NPLD	deci	0.488	1. reverse-J shape	365	47.18	0.304
Funtumia	Apocynaceae	SB	ever	0.586	1. reverse-J shape	21461	35.00	0.176
Ganophyllum	Sapindaceae	SB	ever	0.507	1. reverse-J shape	9521	45.60	0.278
Garcinia	Clusiaceae	SB	ever	0.640	1. reverse-J shape	4324	31.83	0.139
Gilbertiodendron	Fabaceae	SB	ever	0.614	1. reverse-J shape	16776	55.54	0.672
Gilletiodendron	Fabaceae	SB	ever	0.614	1. reverse-J shape	269	43.68	0.265
Gmelina	Verbenaceae			0.586	1. reverse-J shape	60	46.17	0.226
Grewia	Malvaceae	SB	ever	0.484	1. reverse-J shape	9328	37.04	0.185
Guarea	Meliaceae	SB	ever	0.511	1. reverse-J shape	16329	46.18	0.284
Hallea	Rubiaceae	NPLD	ever	0.491	1. reverse-J shape	3774	50.79	0.376
Harungana	Clusiaceae	P	ever	0.640	1. reverse-J shape	277	32.92	0.144
Hexalobus	Annonaceae	SB	ever	0.529	1. reverse-J shape	14392	45.18	0.246
Holoptelea	Ulmaceae	P	deci	0.545	2. deviation from reverse-J	1090	57.74	0.351
Homalium	Salicaceae	SB	ever	0.640	1. reverse-J shape	9909	36.92	0.176
Hylodendron	Fabaceae	P	ever	0.721	1. reverse-J shape	2631	42.97	0.254
Hymenocardia	Euphorbiaceae	P	ever	0.640	1. reverse-J shape	2271	35.89	0.223
Irvingia	Irvingiaceae	SB	ever	0.640	2. deviation from reverse-J	25634	59.73	0.438
Isolona	Annonaceae	SB	ever	0.529	1. reverse-J shape	5435	35.44	0.175
Julbernardia	Fabaceae	SB	ever	0.614	1. reverse-J shape	70	36.29	0.227
Keayodendron	Euphorbiaceae	SB	ever	0.640	1. reverse-J shape	9517	44.72	0.253
Khaya	Meliaceae	NPLD	deci	0.538	2. deviation from reverse-J	2460	68.17	0.520
Klainedoxa	Irvingiaceae	P	deci	0.640	2. deviation from reverse-J	10269	67.35	0.503
Lasiodiscus	Rhamnaceae	SB	ever	0.547	1. reverse-J shape	87	32.53	0.119
Lepisanthes	Sapindaceae			0.507	1. reverse-J shape	49	40.41	0.179
Librevillea	Fabaceae			0.614	1. reverse-J shape	81	48.15	0.320
Lophira	Ochnaceae	P	deci	0.864	2. deviation from reverse-J	8322	61.66	0.508
Lovoa	Meliaceae	NPLD	deci	0.440	2. deviation from reverse-J	3021	64.29	0.476
Macaranga	Euphorbiaceae	P	ever	0.640	1. reverse-J shape	30959	37.00	0.214

Maesobotrya	Euphorbiaceae	SB	ever	0.640	1. reverse-J shape	59	32.71	0.180
Mammea	Clusiaceae	SB	ever	0.586	2. deviation from reverse-J	3413	58.91	0.387
Manilkara	Sapotaceae	SB	ever	0.658	1. reverse-J shape	54270	48.80	0.387
Mansonia	Malvaceae	NPLD	deci	0.550	1. reverse-J shape	8222	45.31	0.301
Maranthes	Chrysobalanaceae	SB	ever	0.640	1. reverse-J shape	4322	50.45	0.300
Mareyopsis	Euphorbiaceae	SB	ever	0.640	1. reverse-J shape	78	33.59	0.125
Meiocarpidium	Annonaceae	SB	ever	0.529	1. reverse-J shape	334	31.62	0.158
Milicia	Moraceae	P	deci	0.547	2. deviation from reverse-J	3279	66.03	0.492
Millettia	Fabaceae	P	deci	0.612	1. reverse-J shape	19527	47.57	0.334
Mimusops	Sapotaceae			0.658	1. reverse-J shape	48	38.33	0.183
Morinda	Rubiaceae	P	ever	0.586	1. reverse-J shape	555	40.00	0.188
Morus	Moraceae	NPLD	deci	0.725	2. deviation from reverse-J	465	52.04	0.322
Musanga	Urticaceae	P	ever	0.250	1. reverse-J shape	22656	43.62	0.337
Myrianthus	Rubiaceae	NPLD	ever	0.586	1. reverse-J shape	18105	36.04	0.218
Nauclea	Rubiaceae	P	ever	0.586	1. reverse-J shape	2978	53.30	0.326
Neosloetiopsis	Moraceae	SB	ever	0.547	1. reverse-J shape	280	35.86	0.148
Newtonia	Euphorbiaceae		ever	0.640	2. deviation from reverse-J	124	50.48	0.280
Oddoniodendron	Fabaceae	SB	ever	0.614	1. reverse-J shape	120	38.17	0.257
Odyendyea	Simaroubaceae	NPLD	ever	0.507	1. reverse-J shape	944	44.85	0.290
Olax	Olacaceae	SB	ever	0.586	1. reverse-J shape	549	38.14	0.178
Oldfieldia	Euphorbiaceae			0.743	1. reverse-J shape	1275	51.38	0.300
Omphalocarpum	Sapotaceae	SB	ever	0.658	1. reverse-J shape	3067	43.14	0.226
Oncoba	Salicaceae	P	ever	0.640	1. reverse-J shape	1736	32.80	0.145
Ongokea	Olacaceae	NPLD	ever	0.715	1. reverse-J shape	10958	52.60	0.302
Ormocarpum	Fabaceae	NPLD		0.612	1. reverse-J shape	39	47.95	0.254
Pachyelasma	Fabaceae	SB	deci	0.614	2. deviation from reverse-J	1344	89.46	0.851
Pancovia	Sapindaceae	SB	ever	0.507	1. reverse-J shape	8409	31.79	0.153
Panda	Pandaceae	SB	ever	0.640	1. reverse-J shape	19626	42.50	0.237
Parinari	Chrysobalanaceae	NPLD	ever	0.640	1. reverse-J shape	5701	50.76	0.350
Parkia	Fabaceae	NPLD	deci	0.574	1. reverse-J shape	1094	51.95	0.312
Pausinystalia	Rubiaceae	SB	ever	0.586	1. reverse-J shape	11342	39.58	0.222
Pentaclethra	Fabaceae	NPLD	ever	0.793	1. reverse-J shape	23674	51.85	0.360
Pericopsis	Fabaceae	P	deci	0.612	2. deviation from reverse-J	1343	59.81	0.442
Petersianthus	Lecythidaceae	NPLD	deci	0.662	1. reverse-J shape	56233	49.93	0.347
Picralima	Apocynaceae	SB	ever	0.586	1. reverse-J shape	1449	36.12	0.180
Piptadeniastrum	Fabaceae	NPLD	deci	0.587	2. deviation from reverse-J	10030	72.94	0.583
Plagiosiphon	Fabaceae	SB	ever	0.614	2. deviation from reverse-J	42	58.10	0.383
Plagiostyles	Euphorbiaceae	NPLD	ever	0.640	1. reverse-J shape	4623	37.93	0.301
Polyalthia	Annonaceae	SB	ever	0.529	1. reverse-J shape	65553	33.22	0.221
Polyscias	Araliaceae	P		0.586	1. reverse-J shape	881	34.05	0.232
Pouteria	Sapotaceae	NPLD	ever	0.658	1. reverse-J shape	3088	51.61	0.320
Prioria	Fabaceae	NPLD	deci	0.614	2. deviation from reverse-J	10446	64.78	0.474
Pseudospondias	Anacardiaceae	P	ever	0.507	1. reverse-J shape	2499	42.46	0.255
Psydrax	Rubiaceae	P	deci	0.586	1. reverse-J shape	1060	40.25	0.195
Pteleopsis	Combretaceae	P	deci	0.586	2. deviation from reverse-J	7029	59.66	0.386
Pterocarpus	Fabaceae	NPLD	deci	0.612	1. reverse-J shape	20563	50.59	0.295
Pterygota	Malvaceae	NPLD	deci	0.484	1. reverse-J shape	6778	47.65	0.282
Pycnanthus	Myristicaceae	NPLD	ever	0.414	1. reverse-J shape	19046	51.09	0.318
Rauvolfia	Apocynaceae	P	ever	0.586	1. reverse-J shape	1075	44.20	0.232
Ricinodendron	Euphorbiaceae	P	deci	0.216	2. deviation from reverse-J	14703	63.01	0.470
Rinorea	Violaceae	SB	ever	0.640	1. reverse-J shape	982	33.32	0.168
Rothmannia	Rubiaceae	SB	ever	0.586	1. reverse-J shape	631	43.28	0.246

Santiria	Burseraceae	SB	ever	0.521	1. reverse-J shape	12042	39.08	0.200
Schrebera	Oleaceae			0.586	1. reverse-J shape	674	49.08	0.272
Scorodophloeus	Fabaceae	SB	ever	0.614	1. reverse-J shape	3121	38.56	0.291
Scottellia	Salicaceae	SB	ever	0.552	1. reverse-J shape	7311	40.33	0.208
Shirakiopsis	Euphorbiaceae	NPLD	ever	0.640	1. reverse-J shape	1791	44.15	0.224
Sorindeia	Anacardiaceae	SB	ever	0.507	1. reverse-J shape	741	34.78	0.147
Spathodea	Bignoniaceae	P	deci	0.586	1. reverse-J shape	69	43.33	0.215
Spondianthus	Phyllanthaceae	SB	ever	0.640	1. reverse-J shape	31	42.26	0.222
Stachyothyrsus	Fabaceae			0.614	1. reverse-J shape	41	48.78	0.297
Staudtia	Myristicaceae	SB	ever	0.744	1. reverse-J shape	32314	41.81	0.242
Stemonocoleus	Fabaceae	NPLD		0.548	2. deviation from reverse-J	181	66.08	0.557
Sterculia	Malvaceae		deci	0.484	1. reverse-J shape	12098	37.28	0.215
Stereospermum	Bignoniaceae	P	deci	0.586	1. reverse-J shape	538	40.69	0.194
Strephonema	Combretaceae	SB	ever	0.586	2. deviation from reverse-J	67	59.10	0.373
Strombosia	Olacaceae	SB	ever	0.586	1. reverse-J shape	62974	39.10	0.244
Strombosiopsis	Olacaceae	SB	ever	0.586	1. reverse-J shape	24582	40.30	0.221
Symphonia	Clusiaceae	SB	ever	0.541	1. reverse-J shape	298	42.35	0.203
Synsepalum	Sapotaceae	SB	ever	0.658	1. reverse-J shape	9921	34.99	0.171
Syzygium	Myrtaceae	SB	ever	0.586	1. reverse-J shape	2427	45.98	0.256
Tabernaemontana	Apocynaceae		ever	0.586	1. reverse-J shape	700	33.81	0.156
Terminalia	Combretaceae	P	deci	0.586	2. deviation from reverse-J	34111	63.60	0.494
Tessmannia	Fabaceae	SB	ever	0.614	1. reverse-J shape	9407	52.44	0.316
Tetraberlinia	Fabaceae	SB	ever	0.614	1. reverse-J shape	77	41.17	0.313
Tetrapleura	Fabaceae	P	deci	0.519	1. reverse-J shape	4838	42.73	0.215
Treculia	Moraceae	SB	ever	0.547	1. reverse-J shape	2836	43.63	0.223
Trichilia	Meliaceae	SB	ever	0.511	1. reverse-J shape	21051	36.46	0.188
Trichoscypha	Anacardiaceae	NPLD	ever	0.507	1. reverse-J shape	1063	42.33	0.225
Tridesmostemon	Sapotaceae		ever	0.658	1. reverse-J shape	3471	48.35	0.289
Trilepisium	Moraceae	SB	deci	0.547	1. reverse-J shape	10582	39.59	0.236
Triplochiton	Malvaceae	P	deci	0.327	2. deviation from reverse-J	13019	87.43	0.907
Uapaca	Euphorbiaceae	P	ever	0.640	1. reverse-J shape	9820	42.33	0.299
Usteria	Loganiaceae			0.586	1. reverse-J shape	78	43.59	0.214
Uvariastrum	Annonaceae	SB	ever	0.529	1. reverse-J shape	76	34.21	0.131
Vangueriopsis	Rubiaceae			0.586	1. reverse-J shape	41	40.00	0.261
Vepris	Rutaceae	SB	ever	0.507	1. reverse-J shape	474	38.80	0.191
Vitex	Verbenaceae		ever	0.586	1. reverse-J shape	6737	35.64	0.164
Xylopia	Annonaceae		ever	0.529	1. reverse-J shape	29500	38.53	0.204
Zanthoxylum	Rutaceae	P	ever	0.507	1. reverse-J shape	7162	45.85	0.256

Appendix 7

Chapter 5 – Age data for the four study species based on published tree-ring data. Mean ages and corresponding estimated dates are shown in *Figure 5.2*.

C = Cameroon; RC = Republic of the Congo; CAR = Central African Republic; n = number of stem discs; SD = standard deviation.

Species	Location	Date of collection	N discs	Mean ring width (cm ± SD)	Mean age (yr)	Estimated date (AD)	References
P. elata	Kisangani (DRC)	2008	24	0.298 ± 0.54	137	1871	De Ridder et al. 2014
T. superba	Luki & Tschela (DRC)	2008	12	0.719 ± 0.267	47	1961	De Ridder et al. 2013a, 2013b
T. superba	Scio (IC)	2008	29	0.719 ± 0.267	55	1954	De Ridder et al. 2013a, 2013b
T. scleroxylon	Biakoa (C)	1993	18	0.620 ± 0.28	124	1869	Worbes al. 2003

Appendix 8

Chapter 5 – Relative performance of commonly used growth models for the four genera that are monospecific in the SRI.

Growth model functions used to analyze the variation in tree growth (MAI_d, in cm.yr^1) with tree size (DBH, in cm) are detailed below. For the biological interpretation of parameters, Max is the maximum growth or growth optimum (in cm.yr^1), D_{opt} is the diameter at growth optimum (in cm), and D_{max} is the maximum diameter (in cm). Linear and mean models were additionally fitted to the data. For each model fitted to the growth and diameter data of each species, the Bayesian Information Criterion (BIC) is provided. The models with the best performance for each species are highlighted.

Model	**Equation and parameter**		**BIC values**			
			E. suaveolens	***P. elata***	***T. superba***	***T. scleroxylon***
Canham	$MAI_d = a\times\exp\left[-\frac{1}{2}\times\left(log\left(\frac{\mathrm{DBH}}{b/c}\right)\right)^2\right]$	a = Max b = D_{opt} c	196.6	-96.8	256.1	372.1
Gompertz	$MAI_d = a\times DBH\times log\,(\frac{b}{DBH})$	a b = D_{max}	219.5	-98.8	277.4	397.6
Logistic (Verhulst)	$MAI_d = a\times DBH\times\left(1-\frac{DBH}{b}\right)$	a b = D_{max}	246.1	-90.2	289.4	398.7
Power	$MAI_d = a\times DBH^b$	a b	235.5	-97.8	263.3	397.5
Power modified multiplier	$MAI_d = a\times\exp\,(-c\times DBH)\times DBH^b$	a b c	198.2	-96.3	257.8	372.1
Lognormal	$MAI_d = a\times\exp\left[-\left(b\times\log\left(\frac{c}{DBH}\right)\right)^2\right]$	a = Max b c = D_{opt}	210.1	-95.8	266.0	403.1
Linear	$MAI_d = a + b\times DBH$	a b	223.5	-96.5	265.0	398.1
Mean	$MAI_d = a$	a	241.2	-99.1	267.5	411.4

Appendix 9

Chapter 5 – Age estimations of the trees at the mode of the diameter distribution for the four genera that are monospecific in the SRI.

The mode of the diameter distribution across the SRI, information on growth data, including number of trees (n), the diameter (dbh) range and the mean and standard error of the annual diameter increment (SE), and age estimations of the mode based on the mean annual diameter increment (MAI_d) calculated for 982 monitored trees in the SRI are provided for the four study species (see ***Figure 5.4***). For all study species, eight growth models (i.e. Canham, Gompertz, Verhulst, Power, Power mult, Lognormal, Linear and Mean) were fitted to the data, and age estimations were obtained with numerical solutions to ordinary differential equations (ODE) (see ***Figure 5.4***). The most reliable age estimations according to age data from published tree-ring studies are highlighted.

		Study species			
		E. suaveolens	*P. elata*	*T. superba*	*T. scleroxylon*
Mode of the distribution					
	Weibull	72.0	65.3	69.5	90.3
Growth data					
	n	367	199	152	265
	Sites (Fig. 1 Main Text)	1, 2, 3, 4, 5, 6, 7	3, 4	1, 3, 5, 6, 7	1, 3, 5, 6
	dbh range (cm)	12.2 - 151.6	14.7 - 104.7	10.6 – 80.7	10.7 – 149.4
	MAI_d (mean ± SE)	0.44 ± 0.033	0.45 ± 0.026	0.53 ± 0.112	0.58 ± 0.061
Age estimations (yrs) based on					
	Mean growth (± SE)				
ODE numerical solving	**Canham**	**-**	236	177	193
	Gompertz	189	223	168	254
	Logistic (Verhulst)	444	625	322	866
	Power	-	48	-	76
	Power modified exponent	129	148	131	170
	Power modified multiplier	274	176	129	193
	Lognormal	-	384	212	223
	Linear	133	152	135	186
	Mean	105	166	86	316

Appendix 10

Chapter 5 – Data documenting paleoenvironmental changes (*Figures 5.1* and *5.5*) during the last 1000 years in the SRI.

C = Cameroon; RC = Republic of the Congo; CAR = Central African Republic; W Africa = West Africa. Numbers refer to the map (***Figure 5.1***). References are indicated.

Country	**Site**	**Fig. 1**	**Latitude**	**Longitude**	**Data type**	**References**
C	Belabo (upper Sanaga catchment)	1	4.56390	13.17200	Grain size, chemical elements	Sangen et al. 2011
C	Benana C22 (Nyong valley)	2	4.00000	13.00000	Grain size, chemical elements	Runge et al. 2014
C	Mankako (upper Boumba catchment)	3	3.18000	14.04000	Grain size, chemical elements	Sangen et al. 2011
C	Ouesso region (Boumba catchment)	4	3.24000	14.32000	Grain size, chemical elements	Sangen et al. 2011
C	Lobéké Reserve	5	2.17300	15.42590	Phytoliths, $\delta^{13}C$	Runge and Fimbel 2001
C	Moukounounou (upper Ngoko catchment)	6	1.56390	15.20090	Grain size, chemical elements, $\delta^{13}C$	Sangen 2012, Sangen et al. 2011
C	Mokounounou N01 (upper Ngoko catchment)	6	1.56390	15.20090	Grain size, chemical elements, $\delta^{13}C$	Sangen 2012, Sangen et al. 2011
C	Mokounounou N02 (upper Ngoko catchment)	6	1.56390	15.20090	Grain size, chemical elements, $\delta^{13}C$	Sangen 2012, Sangen et al. 2011
C	Mokounounou N04 (upper Ngoko catchment)	6	1.56390	15.20090	Grain size, chemical elements, $\delta^{13}C$	Sangen 2012, Sangen et al. 2011
C	Mokounounou N06 (upper Ngoko catchment)	6	1.56390	15.20090	Grain size, chemical elements, $\delta^{13}C$	Sangen 2012, Sangen et al. 2011
RC	Mopo Bai	7	2.23300	16.26200	Atmospheric dust signal, pollen, µ-charcoal	Brncic et al. 2009
RC	Mopo Bai Site 1	7	2.24370	16.26190	Charcoal	Tovar et al. 2014
RC	Mopo Bai Site 8	7	2.24120	16.26130	Charcoal	Tovar et al. 2014
RC	Mopo Bai Site 9	7	2.23250	16.26240	Charcoal	Tovar et al. 2014
RC	Mopo Bridge Site 10	8	2.22720	16.28550	Charcoal	Tovar et al. 2014
RC	Mopo Bridge Site 13	8	2.21410	16.25240	Charcoal	Tovar et al. 2014
CAR	Mbeli River Site 5	9	2.28020	16.43290	Charcoal	Tovar et al. 2014
CAR	Mbeli River Site 6	9	2.27880	16.45190	Charcoal	Tovar et al. 2014
CAR	Mbeli River Site 7	9	2.27800	16.45520	Charcoal	Harris 2002
RC	Goualougo Lake	10	2.16400	16.50900	Atmospheric dust signal, pollen, µ-charcoal	Brncic et al. 2007
CAR	Goualougo Site 14	10	2.18430	16.52040	Charcoal	Tovar et al. 2014
CAR	Goualougo Site 15	10	2.16370	16.50960	Charcoal	Tovar et al. 2014
CAR	Goualougo Site 16	10	2.20280	16.50360	Charcoal	Tovar et al. 2014
RC	Pokola Site 17	11	1.27080	16.79700	Charcoal	Tovar et al. 2014
RC	Lake Télé	12	1.20000	17.10000	Pollen	Laraque et al. 1998
CAR	Mbaéré valley	13	3.72500	17.00000	Grain size, chemical elements	Neumer et al. 2008
CAR	Sadika alluvial fan	13	3.72500	17.00000	Grain size, chemical elements	Neumer et al. 2008
CAR	Bagbaya (core FC400)	14	3.50000	17.28000	Pollen, charcoal	Lupo et al. 2015
CAR	Ngotto Forest	15	4.00000	17.30000	Remote sensing	Runge 2008
CAR	Lake Gbali	16	4.81861	18.26278	Charcoal	Aleman et al. 2013
CAR	Oubangui catchment	17	4.62000	18.59000	Flood & erosion data 1911-1999	Runge and Nguimalet 2005
CAR	Lake Doukoulou	18	4.25278	18.42361	Charcoal	Aleman et al. 2013
CAR	Lake Nguengué	19	3.76111	18.12194	Charcoal	Aleman et al. 2013
W Africa	Marine core ODP 658C	**Fig. 3**	20.4500	-18.35000	SSTs (foraminifera)	DeMenocal et al. 2000

Appendix 11

Chapter 5 – Synthesis of the 63 AMS radiocarbon and the two OSL dates documenting human activities (*Figure 5.5*) during the last 1000 years in the SRI.
C = Cameroon; RC = Republic of the Congo; CAR = Central African Republic; AA = AMS Laboratory, University of Arizona (USA); Beta = Beta Analytic (USA); Erl = Erlangen AMS Facility (Germany); Gif = Gif-sur-Yvette (France); KI = Kiel (Germany); KIA = Kiel AMS (Germany); Ly = University of Lyon (France); OBDY = ORSTOM Bondy (France); Poz = Poznań Radiocarbon Laboratory (Poland). Numbers refer to the map (***Figure 5.1***). Dated material, identified species, lab codes, raw and calibrated dates Before Present (BP) and Anno Domini (AD), source references, and pottery (i.e. potsherds), smelting (i.e. iron slags and identified tuyères), salt (Richard Oslisly pers. obs.) and charred oil palm endocarps evidence are indicated. We assumed that charred oil palm endocarps found in combination with potsherds were consumed during the occupation of the sites (Morin-Rivat et al. 2016).

Country	Name	Fig. 1	Latitude	Longitude	Dated mat.	Identified sp.	Lab nr	BP	±	Cal. BP	Cal. AD	Reference	Pottery	Smelting	Salt	Oil palm
C	Bagofit	1	4.00000	13.12000	charcoal	.	Erl-12252	268	39	463-0	1719	Meyer et al. 2009	x	x	.	.
C	Mindourou 2	2	3.64660	13.52290	seed	*E. g.*	KIA-45496	1050	25	1049-925	875	Morin-Rivat et al. 2014	.	.	.	x
C	Mindourou 3	3	3.09592	13.96362	seed	.	Poz-49314	205	30	305-0	1798	Morin-Rivat et al. 2016	.	.	.	.
C	Mindourou 4	4	3.20084	13.95598	charcoal	.	Poz-49316	210	30	305-0	1798	Morin-Rivat et al. 2016	.	.	.	.
C	Mbang 1	5	4.02815	14.17808	seed	*E. g.*	Poz-62627	860	30	901-695	1152	Morin-Rivat et al. 2016	.	.	.	x
C	Mbang 2	6	4.00818	14.18169	charcoal	.	Poz-62629	175	35	298-0	1801	Morin-Rivat et al. 2016	.	.	.	.
C	Mbang 3	7	3.87331	14.21665	charcoal	.	Poz-62630	305	30	462-300	1570	Morin-Rivat et al. 2016	.	.	.	.
C	Mbang 4	8	3.84654	14.22167	seed	*E. g.*	Poz-62634	360	30	500-315	1542	Morin-Rivat et al. 2016	.	.	.	x
C	Bali River 1	9	3.73690	14.73840	charcoal	.	Poz-41774	110	25	268-15	1807	Morin-Rivat et al. 2014	.	.	.	.
C	Bali River 2	10	3.76250	14.79306	charcoal	.	Poz-41775	590	30	652-537	1356	Morin-Rivat et al. 2014	x	.	.	.
C	Mbang 5	11	3.45867	14.31220	charcoal	.	Poz-62638	260	30	431-0	1735	Morin-Rivat et al. 2016	.	.	.	.
C	Mbang 6	11	3.46071	14.31181	charcoal	.	Poz-62637	140	30	281-6	1807	Morin-Rivat et al. 2016	.	.	.	.
C	Mbang 7	11	3.45206	14.31393	charcoal	.	Poz-62640	80	30	260-25	1808	Morin-Rivat et al. 2016	.	.	.	.
C	Messok 3	12	3.07050	14.35570	charcoal	.	KIA-38942	195	30	302-0	1799	Morin-Rivat et al. 2014	.	.	.	.
C	Messok 3	12	3.07052	14.35566	charcoal	.	KIA-38934	205	30	305-0	1798	Morin-Rivat et al. 2014	x	.	.	.
C	Ndangayé Bai	13	2.38333	15.80000	.	.	KIA-31773	1045	30	1050-921	963	Oslisly et al. 2013b	x	.	x	.
C	Djembé Fosse 1	14	2.18333	16.06667	.	.	Gif-12476	585	35	652-534	1357	Oslisly et al. 2013b	.	.	.	.

C	Bolo Bai 1B	15	2.16667	15.71667	.	.	Poz-45694	1160	30	1177-983	870	Oslisly et al. 2013b	x	.	x	.
C	Bolo Bai 1C	16	2.15000	15.71667	.	.	KIA-31772	948	20	925-796	1090	Oslisly et al. 2013b	x	.	x	.
C	Ngoko Island	17	1.93333	15.58333	.	.	Poz-45692	145	30	283-2	1808	Oslisly et al. 2013b	.	.	.	.
C	Mokounounou 1a	18	1.93333	15.33333	.	.	KI-4612	470	65	641-318	1471	Oslisly et al. 2013b	x	.	x	.
C	Mokounounou 1b	18	1.93333	15.33333	.	.	KI-4613	410	55	531-315	1527	Oslisly et al. 2013b	x	.	x	.
RC	Upper Esimbi	19	2.27600	16.42700	seed	*E. g.*	Beta-75799	1150	70	1255-933	856	Fay 1997	.	.	.	x
RC	Mid Esimbi	20	2.34100	16.34400	seed	*E. g.*	Beta-75800	990	80	1064-730	1053	Fay 1997	.	.	.	x
RC	Mid Esimbi	20	2.34100	16.34400	seed	*E. g.*	Beta-75802	1030	80	1174-767	980	Fay 1997	.	.	.	x
RC	Mid Esimbi	20	2.34100	16.34400	seed	*E. g.*	Beta-75805	1110	70	1237-913	965	Fay 1997	.	.	.	x
RC	Bomassa 1	21	2.16300	16.19490	charcoal	.	KIA-37683	200	25	299-0	1800	Morin-Rivat et al. 2014	·	·	·	·
RC	Loundoungou	22	2.43073	16.97062	seed	*E. g.*	Poz-41787	90	30	266-22	1806	Morin-Rivat et al. 2014	.	.	.	x
CAR	Ndakan	23	2.21000	16.90000	pottery	.	X367 (OSL)	1.39	0.99	920/460	.	Brncic 2003	x	.	.	.
CAR	Ndakan	23	2.21000	16.90000	pottery	.	X368 (OSL)	1.15	0.27	380/760	.	Brncic 2003	x	.	.	.
RC	Mokobo	24	2.01560	16.65310	seed	*N.* sp.	KIA-37685	215	25	305-0	1797	Morin-Rivat et al. 2014	·	·	·	·
RC	Djaka River	25	1.71851	16.46576	charcoal	.	Poz-38696	335	35	482-308	1556	Morin-Rivat et al. 2014	x	.	.	.
RC	Komo River	26	1.68030	16.84610	seed	*E. g.*	Poz-41780	1200	30	1236-1010	827	Morin-Rivat et al. 2014	.	.	.	x
RC	Ngombé	27	1.43532	16.17317	charcoal	.	Poz-38703	675	30	679-560	1331	Morin-Rivat et al. 2014	x	x	.	.
RC	Pikounda 2	28	1.29318	16.20120	seed	*E. g.*	Poz-41772	520	30	626-507	1383	Morin-Rivat et al. 2014	x	.	.	x
RC	Pokola 2	29	1.24669	16.66761	seed	*E. g.*	KIA-34142	620	25	658-5551	1346	Morin-Rivat et al. 2014	.	.	.	x
RC	Landjoué	30	0.76502	15.36163	seed	*E. g.*	Poz-41781	290	30	458-288	1577	Morin-Rivat et al. 2014	x	.	.	x
CAR	Sabele 1	31	3.33333	16.16667	charcoal	.	Ly-5921	630	45	667-546	1343	Lanfranchi et al. 1998	.	x	.	.
CAR	Sabele 2	31	3.33333	16.16667	charcoal	.	Ly-5922	715	35	726-564	1305	Lanfranchi et al. 1998	.	x	.	.
RC	Lopola	32	2.99360	17.30260	charcoal	.	Poz-41784	140	25	281-6	1806	Morin-Rivat et al. 2014	·	·	·	·
RC	Ebaleki River	33	3.21733	17.51133	charcoal	.	Poz-38697	315	30	466-302	1566	Morin-Rivat et al. 2014	x	.	.	x
CAR	Bagbaya BB01	34	3.50000	17.28000	charcoal	.	AA94530	168	35	291-0	1804	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya BB01	34	3.50000	17.28000	charcoal	.	AA94531	207	35	309-0	1795	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya BB01	34	3.50000	17.28000	charcoal	.	AA94529	215	34	310-0	1795	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya BB03	34	3.50000	17.28000	charcoal	.	AA94532	148	34	284-0	1808	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya BB05	34	3.50000	17.28000	charcoal	.	AA94534	187	34	303-0	1799	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya BB05	34	3.50000	17.28000	charcoal	.	AA94533	231	34	422-0	1739	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya ND01	34	3.50000	17.28000	charcoal	.	AA95437	160	35	287-0	1807	Lupo et al. 2015	.	x	.	.

CAR	Bagbaya ND02	34	3.50000	17.28000	charcoal	.	AA94538	242	34	429-0	1736	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya NG01	34	3.50000	17.28000	charcoal	.	AA94539	217	48	429-0	1735	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya NZ03	34	3.50000	17.28000	charcoal	.	AA94541	494	34	621-497	1391	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya NZ03	34	3.50000	17.28000	charcoal	.	AA94542	593	34	654-538	1355	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya NZ03	34	3.50000	17.28000	charcoal	.	AA94540	706	35	701-561	1319	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya OB01	34	3.50000	17.28000	charcoal	.	AA94543	152	35	285-0	1808	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya OB02	34	3.50000	17.28000	charcoal	.	AA94544	210	34	309-0	1795	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya OB05	34	3.50000	17.28000	charcoal	.	AA94546	131	34	280-7	1806	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya OB05	34	3.50000	17.28000	charcoal	.	AA94545	188	39	305-0	1797	Lupo et al. 2015	.	x	.	.
CAR	Bagbaya OB06	34	3.50000	17.28000	charcoal	.	AA94547	131	34	280-7	1806	Lupo et al. 2015	.	x	.	.
CAR	Ngara	35	4.03000	18.38000	.	.	Ly-5919	330	40	485-305	1555	Moga 2008	.	x	.	.
CAR	Lingbangbo	36	3.81667	18.53333	charcoal	.	OBDY-463	70	120	424-0	1738	Moga 2008	.	x	.	.
CAR	Lingbangbo	36	3.81667	18.53333	charcoal	.	OBDY-464	110	80	285-0	1808	Moga 2008	.	x	.	.
CAR	Lingbangbo	36	3.81667	18.53333	charcoal	.	OBDY-255	430	180	689-0	1605	Moga 2008	.	x	.	.
CAR	Lingbangbo	36	3.81667	18.53333	charcoal	.	OBDY-582	559	77	673-493	1367	Moga 2008	.	x	.	.
CAR	Sikilongo	37	3.65000	18.56000	charcoal	.	OBDY-303	870	210	1256-518	1063	Moga 2008	.	x	.	.
CAR	Mondongué	38	3.65000	18.56000	charcoal	.	OBDY-253	140	100	428-0	1736	Moga 2008	.	x	.	.

Appendix 12

Chapter 5 – SQL codes for the Bayesian analysis of the radiocarbon dates.

```
Plot()
 {
Sequence()
{
  Sigma_Boundary(“Start”);
  Sum(“Phase”)
  {
R_Date(BP(calBP(70)), 120) +N(0,10);
R_Date(BP(calBP(80)), 30) +N(0,10);
R_Date(BP(calBP(90)), 30) +N(0,10);
R_Date(BP(calBP(110)), 25) +N(0,10);
R_Date(BP(calBP(110)), 80) +N(0,10);
R_Date(BP(calBP(131)), 34) +N(0,10);
R_Date(BP(calBP(131)), 34) +N(0,10);
R_Date(BP(calBP(140)), 30) +N(0,10);
R_Date(BP(calBP(140)), 25) +N(0,10);
R_Date(BP(calBP(140)), 100) +N(0,10);
R_Date(BP(calBP(145)), 30) +N(0,10);
R_Date(BP(calBP(148)), 34) +N(0,10);
R_Date(BP(calBP(152)), 35) +N(0,10);
R_Date(BP(calBP(160)), 35) +N(0,10);
R_Date(BP(calBP(168)), 35) +N(0,10);
R_Date(BP(calBP(175)), 35) +N(0,10);
R_Date(BP(calBP(187)), 34) +N(0,10);
R_Date(BP(calBP(188)), 39) +N(0,10);
R_Date(BP(calBP(195)), 30) +N(0,10);
R_Date(BP(calBP(200)), 25) +N(0,10);
R_Date(BP(calBP(205)), 30) +N(0,10);
R_Date(BP(calBP(205)), 30) +N(0,10);
R_Date(BP(calBP(207)), 35) +N(0,10);
R_Date(BP(calBP(210)), 30) +N(0,10);
R_Date(BP(calBP(210)), 34) +N(0,10);
R_Date(BP(calBP(215)), 25) +N(0,10);
R_Date(BP(calBP(215)), 34) +N(0,10);
R_Date(BP(calBP(217)), 48) +N(0,10);
R_Date(BP(calBP(231)), 34) +N(0,10);
R_Date(BP(calBP(242)), 34) +N(0,10);
R_Date(BP(calBP(260)), 30) +N(0,10);
R_Date(BP(calBP(268)), 39) +N(0,10);
R_Date(BP(calBP(290)), 30) +N(0,10);
R_Date(BP(calBP(305)), 30) +N(0,10);
R_Date(BP(calBP(315)), 30) +N(0,10);
R_Date(BP(calBP(330)), 40) +N(0,10);
R_Date(BP(calBP(335)), 35) +N(0,10);
R_Date(BP(calBP(360)), 30) +N(0,10);
R_Date(BP(calBP(410)), 55) +N(0,10);
R_Date(BP(calBP(430)), 180) +N(0,10);
R_Date(BP(calBP(470)), 65) +N(0,10);
R_Date(BP(calBP(494)), 34) +N(0,10);
R_Date(BP(calBP(520)), 30) +N(0,10);
R_Date(BP(calBP(559)), 77) +N(0,10);
R_Date(BP(calBP(585)), 35) +N(0,10);
R_Date(BP(calBP(590)), 30) +N(0,10);
R_Date(BP(calBP(593)), 34) +N(0,10);
R_Date(BP(calBP(620)), 25) +N(0,10);
R_Date(BP(calBP(630)), 45) +N(0,10);
R_Date(BP(calBP(675)), 30) +N(0,10);
R_Date(BP(calBP(706)), 35) +N(0,10);
R_Date(BP(calBP(715)), 35) +N(0,10);
R_Date(BP(calBP(860)), 30) +N(0,10);
R_Date(BP(calBP(870)), 210) +N(0,10);
R_Date(BP(calBP(948)), 20) +N(0,10);
R_Date(BP(calBP(990)), 80) +N(0,10);
R_Date(BP(calBP(1030)), 80) +N(0,10);
R_Date(BP(calBP(1045)), 30) +N(0,10);
R_Date(BP(calBP(1050)), 25) +N(0,10);
R_Date(BP(calBP(1110)), 70) +N(0,10);
R_Date(BP(calBP(1150)), 70) +N(0,10);
R_Date(BP(calBP(1160)), 30) +N(0,10);
R_Date(BP(calBP(1200)), 30) +N(0,10);
};
  Sigma_Boundary(“End”);
 };
};
```

Appendix 13

Chapter 5 – Chronology of the historical events from the beginning of the 15th century to the present occurring or influencing human populations in the SRI. Precise dates or time spans are related to local or more general events. References are indicated.

Date	Event	References
1400-1650	Kongo Kingdom in the current Rep. of the Congo and Angola. Slave trade by the Portuguese caused the kingdom to collapse by depopulating and destabilizing the area	Gendreau 2010, Stock 2013
1441-1870	Slave trade, including the Triangular trade, with primary period of slaves transported across the Atlantic between 1700 and 1870 (80%)	Stock 2013
1800-1850	In central Africa, slaves were captured far inland (30,000 slaves sent per year)	Manning and Akyeampong 2006
~ 1840-1900	Southward movements of populations into the forests to escape the Fulbe's (and affiliates') slave-raiding: social disorganization and overpopulation in the Sangha region, particularly along rivers	Copet-Rougier 1998, Robineau 1967, Giles-Vernick 2000
	Interethnic wars then social structuration at the end of the 19th c. through marriage exchanges (alliances) in the SRI	Copet-Rougier 1998
	Economic attraction for the Sangha region: fertile soils, natural resources, e.g. iron, and thriving trade	Copet-Rougier 1998
1875	Beginning of the exploration of southeastern Cameroon and of the Congo	Burnham 1996
~ 1880	Beginning of the 'Scramble for Africa'	Stock 2013
1884-1885	Berlin Conference (Partition of Africa): on paper delimitation of the French/German border	Robineau 1967
1885-1890	Arrival of the first Europeans in central Africa (French, Belgians, British and Germans)	Robineau 1967
1887	German military campaign near Abong-Mbang: seething of the Dja populations	Robineau 1967
1891	First arrival of French explorers Gaillard and Fourneau in the Upper-Sangha region. Creation of the Ouesso station	Copet-Rougier 1998, Robineau 1967
1892	De Brazza is appointed as Commissioner General of the Congo	Burnham 1996
	De Brazza describes the Upper-Sangha region as densely populated and rich in resources with a well-organized trade between agriculturists and pastoralists	Copet-Rougier 1998, Coquery-Vidrovitch 1998
	Permanent French occupation of the region	Copet-Rougier 1998
1894	Franco-German Treaty delimiting the border	Burnham 1996, Robineau 1967
	Establishment of the guarding posts from Koundé (north) to Nola (south)	Burnham 1996
1894-1896	Insurrection then repression of the local populations and the Fulbe slave-raiders by the colonial power, particularly near Nola	Copet-Rougier 1998, Coquery-Vidrovitch 1998
1897	Reduction of the French colonial occupation to the post of Carnot only	Copet-Rougier 1998
1898-1899	Twelve French companies dispute the Upper Congo: 30-year concessions to exploit the resources and develop communications. Creation of factories	Vennetier 1963, Coquery-Vidrovitch 1998
1898	Arrival of the Germans at Ouesso (von Carnapp, Plehn, and von Stein) followed by expansion to the north (Yokadouma and Bertoua)	Copet-Rougier 1998
1899	Foundation of the Sangha-Ngoko station at Mouloundou by the Germans. Beginning of the tensions between the Germans and the French	Copet-Rougier 1998
~ 1900	Gathering of the populations in the European trading centers (admin. or military posts) and in traditional centers (implantation of colonial factories and trading posts)	Robineau 1967
1902-1909	Insurrection of the local populations against the companies, followed by repression	Coquery-Vidrovitch 1998

1905-1906	Commercial conflicts between French and German companies in the absence of a clear border	Robineau 1967
1905-1907	Denunciation of brutalities and murders of locals by the concessionaires	Coquery-Vidrovitch 1998
1907-1911	Arming of the populations by the French and German colonists, interethnic conflicts and looting of the factories, military operations with destruction of villages	Robineau 1967
Before 1910	People formerly settled along the rivers: Sangha, Dja, Djouah, and Aïna; empty zones in the forests btw. the Dja and Boumba rivers	Robineau 1967
1910-1930	Forced population displacements, emptying of the riverbanks	Robineau 1967
1911	New physical delimitation of the Franco-German border more southward in exchange for possessions in Morocco	Robineau 1967
1911-1914	France cedes the Sangha Valley to the Germans. French possessions are spilt apart from the Sangha River	Coquery-Vidrovitch 1998
1913	Evacuation of the French posts and factories: draining of the populations to Ouesso	Robineau 1967
1914-1918	Involvement of local populations in WWI (armed), French/German clashes over control of the region, the populations flee	Robineau 1967, Giles-Vernick 2000
1919	Paris Peace Conference: recovery by France of the German possessions ceded in 1911, with French Equatorial Africa (AEF) included	Kaspi 1971
1920s	Implantation of extensive oil palm and coffee plantations in the Sangha River Interval	Giles-Vernick 2000
1920-1930	Permanent settlement of the colonial posts, layout of new trails and roads with forced labor, more accurate census of the populations, increased role of the local chiefs	Robineau 1967, Freed 2010
	Displacements of villages along the main road axes only (*cantonment* in French), destruction of the ancient villages, collapse of the Bakwélé group	Robineau 1967
1921-1932	Enrollment for the construction of the railway (Congo-Ocean): conflicts btw. rubber companies and the colonial admin (AEF; drainage of the workers)	Robineau 1967
	Desertion of the villages, flight of people to Cameroon (particularly the Djem led by their chief Angoula)	Robineau 1967
	Mortality of workers in the construction of the railway: up to 30.3 % (accidents and epidemics)	Robineau 1967
~1923-1925	Christian missions settled in the Sangha River Interval	Giles-Vernick 2000
1923-1945	Exploitation of the natural rubber (in 10-y concessions), only profitable during WWII (war effort); new trails to export the rubber production	Robineau 1967
1925-1928	Decline in the population from 20,000 to 15,000 btw. two censuses	Robineau 1967
1928-1930	Great insurrection in the Upper-Sangha, including Cameroon and northern Congo	Coquery-Vidrovitch 1998
~1930	Beginning of the rural exodus	Vennetier 1963
1938	22% of the population suffers from sleeping sickness in the Nola subdivision	Robineau 1967
1939-1945	Increasing rubber exploitation during World War II	Coquery-Vidrovitch 1998
1945-1957	Collapse of the rubber production and gold extraction, and failure of the coffee plantations: development of the oil palm (e.g. in Ouesso) and cocoa plantations, timber exploitation	Robineau 1967, Coquery-Vidrovitch 1998
	Beginning the abandonment of road construction projects	Robineau 1967, Coquery-Vidrovitch 1998
1960	Independence for three of the studied countries	Robineau 1967
1964	Massive immigration of workers to Ouesso	Robineau 1967
1970-1976	Modern timber exploitation in central Africa	Vennetier 1963, Laporte et al. 2007
1980s-1990s	Social impacts of economic and environmental interventions (reserves and parks). Employment of workers in timber companies (concessions). End of agricultural activities in the forest	Giles-Vernick 2000

Appendix 14

Articles published as first author (by chronological order), corresponding to Chapters 3, 4, and 5, respectively.

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NEW EVIDENCE OF HUMAN ACTIVITIES DURING THE HOLOCENE IN THE LOWLAND FORESTS OF THE NORTHERN CONGO BASIN

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Sylvie Gourlet-Fleury[4] • Richard Oslisly[5] • Laurent Bremond[6] • Ilham Bentaleb[7] •
Hans Beeckman[2] • Jean-Louis Doucet[1]

ABSTRACT. In the last decade, the myth of the pristine tropical forest has been seriously challenged. In central Africa, there is a growing body of evidence for past human settlements along the Atlantic forests, but very little information is available about human activities further inland. Therefore, this study aimed at determining the temporal and spatial patterns of human activities in an archaeologically unexplored area of 110,000 km^2 located in the northern Congo Basin and currently covered by dense forest. Fieldwork involving archaeology as well as archaeobotany was undertaken in 36 sites located in southeastern Cameroon and in the northern Republic of Congo. Evidence of past human activities through either artifacts or charred botanical remains was observed in all excavated test pits across the study area. The set of 43 radiocarbon dates extending from 15,000 BP to the present time showed a bimodal distribution in the Late Holocene, which was interpreted as two phases of human expansion with an intermediate phase of depopulation. The 2300–1300 BP phase is correlated with the migrations of supposed farming populations from northwestern Cameroon. Between 1300 and 670 BP, less material could be dated. This is in agreement with the population collapse already reported for central Africa. Following this, the 670–20 BP phase corresponds to a new period of human expansion known as the Late Iron Age. These results bring new and extensive evidence of human activities in the northern Congo Basin and support the established chronology for human history in central Africa.

INTRODUCTION

In the last decade, the myth of the pristine tropical forest has been seriously challenged (van Gemerden et al. 2003). As these areas are currently covered by dense forest, they were formerly regarded as intact (Willis et al. 2004). Multiple lines of evidence of ancient human activities have been recorded, however, across the tropics and these have likely influenced tropical forest structure and composition (Barton et al. 2012). Indeed, recent research has attested to early agriculture and land management dated to several thousand years ago in currently sparsely populated or depopulated areas (Barker et al. 2007; Summerhayes et al. 2010; Arroyo-Kalin 2012; Barton 2012; Barton et al. 2012; Haberle et al. 2012; Hunt and Premathilake 2012; Kennedy 2012; Kingwell-Banham and Fuller 2012; McNeil 2012; Rostain 2012; Sémah and Sémah 2012; Stahl and Pearsall 2012; Torrence 2012). In central Africa, artifacts (e.g. stone tools, potsherds, and iron slags) and charred botanical remains (e.g. charcoals and endocarps) constitute valuable witnesses of human history in the forests (van Gemerden et al. 2003; Wotzka 2006; Brncic et al. 2007; Höhn and Neumann 2012; Logan and D'Andrea 2012; Neumann et al. 2012a; Gillet and Doucet 2013; Oslisly et al. 2013a).

In tropical Africa, the current forest composition, specifically the dominance of long-lived light-demanding species in the canopy, have been mostly interpreted as the result of recent human activities (Aubréville 1947; Letouzey 1968; White and Oates 1999; Brncic et al. 2007; Greve et al. 2011). Recently, Bayon et al. (2012) even asserted that human land-use intensification was the determining factor in the major vegetation change that occurred about 3000 yr ago, when rainforests were abruptly replaced by a forest-savanna mosaic in the course of a few centuries. However, such large-scale human-driven vegetation changes have largely been questioned. Paleoecologists and archaeologists indeed agree on the fact that this "rainforest crisis" was related to a large climate

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Research paper

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High spatial resolution of late-Holocene human activities in the moist forests of central Africa using soil charcoal and charred botanical remains

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Abstract

Palaeoecological and archaeological studies have demonstrated that human populations have long inhabited the moist forests of central Africa. However, spatial and temporal patterns of human activities have hardly been investigated with satisfactory accuracy. In this study, we propose to characterize past human activities at local scale by using a systematic quantitative and qualitative methodology based on soil charcoal and charred botanical remains. A total of 88 equidistant test-pits were excavated along six transects in two contrasting forest types in southern Cameroon. Charred botanical remains were collected by water-sieving and sorted by type (wood charcoals, oil palm endocarps and unidentified seeds). A total of 50 Accelerator Mass Spectrometry ^{14}C dates were also obtained. Results showed that charred macroremains were found at multiple places in the forest, suggesting scattered human activities, which were distributed into two main periods (Phase A: 2300–1300 BP; Phase B: 580 BP to the present). Charred botanical remains indicated two types of land-use: (1) domestic, with oil palm endocarps most often associated with potsherds (villages) and (2) agricultural, with charcoal as probable remnant of slash-and-burn cultivation (fields). Oil palm endocarp abundance decreased with distance from the identified human settlements. Our methodology allowed documenting, at high resolution, the spatial and temporal patterns of human activities in central African moist forests and could be applied to other tropical contexts.

Keywords
archaeology, charred endocarps, human settlements, late-Holocene, oil palm, soil charcoal, tropical Africa

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Introduction

Palaeoecological and archaeological evidence of ancient and scattered human activities have demonstrated that human populations have long inhabited the tropical forests worldwide (Barton et al., 2012; Willis et al., 2004). These biomes therefore cannot be regarded as pristine anymore, as they were occupied for several millennia by groups of hunter-gatherers, followed by farmers who settled in areas that are covered by dense forest today. In tropical Africa, it has been assumed that these human activities have had a substantial impact on vegetation structure and composition (Oslisly et al., 2013b). Specifically, early slash-and-burn shifting cultivation has been assumed to have formed scattered openings in the canopy that have allowed long-lived light-demanding trees to establish two to three centuries ago, and today, these trees represent an important component of canopy trees (Biwolé et al., 2015; Engone Obiang et al., 2014; Gond et al., 2013; Vleminckx et al., 2014). Nonetheless, this assumption raises three issues. The first relates to the distinction between anthropogenic and natural signals in the record, as natural fires have occurred irrespective of human presence, specifically during dry climatic events in the late-Holocene (i.e. after 2500 BP) (Hubau et al., 2015). The second issue concerns the observation scale, whether regional or local, of the anthropogenic disturbances and their impacts. The third deals with the quantitative and qualitative characterization of these human disturbances, especially in underexplored areas, because of difficulties related to fieldwork accessibility.

Numerous studies have documented an increasing human presence since the late-Holocene in tropical Africa (after 2500–2300

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RESEARCH ARTICLE

Present-day central African forest is a legacy of the 19th century human history

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Abstract The populations of light-demanding trees that dominate the canopy of central African forests are now aging. Here, we show that the lack of regeneration of these populations began ca. 165 ya (around 1850) after major anthropogenic disturbances ceased. Since 1885, less itinerancy and disturbance in the forest has occurred because the colonial administrations concentrated people and villages along the primary communication axes. Local populations formerly gardened the forest by creating scattered openings, which were sufficiently large for the establishment of light-demanding trees. Currently, common logging operations do not create suitable openings for the regeneration of these species, whereas deforestation degrades landscapes. Using an interdisciplinary approach, which included paleoecological, archaeological, historical, and dendrological data, we highlight the long-term history of human activities across central African forests and assess the contribution of these activities to present-day forest structure and composition. The conclusions of this sobering analysis present challenges to current silvicultural practices and to those of the future.

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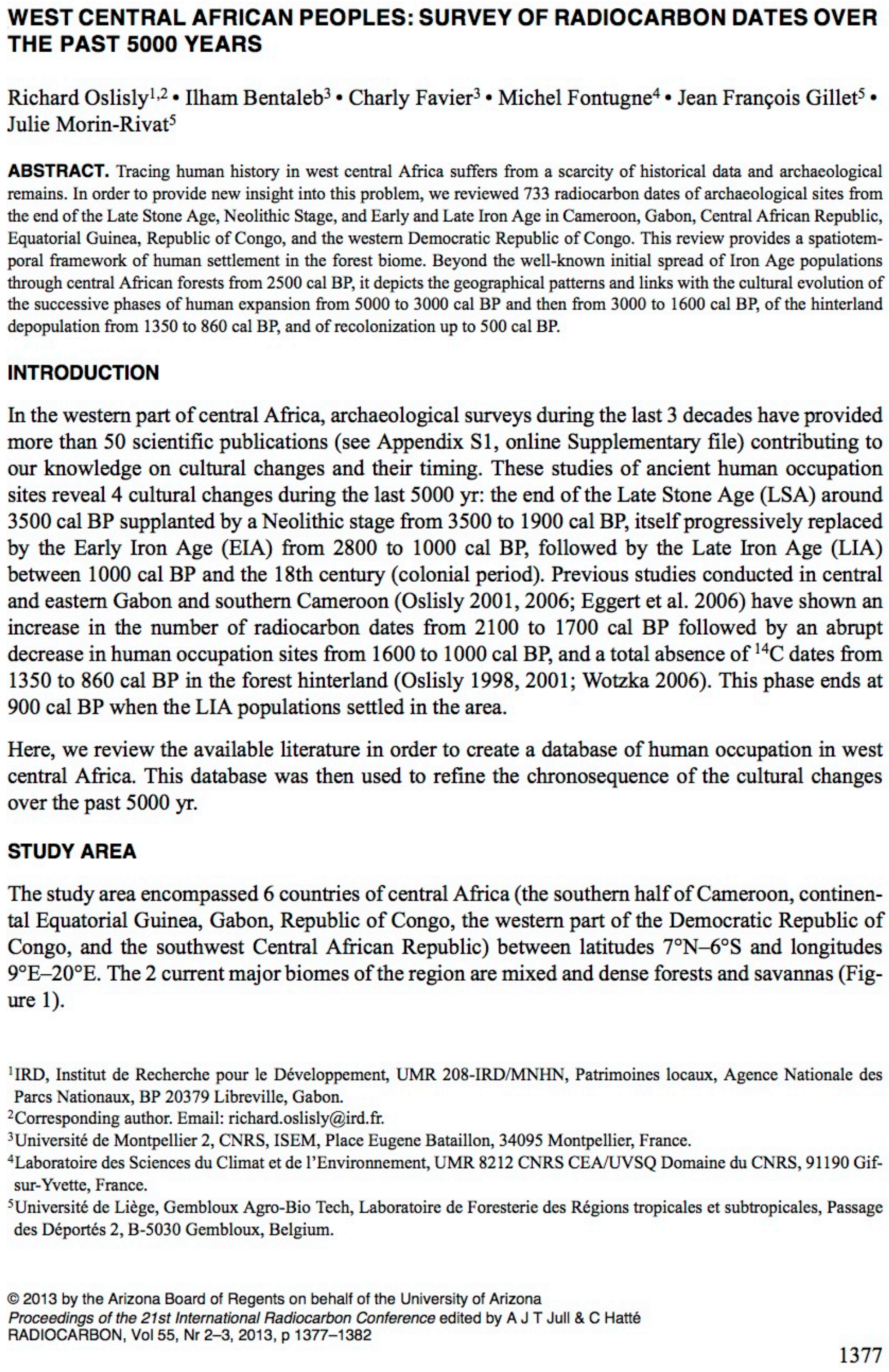
Introduction

Central African forests underwent an unequal history of disturbances during the Holocene (after 10,000 yrs BP) compared with Neotropical forests, which remained relatively stable since the Late Glacial Maximum (LGM, ca. 13,000–10,000 yrs BP) (***Anhuf et al., 2006***). Over the last three millennia, significant changes in the vegetation structure and floristic composition were caused by climate fluctuations (***Maley et al., 2012***; ***Neumann et al., 2012***; ***Lézine et al., 2013***). Specifically, a dry event around 2500 ya caused forest fragmentationan event with a more pronounced seasonality occurred around 2500 ya and caused forest fragmentation, and this fragmented forest included patches of savanna (***Maley, 2002***). This dry episode stopped around 2500 BP, as evidenced from the Mopo Bai site in the Republic of the Congo, where Poaceae pollen severely dropped from 36% to 13% between 2580 and 2400 BP, which is evidence for a retreat of the savannas to the benefit of the forests (***Bostoen et al., 2015***). After 2000 yrs BP, a relatively wet climate in central Africa favored forest recolonization by light-demanding tree species, with few effects imputable to humans (***Maley et al., 2012***; ***Lézine et al., 2013***; ***Brnčić et al., 2009***; ***Bostoen et al., 2015***). The subsequent climatic variations were less important with little effect on the vegetation (***Oslisly et al., 2013a***); however, human

Morin-Rivat *et al.* eLife 2017;6:e20343. DOI: 10.7554/eLife.20343 1 of 18

Appendix 15

Articles published as co-author (by chronological order)



WEST CENTRAL AFRICAN PEOPLES: SURVEY OF RADIOCARBON DATES OVER THE PAST 5000 YEARS

Richard Oslisly[1,2] • Ilham Bentaleb[3] • Charly Favier[3] • Michel Fontugne[4] • Jean François Gillet[5] • Julie Morin-Rivat[5]

ABSTRACT. Tracing human history in west central Africa suffers from a scarcity of historical data and archaeological remains. In order to provide new insight into this problem, we reviewed 733 radiocarbon dates of archaeological sites from the end of the Late Stone Age, Neolithic Stage, and Early and Late Iron Age in Cameroon, Gabon, Central African Republic, Equatorial Guinea, Republic of Congo, and the western Democratic Republic of Congo. This review provides a spatiotemporal framework of human settlement in the forest biome. Beyond the well-known initial spread of Iron Age populations through central African forests from 2500 cal BP, it depicts the geographical patterns and links with the cultural evolution of the successive phases of human expansion from 5000 to 3000 cal BP and then from 3000 to 1600 cal BP, of the hinterland depopulation from 1350 to 860 cal BP, and of recolonization up to 500 cal BP.

INTRODUCTION

In the western part of central Africa, archaeological surveys during the last 3 decades have provided more than 50 scientific publications (see Appendix S1, online Supplementary file) contributing to our knowledge on cultural changes and their timing. These studies of ancient human occupation sites reveal 4 cultural changes during the last 5000 yr: the end of the Late Stone Age (LSA) around 3500 cal BP supplanted by a Neolithic stage from 3500 to 1900 cal BP, itself progressively replaced by the Early Iron Age (EIA) from 2800 to 1000 cal BP, followed by the Late Iron Age (LIA) between 1000 cal BP and the 18th century (colonial period). Previous studies conducted in central and eastern Gabon and southern Cameroon (Oslisly 2001, 2006; Eggert et al. 2006) have shown an increase in the number of radiocarbon dates from 2100 to 1700 cal BP followed by an abrupt decrease in human occupation sites from 1600 to 1000 cal BP, and a total absence of ^{14}C dates from 1350 to 860 cal BP in the forest hinterland (Oslisly 1998, 2001; Wotzka 2006). This phase ends at 900 cal BP when the LIA populations settled in the area.

Here, we review the available literature in order to create a database of human occupation in west central Africa. This database was then used to refine the chronosequence of the cultural changes over the past 5000 yr.

STUDY AREA

The study area encompassed 6 countries of central Africa (the southern half of Cameroon, continental Equatorial Guinea, Gabon, Republic of Congo, the western part of the Democratic Republic of Congo, and the southwest Central African Republic) between latitudes 7°N–6°S and longitudes 9°E–20°E. The 2 current major biomes of the region are mixed and dense forests and savannas (Figure 1).

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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

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Soil Charcoal to Assess the Impacts of Past Human Disturbances on Tropical Forests

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Abstract

The canopy of many central African forests is dominated by light-demanding tree species that do not regenerate well under themselves. The prevalence of these species might result from ancient slash-and-burn agricultural activities that created large openings, while a decline of these activities since the colonial period could explain their deficit of regeneration. To verify this hypothesis, we compared soil charcoal abundance, used as a proxy for past slash-and-burn agriculture, and tree species composition assessed on 208 rainforest 0.2 ha plots located in three areas from Southern Cameroon. Species were classified in regeneration guilds (pioneer, non-pioneer light-demanding, shade-bearer) and characterized by their wood-specific gravity, assumed to reflect light requirement. We tested the correlation between soil charcoal abundance and: (i) the relative abundance of each guild, (ii) each species and family abundance and (iii) mean wood-specific gravity. Charcoal was found in 83% of the plots, indicating frequent past forest fires. Radiocarbon dating revealed two periods of fires: "recent" charcoal were on average 300 years old (up to 860 BP, $n = 16$) and occurred in the uppermost 20 cm soil layer, while "ancient" charcoal were on average 1900 years old (range: 1500 to 2800 BP, $n = 43$, excluding one sample dated 9400 BP), and found in all soil layers. While we expected a positive correlation between the relative abundance of light-demanding species and charcoal abundance in the upper soil layer, overall there was no evidence that the current heterogeneity in tree species composition can be explained by charcoal abundance in any soil layer. The absence of signal supporting our hypothesis might result from (i) a relatively uniform impact of past slash-and-burn activities, (ii) pedoturbation processes bringing ancient charcoal to the upper soil layer, blurring the signal of centuries-old Human disturbances, or (iii) the prevalence of other environmental factors on species composition.

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Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are within the paper and its Supporting Information files.

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Introduction

For a long time, many tropical forests have been viewed as "virgin" or "primary" ecosystems, undisturbed by anthropogenic activities. However, increasing evidence from different continents has suggested that these forests may actually hide influences of past Human disturbances [1]. In South-East Asia for example, it has been suspected that agricultural activities developed as early as 7000 BP in Papua New Guinea [2] and 8000 BP in Thailand [3], in areas covered today by lowland uninhabited rainforests. In Northwest Belize, Ross [4] demonstrated that modern tree species composition appeared to display important differences between areas of high and low settlement of ancient Maya, because of different intensities of past forest gardening (recruitment of useful species). Similarly, in central Amazonia, "terra preta" soils covering an area of about 500 km^2, on which stands apparent "pristine" rainforests, have resulted from intense burning and agricultural activities occurring about 2500 BP, which have considerably enhanced the fertility of these soils and may thus have impacted floristic diversity [5].

In central African moist forests, accumulating evidences show that Human has had a profound impact on the vegetation dynamics during the three last millennia. While only sparse evidence is recorded for Human presence in central Africa during the early and middle Holocene [6,7], archaeological surveys have suggested a dramatic expansion of an ancestral Bantu population coming from the southern part of the actual Cameroon-Nigeria border during the third millennium BP [8]. Archaebotanical data have indicated that this expansion coincided with an increasing seasonality in the precipitation regime that would have generated

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Article

How Tightly Linked Are *Pericopsis elata* (Fabaceae) Patches to Anthropogenic Disturbances in Southeastern Cameroon?

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Abstract: While most past studies have emphasized the relationships between specific forest stands and edaphic factors, recent observations in Central African moist forests suggested that an increase of slash-and-burn agriculture since 3000–2000 BP (Before Present) could be the main driver of the persistence of light-demanding tree species. In order to examine anthropogenic factors in the persistence of such populations, our study focused on *Pericopsis elata*, an endangered clustered timber species. We used a multidisciplinary approach comprised of botanical, anthracological and archaeobotanical investigations to compare *P. elata* patches with surrounding stands of mixed forest vegetation ("out-zones"). Charcoal samples were found in both zones, but were significantly more abundant in the soils of patches. Eleven groups of taxa were identified from the charcoals, most of them also present in the current vegetation. Potsherds were detected only inside *P. elata* patches and at different soil depths, suggesting a long human presence from at least 2150 to 195 BP, as revealed by our charcoal radiocarbon dating. We conclude that current *P. elata* patches most likely result from shifting cultivation that occurred *ca.* two centuries ago. The implications of our findings for the dynamics and management of light-demanding tree species are discussed.

Keywords: Afrormosia; Assamela; Central Africa; tropical rain forest; autecology; forest history; shifting cultivation; past human disturbances; charcoal

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The influence of spatially structured soil properties on tree community assemblages at a landscape scale in the tropical forests of southern Cameroon

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Summary

1. Species distribution within plant communities results from both the influence of deterministic processes, related to environmental conditions, and neutral processes related to dispersal limitation and stochastic events, the relative importance of each factor depending on the observation scale.

2. Assessing the relative contribution of environment necessitates controlling for spatial dependences among data points. Recent methods, combining multiple regression and Moran's eigenvectors maps (MEM), have been proved successful in disentangling the influence of pure spatial processes related to dispersal limitation, pure environmental variables (not spatially structured) and spatially structured environmental properties. However, the latter influence is usually not testable when using advanced spatial models like MEM.

3. To overcome this issue, we propose an original approach, based on torus-translations and Moran spectral randomizations, to test the fraction of species abundance variation that is jointly explained by space and seven soil variables, using three environmental and tree species abundance data sets (consisting of 120, 52 and 34 plots of 0·2 ha each, located along 101-, 66- and 35-km-long transect-like inventories, respectively) collected in tropical moist forests in southern Cameroon.

4. The overall abundance of species represented by ≥30 individuals, and 27% of these species taken individually, were significantly explained by fine-scale (<5 km) and/or broad-scale (5–100 km) spatially structured variations in soil nutrient concentrations (essentially the concentration of available Mn, Mg and Ca) along the 120-plots area. The number of significant tests considerably decreased when investigating the two smaller data sets, which mostly resulted from low statistical power rather than weaker floristic and/or edaphic variation captured among plots.

5. *Synthesis*. Our results provide evidence that tree species turnovers are partly controlled by spatially structured concentrations in soil nutrients at scales ranging from few hundreds of metres to c. 100 km, a poorly documented subject in Central African forests. We also highlight the usefulness of our testing procedure to correctly interpret the space-soil fraction of variation partitioning analyses (which always accounted here for the most important part of the soil contribution), as this fraction was sometimes relatively high (R^2 values up to c. 0·3) but nearly or not significant.

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